Environmental and maternal effects on infant development in wild Verreaux's sifakas (*Propithecus verreauxi*)

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“It takes a village to raise a child”

African proverb

Mother-infant *Propithecus verreauxi* (© 2017. Malalaharivony)

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Young *Propithecus verreauxi* (© 2018. Malalaharivony)

SUMMARY

Organisms' life cycles vary tremendously between and within species leading to differences in life histories. Early development plays an important role in the life trajectory of an individual and shapes its entire life. Acceleration or delay of the developmental schedule can influence the age at maturation and reproduction and even the fitness of an organism. Whereas the factors, which could influence the early development of an individual have been well documented, little is known about the developmental milestones and the mechanisms that link environmental stressors and maternal stress to infant physical and behavioral development and infant early survival. Most of the studies are from captive populations under experimental conditions.

In this study, I contribute new information to this subject by studying the effects of environmental stressors and maternal stress on infant development in a wild lemur species, Verreaux's sifakas *(Propithecus verreauxi)*. These group-living primates give birth to a single infant per year, which is characterized by slow development and late maturity compared to other lemur species. They inhabit the dry forest of south-western Madagascar where they are exposed to pronounced seasonal changes in food availability, rainfall, and temperatures. Allomaternal care is rare in this species, hence mothers are the primary caregivers and invest more in the infant. Infant mortality is high and mostly occurs during the first year of life. In this study, I explored growth pattern and developmental milestones, i.e. the age at the first occurrence of each behavior such as foraging, solitary play, social play, grooming, and independent locomotion and assessed the influence of infant's age and sex, mother's age and food availability on these developmental processes in 16 infants in Kirindy forest. I also examined the influence of seasonality as well as the impact of previous reproduction on maternal stress (glucocorticoid concentration, GCc) and investment to the infants, and their potential influence on infants' physical and behavioral developments and their early survival.

I found strong inter-individual variation in the developmental milestones of the infants. Motor skills emerged earlier than social skills and foraging occurred at an early age compared to other lemur species. Independent locomotion, however, occurred comparably late, indicating the complexities of the species' socio-ecological environment. The results of this study also show sex differences in infants' early growth rates and grooming activities. Females grew faster whereas males spent time grooming conspecifics, reflecting Verreaux’s sifakas’ reproductive strategies and social organization. Neither mothers’ age nor food availability significantly influenced infants' physical and behavioral development. However, the here found inter-individual differences in infants' development reflected the variation of the received investment which are related to maternal condition and their socio-ecological environment. Low rainfall and previous reproduction were associated with increased maternal GC levels, which in turn resulted in a decrease of maternal investment in terms of infant carrying. This indicates that mothers in this species face strong energetic challenges and carry high costs of reproduction. Elevated maternal GC levels strongly influenced infant behavioral and physical development. Although mothers with higher GC levels exhibited lower maternal investment, their infants appeared to be more developed, i.e. played and foraged more. Infants that were less carried more likely survived the first year of their life. The results of this study show the impact of environmental stressors on maternal condition and reflect the adaptive responses of infant Verreaux’s sifakas to early maternal stress.

In conclusion, the early development of the infants seems to be adjusted to their socio-ecological environment and their future life strategies. The early physical and social development of males and females infant Verreaux’s sifakas reflected their future reproductive strategies and social organization. Infant development is strongly shaped by maternal condition and investment, which is in turn influenced by environmental changes. The cost of reproduction is very high for mothers resulting in elevated GC levels and reduced maternal investment. Elevated maternal stress appears to be adaptive for the infants during their first year of life. More studies on early development conducted in natural environment and especially in lemurs are needed to improve our understanding of the lemurs’ life history strategies.

ZUSAMMENFASSUNG

Der Lebenszyklus von Organismen variiert enorm zwischen und innerhalb von Arten, was zu Unterschieden in der Lebensgeschichte führt. Die frühe Entwicklung spielt für Individuen eine wichtige Rolle und prägt deren gesamtes Leben. Beschleunigte oder verzögerte Entwicklungsphasen beeinflussen dabei nicht nur das Erreichen der körperlichen und physiologischen Reife, sondern auch die Fitness eines Organismus. Die Faktoren, die die frühe Entwicklung eines Individuums beeinflussen können, sind weitestgehend dokumentiert. Im Gegensatz dazu ist wenig bekannt über die Meilensteine und dahinterliegenden Mechanismen, die natürliche Umweltstressoren und mütterlichen Stress mit der Entwicklungvon Körper und Verhalten sowie dem Überleben von Säuglingen verbinden. Die meisten Studien dazu stammen von Experimenten mit in Gefangenschaft lebenden Populationen.

In dieser Studie trage ich neue Informationen zu diesem Thema bei, indem ich die Auswirkungen von Umweltstressoren und mütterlichem Stress auf die Entwicklung von Säuglingen bei einer wildlebenden Lemurenart, Larven sifakas (*Propithecus verreauxi*), untersuche. Diese gruppenlebenden Primaten gebären ein einziges Jungtier pro Jahr, das sich im Vergleich zu anderen Lemurenarten durch eine langsame Entwicklung und späte Geschlechtsreife auszeichnet. Die Spezies bewohnt Trockenwälder im Südwesten Madagaskars, wo sie ausgeprägten jahreszeitlichen Schwankungen von Nahrungsangebot, Niederschlägen und Temperaturen ausgesetzt ist. Mütter ziehen den Nachwuchs bei dieser Spezies in der Regel allein groß, weshalb sie viel Zeit und Energie in die Aufzucht investieren müssen. Die Sterblichkeitsrate des Nachwuchses ist hoch und tritt meist im ersten Lebensjahr auf. Bei 16 Jungtieren im Kirindy-Wald untersuchte ich Wachstumsmuster und Entwicklungsmeilensteine, d.h. das Alter beim ersten Auftreten von Verhaltensweisen wie Futtersuche, Spielen allein, Spielen mit Artgenossen, Körperpflege und unabhängige Fortbewegung, und bewertete den Einfluss von Alter und Geschlecht des Säuglings, Alter der Mutter und Nahrungsverfügbarkeit auf diese Entwicklungsprozesse. Ich ermittelte auch den Einfluss der Saisonalität und den Einfluss der vorangegangenen Reproduktion auf den mütterlichen Stress (Glukokortikoid-Konzentration, GCc) und die mütterliche Investition in den Nachwuchs sowie den möglichen Einfluss auf die Entwicklung von Körper und Verhalten und das Überleben.

Ich fand starke inter-individuelle Variationen in den Entwicklungsmeilensteinen der Säuglinge. Motorische Fähigkeiten entwickelten sich früher als soziale Fähigkeiten und die Nahrungssuche fand in einem frühen Alter statt. Die eigenständige Fortbewegung trat relativ spät auf, was auf die Komplexität des sozio-ökologischen Umfelds der Art hinweist. Die Ergebnisse dieser Studie zeigen auch Geschlechtsunterschiede in den frühen Wachstumsphasen und beim Auftreten der gegenseitigen

Fellpflege. Weibchen wuchsen schneller, während Männchen mehr Zeit mit der Pflege von Artgenossen verbrachten, was die Fortpflanzungsstrategien und die soziale Organisation der Larven sifakas wider spiegelt. Weder das Alter der Mütter noch die Nahrungsverfügbarkeit beeinflussten die Entwicklung der Säuglinge. Im Gegensatz dazu hatten Energieaufnahme und erhaltene mütterlicher Fürsorge, die mit dem Zustand der Mütter und ihrer sozio-ökologischen Umgebung zusammenhängen, einen Einfluss auf die Entwicklung des Nachwuchses. Geringe Niederschläge und frühere Reproduktion korrelierten mit erhöhten mütterlichen GC-Werten, was wiederum zu einer Abnahme der mütterlichen Fürsorge in Bezug auf das Tragen der Säuglinge führte. Dies deutet darauf hin, dass Larven sifaka-Mütter starken energetischen Herausforderungen ausgesetzt sind und hohe Fortpflanzungskosten tragen. Erhöhte mütterliche GC-Spiegel beeinflussten stark das Verhalten und die körperliche Entwicklung der Säuglinge. Obwohl Mütter mit höheren GC-Spiegeln weniger in ihren Nachwuchs investierten, schienen ihre Säuglinge besser entwickelt zu sein, d.h. sie spielten mehr, verbrachten mehr Zeit mit der Futtersuche. Säuglinge, die weniger getragen wurden, überlebten häufiger das erste Lebensjahr. Die Ergebnisse dieser Studie zeigen den Einfluss von Umweltstressoren auf den mütterlichen Zustand und spiegeln die adaptiven Reaktionen der Larven sifakas auf frühen mütterlichen Stress wider.

Zusammenfassend scheint die frühe Entwicklung der Säuglinge an ihre sozio-ökologische Umgebung und ihre zukünftigen Lebensstrategien angepasst zu sein. Die frühe körperliche und soziale Entwicklung männlicher und weiblicher Larven sifakas spiegelt deren zukünftigen Fortpflanzungsstrategien und ihre soziale Organisation wider. Die Entwicklung der Säuglinge wird stark von der mütterlichen Kondition und Fürsorge geprägt, die wiederum von Umweltveränderungen beeinflusst wird. Die Kosten der Reproduktion sind für Mütter sehr hoch, was zu erhöhten GC-Werten und reduziertem mütterlichen Engagement führt. Erhöhter mütterlicher Stress scheint für die Säuglinge adaptiv zu sein im ersten Lebensjahr. Weitere Studien zur frühen Entwicklung, vor allem bei frei lebenden Populationen und insbesondere bei Lemuren, sind notwendig, um das Verständnis der Lebensstrategien der Lemuren zu verbessern.

GENERAL INTRODUCTION

Ontogeny is one of the most crucial processes in life history and constitutes a principal subject of concern to evolutionary biologists (Pereira & Fairbanks, 2002). Gestation length, number, and size of the offspring as well as age at maturation and first reproduction are among the essential life-history traits (Charnov, 1991; Pereira & Fairbanks, 2002) and are highly variable between and within species (Harvey & Zammuto, 1985; Kappeler & Pereira, 2003; Millar & Zammuto, 1983). Some species exhibit a slow life history that is characterized by slow growth and late maturation, while other species exhibit a fast life history, with rapid growth and reach maturity earlier.

All placental mammals share the same essential life cycle traits, described by placental gestation, viviparity, and lactation (Kappeler & Pereira, 2003); however, they show considerable variation in many other characteristics, especially in growth and maturation times (Harvey & Zammuto, 1985; Millar & Zammuto, 1983). Among mammals, primates generally have very slow life histories (Pereira & Fairbanks, 2002; Charnov, 1991). They have a long gestation period, slow growth rate, and mature late, compared to non-primate mammals (Charnov, 1991; Charnov & Berrigan, 1993; van Schaik & Isler, 2012). Their extended juvenile period has been presumed to provide training and learning to young primates to prepare them for their physical and social environment, including the complexities of their behavior (Gavan, 1982; Maynard et al., 2021; Whiten & van de Waal, 2018). Learning many complex skills may need a long time (Poirier & Smith, 1974). Besides, prolonged development may be required for their brain and somatic development (Barton & Capellini, 2011; Kappeler & Pereira, 2003; Martin et al., 2010). Multiple explanations have been reported for this long developmental period in primates and the vast diversities in their life history (Charnov, 1991;Kappeler & Pereira, 2003; Promislow & Harvey, 1990). However, many questions remain answered. For instance, why do variations exist even within the same species living in the same habitat? Why do some species exhibit slower growth with delayed behavioral and physical development than others of similar size? Why do infants from the same mother may present different developmental trajectories?

1. Variation in mammalian life-history traits

In general, some life-history traits seem to be unvaried for the average of individuals in the same species (Kappeler & Pereira, 2003). For instance, an elephant's mean longevity is always around 100 years (Kappeler & Pereira, 2003). Similarly, the gestation length is mostly stable within a species and is positively correlated with individual body size (Clutton-Brock, 2016; Lee, 2012). For instance, humans will always give birth after nine months of pregnancy. However, there are enormous variations in some other life-history characteristics in mammals (Charnov, 1991; Kappeler & Pereira, 2003). One of the early theories is that most of the life-history traits of an organism are correlated with its body size (Millar & Zammuto, 1983). For instance, large mammals tend to have greater age at maturity and longer life span than smaller ones; however, they also have a lower reproductive rate with a smaller number of offspring (Millar & Zammuto, 1983). Hence, they show "fast" and "slow" characteristics, which is called the "slow-fast continuum"(Bielby et al., 2007). Previous explanations also argued that life-history traits are correlated with the brain size or metabolic rate (Barton & Capellini, 2011; de León et al., 2008; Western & Ssemakula, 1982). Species that have high metabolic rates and complex brains require a long developmental period. However, those theories were not supported, as the "slow-fast continuum" persists even after controlling for body size, brain size, and metabolic rate (Barton & Capellini, 2011; Bielby et al., 2007; de León et al., 2008; Promislow & Harvey, 1990).

The "slow-fast continuum" is also found among primates. Large primate species develop slower and have longer developmental period and smaller litter size (Kappeler & Pereira, 2003; Millar & Zammuto, 1983; Walker et al., 2006) compared to the smaller species. For instance, some small nocturnal primates can bear large litters, and reach maturity after less than one year (Harcourt & Bearder, 1989, Boulinguez-Ambroise et al., 2020); chimpanzees (*Pan troglodytes)* on the other hand are sexually mature at around seven to fourteen years of age and can only have a single infant per year (Kappeler & Pereira, 2003; Watts & Pusey, 1993). This divergence in life-history traits also exists among the strepsirrhine primates including the Malagasy lemurs (Kappeler, 1995, 1996). For instance, Verreaux's sifakas (*Propithecus verreauxi*), which are relatively large among lemurs, reach sexual maturity at around three to four years and can only have one infant per year (Richard, 1976); however, the small mouse lemur (*Microcebus murinus*) reaches maturity at about six months and can have more than one offspring (Kappeler, 1995; Boulinguez-Ambroise et al., 2020).

Diversities in life-history traits are also found even among individuals within the same species (Kappeler & Pereira, 2003). Variations are mostly found in body size and age at maturation, which relates to an individual early developmental process (Dmitriew, 2011; Kappeler & Pereira, 2003; Pontzer et al., 2014; Stearns, 1992). Early development and survival during the infancy period will determine the age at maturation and reproduction of an individual (Dmitriew, 2011; Stearns, 1992). Hence, intrinsic factors, such as adult body size and brain size, are not enough to explain the variation found in life history. Intraspecific variation in age and body size at maturation may occur due to the influence of various extrinsic factors such as food availability, seasonality, predation, environmental changes, including maternal investment and condition (Janson & van Schaik, 1993; Lee et al., 2020; Stoinski et al., 2013; Dmitriew, 2011; Kappeler, 1996; Kappeler & Pereira, 2003). Some particular life-history characteristics evolve through adaptation to socio-ecological parameters (Charnov, 1991; Gaillard & Yoccoz, 2003). Hence, many factors can directly or indirectly influence the early development of an individual and induce changes in their life trajectories. Body size and age at maturation are the aspects which vary the most and constitute the principal life-history traits that are connected to life during infancy. It is therefore important to understand the process of early development to explain variation in life history, especially the intraspecific variation.

2. Variation in infant development (one aspect of life-history traits)

Infant growth rate and environmental stressors

The process of the early development of an individual will shape its future life and fitness (Dmitriew, 2011; Kappeler & Pereira, 2003; Pontzer et al., 2014; Stearns, 1992). Some studies suggested that variations concerning maturation age and growth rate can be explained by the Ecological Risk Aversion Hypothesis (ERAH), particularly among the great apes (Janson & van Schaik, 1993; Galbany et al., 2017; Stoinski et al., 2013). This hypothesis is based on the link between the species' growth rates and their socio-ecological environment, such as resource availability, feeding competition, energetic cost, and predation risk (Janson & van Schaik, 1993). According to this hypothesis, species with low resource availability and high feeding competition should grow slowly to save energy, particularly frugivorous species. However, species with high food intake and low feeding competition should grow faster to reduce predation risk, especially folivorous species (Janson & van Schaik, 1993; Lee et al., 2020). In support of this hypothesis, previous studies assessing growth rates in captive apes species showed that gorillas (*Gorilla gorilla gorilla*), which are relatively folivorous, reach adult body mass earlier compared to bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) that are more frugivorous (Leigh & Shea, 1996). These differences are also found even within species. For example, among gorillas, Eastern mountain gorillas (*Gorilla beringei*

beringei), that have a more folivorous diet, grow faster than the more frugivorous Western lowland gorillas (*Gorilla gorilla gorilla*) (Galbany et al., 2017; Robbins & Robbins, 2018; Nowell & Fletcher, 2007).

It has also been shown that infants' growth rates are positively correlated to energy intake via food or breast milk (Hinde & Milligan, 2011). Thus, a reduction in food availability induces a decrease in the growth rate of an infant (Garcia et al., 2009; Onyango et al., 2013). However, food availability is, in turn, related to climate conditions and seasonal variation (Dmitriew, 2011). Most of the primate species inhabit the tropical forest, where the availability of resources is mostly unpredictable. Low food availability may increase starvation risk and reduce energy intake, which results in slow growth (Pontzer et al., 2014). Also, the growth rate is affected directly by food intake and indirectly by the trade-off between foraging and predation risk (Dmitriew, 2011). Predation is one of the main stressors faced by species in their natural habitat. To increase the growth rate, individuals must increase their food intake; however, this increases the risk of exposure to predators (Dmitriew, 2011). Hence, for populations living in an area with high predation risk, infant growth rates may be reduced due to limited foraging time to avoid predators and increase vigilance (Carthey & Banks, 2015; Dmitriew, 2011).

Age and body size at maturation are among the most important life-history traits; most of the energy gained is allocated to the physical growth rates (Berghänel et al., 2016, 2017; Dmitriew, 2011). However, infant’s growth and survival also depends on their ability and performance in many activities, such as locomotor skills, which enhance their competence to travel and escape the predators (Berghänel et al., 2015), but also foraging and social skills (Galef & Giraldeau, 2001; Janson & van Schaik, 1993). Overall, an individual's life trajectories are shaped by the conflict between mortality during the immaturity period and the time necessary to acquire adult characteristics (Dmitriew, 2011). For instance, the time required to learn foraging and social skills vary among infants (Maynard et al., 2021; Whiten & van deWaal, 2018; Bründl et al. 2020). Below, I will discuss variations in the development of such skills and other developmental milestones.

Variation in infant’s skills acquisition

Apart from the variation in age and body size at maturation, there is also variation in the development of various activities, behavior, and socialization of an infant. Variations are primarily found in the timing of the acquisition of different skills. All young must acquire all necessary physical and social skills to adapt to their environment, particularly for gregarious species like primates. Long experience and training are needed for developing individuals to learn various skills and survive independently from their mother in their natural habitat (Janson & van Schaik, 1993; Poirier & Smith, 1974). However, infants acquire those necessary skills at different ages and times, even within the same species. Some individuals acquire some behavior and competence at an early age, some later. These differences may also induce variations in their life history (Maynard et al., 2021; Whiten & van de Waal, 2018; Young & Shapiro, 2018; Bründl et al., 2020). For example, in chimpanzees, social skills emerge very late compared to motor skills with huge inter-individual variation (Bründl et al., 2020). The timing of the acquisition of the various milestones can contribute to the acceleration or reduction of an infant's growth rate, reproduction, and affects their survival. For instance, the acquisition of locomotion skills can influence the developmental process and the life history of an individual (Bekoff, 1988; Berghänel et al., 2015; Young & Shapiro, 2018; Godfrey et al., 2004; Wunderlich et al., 2011).

In some primate species, young animals need to be carried for a more extended period until they can locomote independently (Kappeler, 1998; Ross & Lehman, 2016; Ross, 2003). Acquisition of independent locomotion is positively correlated to body and brain size, suggesting that larger species reach locomotor independence later than smaller ones (Young & Shapiro, 2018). For instance, the first independent locomotion in chimpanzees occurs at around seven months (Bründl et al., 2020); whereas, mouse lemurs start independent locomotion at about ten days (Boulinguez-Ambroise et al., 2020). Similarly, independent travel is also strongly correlated with age at weaning. Species that are weaned at a later age have slow locomotion development and acquire it late (Young & Shapiro, 2018). Also, it has been suggested that the acquisition of independent locomotion is shaped by the locomotion mode of the species (Sussman, 1977; Wunderlich et al., 2011) and their ecological habitat (Boulinguez-Ambroise et al., 2020). Arboreal species living in a complex habitat need more time to acquire efficient locomotion, such as climbing and vertical clinging than terrestrial species (Sussman, 1977, Wunderlich et al., 2011). However, Young & Shapiro (2018) did not find the effect of locomotion mode on independent locomotion timing. Besides, the timing of developing these locomotor skills is highly variable within species (Boulinguez-Ambroise et al., 2020; Bründl et al., 2020; Young & Shapiro, 2018). Thus, the age of independent locomotion is not only influenced by species body size or weaning age (Young & Shapiro, 2018). For instance, there is a significant inter-individual variation in the emergence of independent locomotion, ranging between 4.2 and 9.7 months of age in chimpanzees (Bründl et al., 2020). Similarly, infant mouse lemurs acquire motor coordination at different ages (Boulinguez-Ambroise et al., 2020). Nevertheless, efficient locomotion is essential and beneficial for food searching and predation escape, thus crucial in the individual's fitness (Bekoff, 1988; Berghänel et al., 2015; Young & Shapiro, 2018). It has been shown that the acquisition of this skill can be improved from locomotory play (Berghänel et al., 2015).

Another essential activity is foraging. The growth rates of infants are related to their energy intake via lactation and solid food (Hinde & Milligan, 2011). Foraging cognition is crucial for the survival of an individual. Learning foraging strategies may also require a long time, especially for species that have a special diet (Maynard et al., 2021). Social learning facilitates the acquisition of foraging strategies in many species (Fragaszy et al., 2002; Galef & Giraldeau, 2001; Galef, 1990; Galef& Bennett, 1995; Maynard et al., 2021; O'Mara & Hickey, 2012; Perry, 2020), but these are also enhanced by individual exploration (Boinski & Fragaszy, 1989; O'Mara & Hickey, 2012). According to Galef & Giraldeau (2001), "infants learn what to eat," "when to eat," and "where to eat" during their first months of life. Infants improve their foraging skills through contact with their mother but also with other older and more experienced conspecifics (Milton, 1993), such as in the case in white-faced capuchins (*Cebus capucinus*) (Perry, 2020) and ring-tailed lemurs (O'Mara & Hickey, 2012). However, the timing of this nutritional development varies among species and even within individuals of the same species. For instance, infant squirrel monkeys (*Saimiri sciureus*) start to ingest solid food at an age ranging from 43 to 54 days (King & King, 1970), while in howler monkeys (*Allouatta guariba clamitans*), this age span varies from 3 to 4 months (Podgaiski et al., 2009). Similarly, in infants of brown lemurs *(Eulemur fulvus)*, the age at first solid food consumption ranges from 6 to 12 weeks (Taurnaud, 2004). Hence, the timing of acquisition of some important skills varies largely between and within species and is mostly influenced by social context. However, the acquisition of those important skills influences an infant's developmental process, including growth rate, body size, and age at maturation but also their fitness (Berghänel et al., 2015; Dmitriew, 2011; Maynard et al., 2021; Young & Shapiro, 2018).

In gregarious species, infants must also acquire their social behavior skills. Since their birth, they are part of social groups, with one or several conspecifics of the same or different age and sex (Campan & Scapini, 2002). The interaction between infants and their conspecifics during many social activities improves their skill acquisition such as locomotion and foraging (Maynard et al., 2021; O'Mara & Hickey, 2012; Perry, 2020). Also, interaction allows young individuals to predict their future social status and their role inside the group (Campan & Scapini, 2002). Below, I will briefly report the role of play and grooming in infant development which are among the most essential social activities in gregarious species.

For young mammals, especially primates, play is one of the main social activity characteristics (Burghardt, 2005; Graham & Burghardt, 2010). Play is essential in infant development through which infants can obtain many social skills and enhance physical ability, which is useful especially for males during the reproduction period (Berghänel et al., 2015; Laplante et al., 2007). For instance, according to Rijksen (1978), immature male orangutans used rough play to test each other's physical ability and establish and maintain rank. Despite the importance of play during ontogeny, it remains poorly studied (Graham & Burghardt, 2010). There is also variation in age at emergence and frequencies of play between and within species and even between sexes (Rijksen, 1978; Berghänel et al., 2015; Barale et al., 2015). Sex differences in the amount of play have been found in gorillas (Watts & Pusey, 1993), chimpanzees (Pusey, 1990), and orangutans (Rijeksen, 1978) where males show more interest and involvement in play than females. Similarly, in wild Assamese macaques (Berghänel et al., 2015) and geladas (*Theropithecus gelada*) (Barale et al., 2015), males play more and have more play partners.

Grooming is another essential activity for socialization and an important key behavior to establish and maintain affiliative relationships (Thompson & Cords, 2020). Many studies on primates report that grooming activity is influenced by age and sex (Thompson & Cords, 2020; Pereira & Altmann; 1985; Pusey, 1990). For instance, in baboons, males and females differ in grooming frequencies and partners (Pereira &Altmann, 1985). Immature male baboons interact and groom at lower rates than females (Cheney, 1978). Besides, it has been reported that an infant's grooming behavior is influenced by its mother's behavior during early life in blue monkeys (*Cercopithecus mitis*) with sex-specific differences, where, juvenile males invest more in grooming than females (Thompson & Cords, 2020). Investment in social activities enhances survival by reducing resource competition on the one hand and improving learning skills on the other hand. It has been shown that an individual's energy intake is affected by resource competition, especially in gregarious species (Dmitriew, 2011; Kappeler & Fichtel, 2015). Social interactions can also reduce predation risk by allowing to form partnerships with other conspecifics, to learn skills to escape from predators (Schultz et al., 2011). Additionally, They can increase future reproductive success by forming social bonds (Schülke et al., 2010). Thus, in general, skill acquisition and social interactions influence the life history of an individual. However, there is an inter-individual variation in the time of acquisition, and the time spent learning and engaging in those necessary, which depends on infants' socio-ecological conditions but also maternal investment.

Infant development and maternal care

In altricial species, like primates, infants cannot care for themselves and completely depend on their mothers or helpers. Maternal pre-and postnatal investment strongly influences offsprings' development and survival in mammals, at least, until infants reach their independence. This includes both maternal "style" and survival (Kappeler, 1998; Hinde & Milligan, 2011; Zipple et al., 2021; Bardi & Huffman, 2002; Thompson & Cords, 2020). Maternal investment supports not only the offspring's physical but also behavioral development (Thompson & Cords, 2020; Hinde, 2013). For example, the death of mothers has been shown to reduce offspring survival in baboons (Zipple et al., 2021). Similarly, the mother's affiliative behaviors influence offspring's behavioral development later on in blue monkeys and Japanese macaques (*Macaca fuscata*) (Bardi & Huffman, 2002; Thompson & Cords, 2020).

The offspring's development can be influenced not only by maternal lactation but also by maternal care which is related to maternal behavior and physical condition (Hanson & Gluckman, 2014*;* Hinde, 2013; Love et al., 2013). Lactation is the maternal investment specific to and present in all mammals. Still, in some other mammals species, mothers also show additional investment, such as carrying their infants from birth until they acquire locomotion independence (Kappeler, 1998; Hinde, 2013). Maternal behavior toward infants or maternal "style", distinguishes between active or passive mothers (King & King, 1970). Active mothers invest more in their infants and are more supportive. For example, they spend more time carrying their infants and always keep a close distance; whereas, passive mothers invest less and are less supportive. Maternal effects on offspring development have been well documented in many taxa but the effects are highly variable (King & King, 1970; Mason, 1968; Bardi & Huffman, 2002, 2006; Hinde et al., 2015; Love & William, 2008*;* Love et al., 2013; Schai-Braun et al., 2021; Thompson & Cords, 2020; Zipple et al., 2019, 2021).

Two contradictory hypotheses have been reported concerning the effects of maternal "style" on offspring development. First, King & King (1970) argued that infants with passive, less supportive mothers, show slower behavioral growth and reach independence later than infants with active and supportive mothers. In contrast to that, Mason (1968) reported that infants from non-supportive mothers are less dependent than infants in species characterized by supportive maternal behavior, which manifests more dependence on their mothers. In line with the findings of King & King (1970), King and colleagues (1974) also found that tamarins (*Saguinus oedipus*) and squirrel monkeys (Saimiri sciureus) have slower maturation as they have less supportive mothers (see also Rosenblum, 1968). In rhesus macaques (*Macaca mulatta*), mothers show active and supportive behavior, and infants exhibit faster maturation (Hansen, 1966). However, in Japanese macaques (*Macaca fuscata*), infants from protective mothers show more dependence and are less explorative than those from less protective mothers (Bardi& Huffman, 2002; Schino et al., 2001) which supports Mason's finding (1968). Hence, there are still divergences even within the same species concerning the effects of maternal "style" on offspring's development.

Besides, it has been shown that milk nutrients are strongly correlated to the maternal "style" and ecological condition (Hinde & Milligan, 2011). For instance, the milk of species living in the arctic environment has higher density and fat content to provide more energy for offspring. Species that live in a dry and arid habitat on the other hand produce more diluted milk to provide hydration for their infants (Oftedal, 2000; Hinde & Milligan 2011). Similarly, mothers that carry their offspring all the time have more diluted milk than those that park their infants (Hinde & Milligan, 2011). For example, among lemur species, black and white ruffed lemurs (*Varecia variegata*) have more concentrated milk than brown lemurs (*Eulemur fulvus*) (Tilden & Oftedal, 1997). Variation in milk nutrients has also been shown to influence infant physical and behavioral development. Feeding on milk that has higher protein content and, therefore, provides more energy, has been shown to increase infants' growth rates (Oftedal, 1984; Power et al., 2002), and infants' exploration behavior and competence (i.e., in *Macaca mulatta*, Hinde & Capitanio, 2010).

However, lactation and infant carrying impose energetic costs on mothers, affecting their physiology and body condition (Koch et al., 2017; McCabe & Fedigan, 2007; Ross & Lehman, 2016; Serio-Silva et al., 1999). Reproductive status has been shown to influence females feeding behavior and diets (Serio-Silva et al., 1999, Koch et al., 2017 McCabe &Fedigan, 2007). For example, lactating females have greater food intake than non-lactating females in white-faced capuchins (*Cebus capucinus*) (McCabe & Fedigan, 2007). Similarly, in howler monkeys (*Alouatta palliata*), gestating and lactating females ingested more food rich in fat and protein (Serio-Silva et al., 1999). Consequently, many species adopt allomaternal care strategies such as allomaternal nursing, transport, and carrying, which reduce lactation costs and enhance reproductive success (Tecot et al., 2013). Allo-maternal care has been shown to increase an infant's growth rate and accelerates the weaning process (Ross, 2003; Tecot et al., 2013). However, for species that express less or no allomaternal care, mothers must provide all necessary care for their offspring, which results in high energetic demands, such as the case in many lemur species (Tecot et al., 2013). Besides, maternal energy is influenced by their socio-ecological environment (Hanson & Gluckman, 2014, Sheriff & Love, 2013).

Many parameters can directly or indirectly affect infant development. In the previous section, I highlighted that for altricial species, infants are entirely dependent on their mothers until they are able to locomote and forage independently. Infants’ growth rates and skill acquisition vary among individuals and are influenced not only by their socio-ecological environment but also by maternal behavior and investment. Many socio-ecological stressors influence maternal body condition, behavior, and, thus maternal investment in the offspring (Hanson & Gluckman 2014, Sheriff & Love 2013). Those ecological stressors can be acute or chronic, and induce maternal stress and disturbances, which can also affect the immature directly or indirectly (Love & William, 2008; Love et al., 2013; Sheriff & Love, 2013). Below, I will briefly discuss the effects of various socio-ecological stressors on mothers and their impact on their offsprings’ development.

3. Maternal stress and infant development

Steroid hormones, glucocorticoids (GCs), play an essential role in mediating the link between environmental stressors, organism behavior, and life history strategies (Love & William, 2008; Love et al., 2013; Sheriff et al., 2009; Breuner et al., 2008). The primary function of GCs is to regulate energetic balance inside the organism (Landys et al., 2006; Love et al., 2013), but it is also involved in mediating organism’s behavioral and physiological responses to various environmental stressors (Landys et al., 2006; Love et al., 2013; Wingfield, 2005). Due to stress caused by various socio-environmental challenges, the organism releases GC hormones (Breuner et al., 2008; Love et al., 2013), hence, GCs is also commonly used as a proxy for stress levels (Love et al., 2013; Rudolph et al., 2020; Ostner et al., 2008; Berghänel et al., 2016; Fichtel et al., 2007). Different levels of GCs secretion affect an organism's behavioral and physiological state and can induce consequences in its life history and fitness (Breuner et al., 2008; Landys et al., 2006; Love et al., 2013; Campos et al., 2021). This mechanism is different between individuals, and each individual can respond differently to various environmental challenges (Breuner et al., 2008; Bonier et al., 2009). Hence, it also could be one of the significant causes of life history variations (Bonier et al., 2009; Hadany et al., 2006). Related to that, it has been reported that maternal GCs can also be transmitted to the offspring and influence their prenatal and postnatal development (Love et al., 2008; Sheriff et al., 2010). This phenomenon has been well studied in diverse taxa, such as in birds (Love et al., 2005; Love & Williams, 2008; Khan et al., 2016), reptiles (Liu et al., 2020; Meylan et al., 2002; Vercken et al., 2007), fish (Eriksen et al., 2011; McCormick, 2006; McGhee et al., 2021) and mammals, including humans (Berghänel et al., 2016; Cao et al., 2014; Emack et al., 2008; Grey et al., 2013; Hauser et al., 2007; Mumby et al., 2015; Sheriff et al., 2009); however, the effects on offspring are highly variable even within the same population and between sexes, ranging from positive to negative (Love & William, 2008; Love et al., 2013; Sheriff & Love, 2013; Sheriff et al., 2010, 2017; Berghänel et al., 2017).

Maternal stress and environmental stressors

Variation in food availability represents the main challenge faced by species living in seasonal climates, especially for females, because of the high energetic costs of reproduction (Koch et al., 2017; Love et al., 2005). Indeed, unpredictable changes in food quantity or quality are reported to increase female GC levels in birds and mammals (Chapman et al., 2015; Cinque et al., 2021; Dantzer et al., 2011; Jenni-Eiermann et al., 2008; Love et al., 2005; Welcker et al., 2009). For example, experimental changes in the diet have been shown to increase female GC levels in red squirrels (*Sciurus vulgaris*) (Dantzer et al., 2011). Low food quality has been found to increase individual's GC levels in red colobus monkeys (*Procolobus rufomitratus*) (Chapman et al., 2015). Low fruit availability has been reported to increase an individual's GC levels in many species (Behie & Pavelka, 2013; Pride, 2005; Rudolph et al., 2020). Reduction in food availability induces reduction of energy intake, thus leading to an increase of GC levels.

Besides, energy intake can also be influenced by feeding competition among conspecifics leading to an increase in individual GC levels (Dantzer et al., 2013; Foerster et al., 2011). For instance, a high population density has been shown to increase maternal GC levels in red squirrels (Dantzer et al., 2013). Similarly, in ring-tailed lemurs (*Lemur catta),* female GC levels are elevated in larger groups (Pride, 2005). Further, GC levels may vary between females within groups because dominant females dispose high priority of food over subordinate females (Altmann & Alberts, 2005), resulting in high GC levels in subordinate females (Creel, 2001). For instance, high-ranking mothers exhibit lower GC levels than low-ranking mothers during low fruit availability in blue monkeys (*Cercopithecus mitis*) (Foerster et al., 2011). However, in cooperative breeding mammals, the dominant females have higher GC levels (Creel, 2001). Hence, feeding competition, female rank inside the groups, and social interaction have been shown to increase females' GC levels.

Moreover, increased predation risk can also increase stress hormone levels, particularly in pregnant and lactating females in many taxa (Love et al., 2013; Sheriff et al., 2010). For example, in birds (e.g., European starlings (*Sturnus vulgaris*) and fish (e.g., in sticklebacks), elevation in predation risk, induces an increased maternal GC secretion into the eggs (Love et al., 2008; Giesing et al., 2011). The same pattern has been found in yellow-bellied marmots (*Marmota flaviventris*); increased predator pressure induces an increase of maternal GC levels (Monclús et al., 2011). Besides, resource allocation and predation risk can both increase maternal GC levels due to the conflict between foraging and survival (Sheriff et al., 2011; Dmitriew, 2011). Predation can induce mortality directly and indirectly through the trade-off between foraging and escaping predators (Heithaus& Dill, 2002). Maternal stress may also vary across years due to variation in resource availability or quality or other environmental factors (Lea et al., 2015*;* Love et al., 2013). It may also differ among females in neighboring groups because their territories may vary in quality (Altmann & Alberts, 2005).

Maternal stress and offspring's responses

In mammals, maternal stress and elevated maternal GCs have been reported to influence pre-and postnatal maternal investment into the offspring (Bowen, 2009; Cottrell et al., 2012; Sheriff & Love, 2013; Berghänel et al., 2017). Elevated stress during pregnancy or lactation induces changes in maternal behavior, such as increased rejection, aggression, anxiety, and depression in many species, including humans (Bardi et al., 2003, 2004; Berghänel et al., 2016; Kammerer et al., 2006; Klaus et al., 2013). These changes in maternal behavior will in turn influence maternal investment and affect infant development (Bowen, 2009; Cottrell et al., 2012; Sheriff & Love, 2013).

Elevated maternal GCs can also affect directly infant development during gestation through placenta and during lactation through milk in mammals (Love et al., 2013; Sheriff et al., 2017; Sullivan et al., 2011). High maternal GCs have been shown to influence infant physical development, skill acquisition (Berghänel et al., 2016; Cao et al., 2014), immune function (Berghänel et al., 2016; Veru et al., 2014), and offspring behavior (Bardi& Huffman, 2002; Sullivan et al., 2011; Sheriff et al., 2017) in many taxa. The effects of prenatal maternal GCs on infants can vary according to the time of occurrence of the stress during the gestation phase (Sheriff et al., 2017; Hauser et al. 2007). In Assamese macaques, early and mid-prenatal GCs were positively correlated with infants' growth rates (Berghänel et al., 2016). In humans, prenatal stress during late pregnancy has been reported to reduce the motor skills function in daughters (Cao et al., 2014). Some researchers even found that stressors faced by the mothers during reproduction can affect their offspring's phenotype (Love & Williams, 2008). Additionally, maternal stress effects can also be transmitted to the next generation (Zipple et al., 2019). Recently, there has been an increase in research focused on the impact of maternal GC levels on offspring development (Berghänel et al., 2016, 2017; Dettmer et al., 2018; Hauser et al., 2007; Zipple et al., 2019). However, the effects are highly variable and it is still debated whether maternal GCs can induce adaptive or maladaptive effects on the offspring (Berghänel et al., 2017; Lea et al., 2015; Love & Williams, 2008; Sheriff & Love, 2013; Sheriff et al. 2017).

Several hypotheses have been suggested to predict the offspring's response to maternal stress and early adversity conditions. First, the developmental constraints hypothesis argued that early adversity experienced during the prenatal and postnatal phase, including elevated maternal GCs would decrease infants' growth rates, body condition, health and affects negatively their behavior; those effects will last during their adult life and decrease their fitness (Grey et al., 2013; Cao et al., 2014; Emack et al., 2008; Lea et al., 2015; Monaghan, 2008; Hayward et al., 2013; Hayward & Lummaa, 2013; Sullivan et al., 2011). For instance, elevated prenatal maternal GC reduces motor skills, induces "negative temperament" in daughters in humans (Grey et al., 2013, Cao et al., 2014) and rhesus macaques (Sullivan et al., 2011). Information on the link between GC levels and individual fitness is poorly documented (Campos et al., 2021; Beehner & Bergman, 2017). However, studies assessing the effects of early adversities on adult survival and reproduction supported the developmental constraints hypothesis in many long-lived species, including humans (Douhard et al., 2014; Hayward et al., 2013; Hayward & Lummaa, 2013; Lea et al., 2015; Campos et al., 2021). For instance, Hayward and colleagues (2013) found that the human populations experienced challenging early environments (e.g. insufficient nutrition) have lower survival and fertility during their adult life under similar environmental conditions. Similarly, Douhard and colleagues (2014) found that early life adversities (e.g. low resource availability) induce negative developmental consequences and reduce fitness in roe deer (*Capreolus capreolus*).

In contrast to that, it has been suggested that infants can develop predictive adaptive responses (PAR hypothesis). According to this hypothesis, mothers can inform their offspring about the current environmental conditions through GCs. Thus, infants can predict their future environment and will be able to regulate their phenotype to match these conditions (Gluckman et al., 2005; Nettle et al., 2013). However, this mechanism is only adaptive when the future environmental conditions are similar to the maternal conditions. For long-lived species living in an unpredictable environment like primates, the PAR hypothesis is still debated (Lea et al., 2015). It has been suggested that the PAR hypothesis is suitable only for short-lived animals (Lea et al., 2015). A hypothesis of compensatory growth has also been proposed, suggesting that individuals accelerate their development, especially their growth rate, to compensate for the effects of early adversity (Dmitriew, 2011). This case was found in many non-human and human species (Ali et al., 2003; Sanna et al., 2015). Indeed, infants' responses to early adversities including elevated maternal GCs are highly variable.

Hence, many factors have been shown to affect infant development, including intrinsic (sex, body condition) and extrinsic (environment, maternal care, maternal stress) parameters. Those factors can contribute to the variation of its physical growth rate but also behavioral development and skills acquisition, which are all related and essential for their survival and fitness. Each factor can also be linked to each other and form puzzling trade-offs during infant development, leading to variations in the species’ life history. Thus, immaturity is a critical period, especially for primates, during which young learn and acquire all useful skills that can affect its success of survival (Lee et al., 2020; van Noordwijk & van Schaik, 2005;Thompson & Cords, 2020). It is therefore important to assess infant development and evaluate the intrinsic and extrinsic factors influencing this early life stage to understand the variation in life history (Bard & Leavens, 2014; Kappele & Pereira, 2003, Lonsdorf &Ross, 2012; van Schaik & Isler, 2012).

However, there is a lack of studies concerning early development, including the various developmental milestones and the factors that influence them, especially in the wild populations of strepsirrhine species, particularly in lemurs. Most of the studies on infant development focused on haplorrhine primates (e.g. Amici et al., 2019; Garber & Leigh, 1997; Lonsdorf et al., 2020; Maynard et al., 2021; Perry, 2020; Ross, 1991; Young & Shapiro, 2018; Berghänel et al., 2016; Bründl et al. 2020). Below, I will give a summary of the lemur’s life history, the so-called “lemur syndrome” (Kappeler & Fictel, 2015), and address why it is interesting to understand the early development of lemurs.

4. Lemur’s life history: “lemur syndrome”

It has been reported that lemurs have different life-history strategies and unique traits than other primates (Wright, 1999; Kappeler & Fichtel, 2015). For example, lemurs have a brief estrus period, most of them do not have sexual dimorphism, females are dominant, and they have a low metabolic rate (Jolly, 1966;Snodgrass et al., 2007; Wright,1999; Kappeler & Fichtel, 2015). Lemurs apply energy conservation strategies and adapt their activity, social organization, and reproduction to reduce energy expenditure (energy conservation hypothesis) (Jolly,1984; Wright, 1999). For instance, most lemurs are seasonal breeders; their reproduction occurs during the period when all the conditions, such as food availability and climate, are good (Wright, 1999). Also, female dominance is a strategy for lemurs to maximize females’ resource acquisition because the cost of reproduction is higher in females (Young et al., 1990). Lemurs have small group sizes to reduce resource competition (Wright, 1999). Lastly, some of the lemur species are cathemeral to maximize food intake and increase foraging time (Wright, 1999). Several hypotheses have been developed to explain lemur syndrome. It has been reported that those traits evolved presumably due to the various environmental stressors faced by lemurs in Madagascar (Kappeler et al., 2019; Wright, 1999), but could also derive from the effects of maternal stress during the infancy period (Kappeler & Fichtel, 2015).

Variation in many life-history traits is also found between lemur species (Godfrey et al., 2004; Kappeler & Fichtel, 2015). Lemuridae and Indriidae families have different life-history strategies (Godfrey et al., 2004). For example, they have different developmental schedules, time at maturation, and first reproduction (Godfrey et al., 2004). For instance, infant ring-tailed lemurs and brown lemurs, both belong to the Lemuridae family, are entirely independent of their mothers around the age of three months (Gould, 1990; Volampeno et al., 2011). However, infant Coquerel’s sifakas (*Propithecus coquereli*), which belong to the Indriidae family, are still carried by their mothers at the age of five months (Ross & Lehman, 2016). It has been reported that infants from Lemuridae species acquire independence and maturity faster and reproduce earlier than those from Indriidae species (Godfrey et al., 2004).

Intraspecific variation in various traits has also been reported in lemurs (Kappeler & Fichtel, 2012; Rudoplh et al., 2020; Dinter et al., 2021). Several studies found intraspecific differences in behavior, diet, group size, infant development, and even in reproductive success and survival (Harcourt &Thornback, 1990; Kappeler & Watts, 2012). For instance, in the ring-tailed lemur population, larger groups have low reproductive success but have higher surviving infants than smaller ones (Koyama et al., 2002; Pride, 2005). In diademed sifakas *(Propithecus diadema*), juveniles from fragmented areas exhibit slow growth than those from continuous areas (Irwin et al., 2010). Similarly, reproductive success and infant survival differ between females caused by their physical differences or social status. For instance, in Verreaux's sifakas, females with larger body sizes have a higher chance of reproducing and giving birth than those with lower body sizes (Richard et al., 2000). In ring-tailed lemurs, mid-rank females have a higher survival rate of infants compared to highest or lowest-rank females (Koyama et al., 2002). Intraspecific variation in the physiological responses to various environmental stressors has also been reported. For instance, in Verreaux's sifakas, populations that live on the edge exhibit higher GC metabolite concentration, and females have lower birth rates than those who live in the forest's interior (Dinter et al., 2021).

Hence, there is also inter-and intraspecific variation in lemur's life-history traits, especially in infant developmental schedules and fitness. Previously, it has been suggested that those life-history traits result from reproductive stress (Jolly, 1984). Female lemurs face high reproduction costs (Young et al, 1990). Another suggestion is that lemur life-history traits could be related to their environmental or nutritional stress because of the variations across habitats and microhabitats (Kappeler, 1996; Wright, 1999). Madagascar's ecological conditions are very different to other tropical forests because of the high seasonal climate changes, low soil fertility, slow tree growth with small diameter, low fruit availability, but also due to the huge impact of human disturbances (Ganzhorn, 2003a; Ganzhorn et al., 2003b; Kappeler & Fichtel, 2015; Wright, 1999). It is therefore interesting to assess maternal care and infant development in lemurs to understand how mothers face this harsh environment and can ensure infant survival.

Despite the importance of studying the life history of lemurs, few studies assessed infant development of lemur species, and most of the studies focused on one aspect of behavior. Also, those studies did not give detailed information concerning the schedule of various milestones and the factors which influence this developmental process (e.g., Jolly, 1966; Richard, 1976; Gould, 1990; Morlland, 1990; Gresier, 1992; Taurnaud, 2004; Volampeno, 2011; Ross & Lehman, 2016; Godfrey et al., 2004). Until now, detailed information concerning the timing of occurrence of various developmental milestones is only available for humans and chimpanzees (Bründl et al., 2020; Flensborg-Madsen & Mortensen, 2018). Moreover, there is a lack of information concerning the link between natural environmental stressors, maternal stress, and infant development. Therefore, in this study, I aim to assess this subject by analyzing original data from a wild lemur species, the Verreaux's sifakas (*Propithecus verreauxi*), and adding a comparative analysis on infant development in other primates. Below, I will explain why this species is suitable for this topic.

Why Verreaux's sifakas are a suitable study subject

Verreaux's sifakas are strepsirrhine primates endemic to Madagascar. They belong to the Lemuriformes order and the Indriidae family. They are among the largest group of lemurs, their adult body mass is around 3 kg (Mittermeier et al., 2008;Kappeler & Fichtel, 2012; Richard et al., 2002).Verreaux's sifakas are highly arboreal, diurnal, and live in groups of 2 to 12 individuals that typically contain multiple adult males and females (Kappeler & Fichtel, 2012).This species is characterized by female dominance; females are philopatric, whereas males disperse from their natal groups (Richard et al., 1993).They inhabit most parts of the remaining dry forest of Madagascar, where they feed mainly on leaves but also on fruits and flowers (Koch et al., 2017*;* Richard, 2003). Their home ranges vary among study sites between 5 to about 200 ha (Kappeler & Fichtel, 2012; Koch et al., 2017). They are exposed to environmental stressors, their habitats experience extreme seasonal variation, resulting in annual food availability fluctuations (Dewar & Richard, 2007). Besides, they also face another challenge which is predation. Fossas (*Cryptoprocta ferox*), harrier hawks (*Polyboroides radiatus*), and boas (*Acrantophis spp.*) constitute the main predators of Verreaux's sifakas in their natural habitat (Rasoloarison et al., 1995, Kappeler & Fichtel, 2012).

Verreaux's sifakas belong to the group of primates that reproduce slowly and produce only one offspring per year; their longevity is around 30 years (Kappeler & Fichtel, 2012; Richard et al., 2002). The mating period is very short and lasts only a few days, however, they have a relatively long gestation period of around 165 days (Richard, 2003). Infant are born, between July and August, during the extreme dry season period, where food availability is deficient, and are weaned until the age of six months, between January and February, during the wet season (Richard, 1976).Young Verreaux's sifakas achieve sexual maturity later than other larger lemur species, which is at around 4 to 5 years (Kappeler & Fichtel, 2012; Richard et al., 2002). Infants are entirely dependent on their mother during their first three months of life (Jolly, 1966), and mothers constitute their primary caregiver and invest more in transport than the other group members (Patel, 2007; Ross & Lehman, 2016). Infant mortality is very high in this species, about 62% during the first year of life of the infants (Richard, 1976, Kappeler&Fichtel, 2012). Besides, due to climate change and human disturbances in their natural habitat, Verreaux’s sifakas are recently classified among the critically endangered species (IUCN 2020).

Moreover, infant Verreaux’s sifakas are exceptional because they are born with a fully erupted milk dentition, like other Indriidae species(Godfrey et al., 2004; Richard et al., 2002). Therefore, Verreaux’s sifakas are excellently suited for this study. First, it is interesting to explore this mismatch between their dental precocity and their slow development. Second, Verreaux’s sifaka mothers face various socio-environmental stressors. The lactation period coincides with the dry and winter season, during which food availability is very low. Hence, mothers face a trade-off between infant's survival and her fitness and investment in future reproduction (Richard, 1976; Ross & Lehman, 2016). It is therefore important to understand the early development of this species and to understand how mother sifakas face the trade-off between the variable socio-environmental stressors and the investment to the offspring, to add information explaining lemur’s life history strategies under their harsh and challenging environment.

Information concerning the development of infant lemur species is poorly documented, especially from Indriidae family. Only few studies investigated infant development of indriids (Jolly, 1966; Grieser, 1992; Richard, 1976; Ross & Lehman, 2016; Wunderlich et al., 2011). Those studies do not give details concerning the infants’ developmental milestones, the occurrence of various specific skills, including the factors which induce inter-individual variation in infant development. According to Richard’s study (1976), infant Verreaux’s sifakas start to taste solid food at around two weeks of age. Social interactions begin within the first month of life with inter-individual variation, and by about six months of age, infants are weaned (Richard, 1976, Richard et al., 2002). Although studies on the link between environmental stressors, maternal stress, and glucocorticoid variation have been well developed in many lemur species (Brockman et al., 2009; Fardi et al., 2018; Hämäläinen et al., 2015; Ross, 2020; Rudolph et al., 2019, 2020; Tecot, 2013; Tecot et al., 2019; Dinter et al., 2021), studies assessing environmental and maternal effects on infant development remain poorly documented. Therefore, in this study, I aim to fill this gap by analyzing original data from wild Verreaux's sifakas.

5. Study aims and approaches

The aim of this study is to assess the link between environmental variation, maternal stress, and infant development. To explore this subject, I collected data on mother-infant dyads across three birth cohorts in the German Primate Center's field station, Kirindy forest Madagascar. I assessed animals’ social behaviors and activity patterns. I examined the infant’s skeletal and somatic growth rates. To assess maternal stress, I collected pre-and postnatal maternal fecal samples of all mothers for fecal glucocorticoid metabolite analysis. Also, I added phenology data in my project to assess variation in food availability, which is part of long-term data collection in the study site.

In the first study (Chapter 1), I investigated the physical, behavioral, and social development of infants in Verreaux’s sifakas. I assessed infants' developmental milestones and explored how some intrinsic (sex, age) and extrinsic factors (food availability), as well as maternal condition (mother’s age), may influence their physical and social development.

In the second study (Chapter 2), I explored the effects of maternal glucocorticoid concentration (GCc) on infant development. First, I examined the effects of variation in local climate, food availability, and previous reproduction on maternal GCc. Second, I explored the effects of elevated maternal GCc on maternal investment. Lastly, I explored how maternal stress influences the physical and behavioral development of infants.

Chapter I

Infant development and maternal care in wild Verreaux's sifakas *(Propithecus verreauxi)*

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ABSTRACT

Investigating factors influencing infant physical and social development is important to elucidate primate adaptations and life history evolution. Infant sifakas exhibit a puzzling mismatch between dental precocity and relatively slow postnatal growth, but only anecdotal reports of infant development are available for a comparative appraisal of their early life history and maturation. We therefore collected behavioral data on mother-infant dyads of 16 infant Verreaux's sifakas (*Propithecus verreauxi*) from three birth cohorts in Kirindy Forest to assess how infants' age, sex, mothers' age and environmental variation influence infants' development until weaning. We found that somatic growth rates differed between the sexes, with females growing faster than males. Infants began ingesting solid food as early as 3 weeks of age, which is extremely early for a primate of this size and much earlier than in Lemuridae. Social behavior emerged at a later age than motor skills. Despite pronounced variation in the timing and occurrence of various infant activities, none of them differed between the sexes, except that male infants were more engaged in grooming others. Infant sifakas did not develop faster than other lemurs despite the extra available energy gained from ingesting solid food at an early age, but their mothers carry them for a relatively long period, perhaps because vertical clinging and leaping is a locomotor style that requires prolonged physical maturation. The adaptive significance of their dental precocity remains elusive, however. Thus, further studies are required to understand how developmental schedules have coevolved with ecological and anatomical factors.

Key words: infant development, maternal care, developmental milestones, *Propithecus*, life history

INTRODUCTION

Primates have some of the slowest mammalian life histories, characterized by relatively slow growth, long gestation lengths, large neonates, low reproductive rates, slow postnatal growth rates, late age at sexual maturation and long life spans (Charnov 1991; Charnov and Berrigan 1993; Harvey and Clutton-Brock 1985; Ross 1998; van Schaik and Isler 2012), which appear to be driven by comparatively slow metabolic rates (Pontzer *et al*. 2014). However, a pronounced slow-fast continuum of life history speed is also found within the order Primates, where mouse lemurs and smaller bushbabies, for example, begin to reproduce when they are less than one year old and produce one or several litters of up to four infants per year, whereas great apes mature for up to 10 years before they begin producing single offspring every couple of years (Kappeler and Pereira 2003). Variation at this level is driven by variation in age-specific mortality hazards and the spread of reproduction (Healy *et al*. 2019; Promislow and Harvey 1990; Colchero *et al.* 2021; but see Leigh and Blomqvist 2011).

Infant development and mortality risk are influenced by variation in maternal investment i.e. “investment in offspring by the mother that increases the offspring's chances of surviving and hence reproductive success at the expense of the mother's ability to invest in other offspring” (p. 139, Trivers 1972), which, in turn, is shaped by maternal energy intake and physical condition, but also by offspring sex and age (Hanson and Gluckman 2014; Hinde 2013; Hinde and Milligan 2011) as well as maternal survival (Zipple *et al*. 2021). Numerous environmental and social factors, such as predation risk, resource availability, infanticide risk or alloparental care, directly or indirectly impact infant development and survival (Altman and Alberts 2005; Badescu *et al*. 2016; Janson and van Schaik 2000; Love *et al*. 2013). Further, developmental schedules also vary because infants in different species require different amounts of time for social learning of foraging and social skills (Maynard *et al*. 2021; Whiten and de Waal 2018). Thus, studying infant physical and social development as a function of intrinsic, maternal, and environmental variables within and across species is an important objective in elucidating primate adaptations and life history evolution (Bard and Leavens 2014; Kappeler and Pereira 2003; Lonsdorf 2017; Lonsdorf and Ross 2012; Pereira and Fairbanks 2002; van Schaik and Isler 2012).

Whereas the early development of haplorhine primates has been studied in several representatives of different lineages (e.g. Amici *et al*. 2019; Berghänel et al. 2015; Garber and Leigh 1997; Lonsdorf et al. 2020; Ross 1991; Young and Shapiro 2018), wild lemurs and other strepsirrhines remain underrepresented in studies of infant development and maternal care. Based on fundamental studies in captivity (Doyle *et al*. 1969; Klopfer and Boskof 1979; Klopfer and Klopfer 1970), subsequent studies have described various developmental milestones or single aspects of development in some species in the wild (*Lemur catta*: Gould 1990; *Eulemur fulvus*: Tarnaud 2004; *E. flavifrons*: Volampeno *et al*. 2011; *Varecia variegata*: Morland 1990; *Propithecus spp.*: Grieser 1992; King *et al*. 2011 Richard 1976; Ross and Lehman 2016; *Nycticebus javanicus*: Maynard *et al*. 2021). Similarly, patterns of parental care have been detailed in only a few strepsirrhines, focusing on species-specific tactics of care rather than on determinants of individual variation (summarized and reviewed in Tecot *et al*. 2013; but see Tecot and Baden 2018).

The early development of Indridae is of particular interest because they are exceptional in having virtually fully erupted milk dentition at birth in combination with relatively slow overall postnatal growth and maturation (Godfrey *et al*. 2004; Richard *et al*. 2002). However, infant development in Indridae remains poorly documented (Grieser 1992; Richard 1976; Ross and Lehman 2016) to explain this unique combination of life history traits (Godfrey *et al*. 2001; Godfrey *et al*. 2004; Mongle *et al*. 2020).

Therefore, we examined patterns of infant development and maternal care in one member of the Indridae, the Verreaux's sifakas. They are diurnal, arboreal lemurs that live in groups with on average 6 individuals (Kappeler and Fichtel 2012). They inhabit the dry forests of western and southern Madagascar, where they feed on flowers, leaves and fruits (Koch *et al*. 2017; Richard 2003). During their first few months of life, sifaka infants are completely dependent on their mothers (Jolly 1966), who are their primary caregivers (Patel 2007). Young sifakas achieve sexual maturity later than other diurnal lemur species, namely at an age of 4 to 5 years (Godfrey *et al*. 2004; Kappeler and Fichtel 2012; Richard *et al*. 2002). While Godfrey et al. (2004) proposed that, during resource crunches, the relatively low growth rates of young indriids may reduce the risk that they will starve, the relevant details of infant development have not been studied, so that the behavioral correlates of their exceptional dental precocity and slow postnatal growth remain essentially unknown. The aim of our study was, therefore, to describe milestones of physical and social development of wild infant Verreaux's sifakas to provide a basis for functional explanations of their unusual development and life history (see Godfrey *et al*. 2004), and to assess the relative importance of factors that could influence their early physical and behavioral development.

METHODS

Study site and subject

Data on wild Verreaux’s sifaka were collected during the birth season of three successive years (2017, 2018 and 2019) at the field station of the German Primate Center at Kirindy Forest/CNFEREF, located in central western Madagascar (Kappeler and Fichtel 2012). The area is dominated by dry deciduous forest and a climate characterized by a hot wet season from November to March and a cool dry season from April to October. A local population of sifakas living in up to 10 adjacent groups has been studied in Kirindy Forest since 1995. These lemurs are habituated to human observers and are individually marked with unique neck collars when they are about 8 months old or when they immigrate into the study population (Kappeler and Fichtel 2012).

Behavioral observations

A total of 16 singleton infants, whose birth dates were determined during daily group censuses, and their mothers from 7 study groups served as focal animals for this study. Most infants were born in July (see below) and were observed either during the first 8 months of their life in 2017 (N=5 infants) or for the first 6 months in 2018 (N=6 infants) and 2019 (N=4 infants), respectively. All of the mothers included in this study had at least one infant in previous years. The behavior of mothers and infants was simultaneously recorded for 5 daily observation hours, balanced between 3 hours in the morning (8:00 -11:00h) and 2 hours in the afternoon (14:00 -16:00h), using continuous focal animal sampling (Altmann 1974). Focal subjects were chosen in a randomized but counter-balanced manner throughout morning and afternoon observations.

During behavioral observations, we recorded all infant activities, the identity of their social partners, and proximity between mothers and their dependent infants (Table 1). To quantify patterns and milestones of infant development, we recorded the duration of all infant activities such as feeding, self-grooming, solitary play and locomotion. Concerning locomotor development, we distinguished between early locomotory behavior, when infants were still crawling on their mothers’ body, and independent locomotion off their mothers’ body. We also recorded all interactions, including social play, grooming and aggression with other group members to characterize the social development of infants.

Table 1 : Operational definitions of all recorded behaviors exhibited by infant Verreaux´ Sifakas, studied in Kirindy Forest Madagascar, from 2017-2019

Behavior	Definition
Early locomotion	Crawling across the mother's body
Self-grooming	Infant strokes, uses the tooth-comb to stroke through its own fur.
Carried by mother	Being carried by the mother, either ventrally or dorsally.
Independent locomotion	Moving independently over >5m.
Solitary object play	Infant manipulates an object.
Solitary locomotor play	Infant moves alone (locomotes, jumps, climbs) on branches or tree.
Nipple contact	Infant is in nipple contact with its mother or head is on the armpit of the mother.
Tasting food	Infant tastes, and licks solid food
Foraging	Infant ingests solid food
Social play	Infant plays (repetition of movements) with the mother or another group member, which is often accompanied with an open-mouth facial display and an open-arm gesture.
Grooming given	Infant uses its toothcomb to stroke through the fur of another individual
Grooming received	Another individual uses its toothcomb to stroke through the fur of the infant

Growth rate estimates

We used two independent methods to assess infant physical growth rates. First, infants' lower arm length was estimated once a month via photogrammetry. To this end, the length of the lower arm, corresponding approximately to the length of the radius, was estimated from photographs taken with a Canon EOS-D7 camera with a 85-200 mm lens. The size of an object (*o*) can be determined by the ratio of the focal length of the lens and the distance from the camera to the object as follows:

$$(1)\ D/f = o/p$$

where f is the focal length of the lens, D is the distance from the camera to the object, and p is the size (pixel number) of the object in the photo. The direct distance to a focal animal was determined with a Bosch GLM 50 C laser distance measurement tool (accuracy, ±2mm). The length of the infant's lower arm was then calculated by multiplying the distance with the number of pixels in the picture (Breuer *et al.* 2007). Photographs were taken whenever the opportunity for an unobstructed view presented itself, and the mean estimate of the lower arm was calculated from all photographs of an infant taken during a given month.

Second, we recorded the body mass of 13 infants during their first capture at an age of about nine months; three infants died before they could be captured. Captured infants were also sexed and the length of their lower arm was directly measured during brief anesthesia. We also measured the body mass and estimated their somatic growth rate (by fitting a generalized least square regression), assuming a uniform body mass of 58g at day 15 (Kappeler and Fichtel 2012).

Food availability

The relative abundance of leaves, flowers and fruits, was assessed during bi-weekly phenology transects of 784 trees in the study area detailed elsewhere (Koch *et al.* 2017). Briefly, we applied a semi-quantitative method in which the availability for each food item was scored on an ordinal scale ranging from 0 to 4, where 0 reflects the complete absence of the item and 4 represents its maximum abundance. Mean monthly scores for leaves, fruits, and flowers were summed up to obtain one score for food availability per month.

Statistical analyses

To determine growth rates in lower arm length, we used an approach similar to cross-validation. To this end, we fitted a model with the individual growth data as determined from photogrammetry, then predicted the arm length for the age at which the real measure of the arm length was taken during the capture, and finally compared the predicted arm lengths with those actually measured. More specifically, we first fitted a linear mixed model (LMM; Baayen 2008) with age included as the only fixed effect, individual ID included as a random intercepts effect, and a random slope (Barr *et al.* 2013; Schielzeth and Forstmeier 2009) of age. We also included a parameter for the correlation between the random intercept and the random slope. The response in this model were the arm length estimates determined using photogrammetry. Based on this model we determined predicted arm length for each individual and over the age range for which measures for a given individual were available. These predictions were based on the fixed effects estimates and the estimated individual specific deviations (BLUPs; Baayen 2008) from the population level parameters. A comparison of the arm length predicted for the age at which the actual arm length measure was taken with the arm length then allows for an assessment of the accuracy of photogrammetry. To further allow for an assessment of whether the actual arm length significantly deviated from the model, we determined 95% confidence limits (Cl) of the fitted model. The reason for using a linear over than an exponential model was that we had little indication for growth is non-linear within the range of age values we considered (see Results).

The model was fitted in R (version 4.0.3.; R Core Team 2020) using the function lmer of the package lme4 (version 1.1-21; Bates *et al.* 2015). We determined 95% confidence intervals (Cl) by means of a parametric bootstrap (N=1,000 bootstraps; function bootMer of the package lme4). To obtain Cl conditional on the particular individuals in the data set, we set the argument use.u of the function bootMer to TRUE. The sample analysed for this model comprised of 364 photogrammetrically determined arm lengths total of 14 individuals.

The arm length estimates obtained by photogrammetry were compared with the direct estimates, and the estimates of linear and somatic growth rates were correlated with each other (Spearman rank correlation) to assess their relationship. To evaluate potential sex effects on growth rates, both growth rate estimates were compared between the sexes with an exact Mann-Whitney U-test, using the package exactRankTests (Hothorn *et al.* 2019). We also assessed the influence of nutritional behavior, i.e. time spent in nipple contact and time spent foraging, on both growth rates by using Spearman rank correlations. Finally, we compared growth rates across birth cohorts, using a Kruskal Wallis test, to assess potential variation across years.

Food availability during the course of the study from July to December was compared across years by fitting a linear mixed model (Baayen *et al.* 2008), using the lme4 package (Bates *et al.* 2015) with food availability as response and year and month as fixed factors.

To characterize the pace of infant development, we estimated the age at which developmental milestones were observed for the first time, distinguishing between two categories of skills. “Motor skills” included infants’ early locomotion on the maternal body, being carried dorsally, self-grooming, solitary locomotor and object play, and first food ingestion. Grooming and social play with mothers and non-maternal group members constituted the category “social interactions”. To examine factors influencing the timing of developmental milestones, we fitted a linear mixed model using the package lme4 (Bates *et al*. 2015). Age in weeks was fitted as response, sex and skill as fixed factors, and birth cohort and mother's age as control factors. Infants' identity was included as a random factor.

In an attempt to quantify and explain inter-individual variation in development, we calculated the proportion of time (per hour) for each behavioral activity based on observational data collected between July and December of each study year as well in January and February 2018. We fitted eight different models assessing variation in the proportion of time spent either 1) being carried, 2) engaged in early locomotion, 3) locomotor play, 4) self-grooming, 5) object play, 6) being in nipple contact, 7) foraging, and 8) social play. In all models, we examined the influence of sex, age, food availability, mother's age and birth cohort on the proportion of time individuals were engaged in these behavioral activities by fitting a Generalized Linear Models (GLMM; Baayen 2008) with a beta error distribution and logit link function (package glmmTMB; Bolker 2009; McCullagh and Nelder 1989). In these models, we included sex, age and food availability as fixed effects and mother's age as well as birth cohort as control factors. Subject's and mother's identities were included as random effects. To avoid overconfident model estimates and to keep type I error rate at the nominal level of 0.05, we included random slopes (Barr et al. 2013; Schielzeth and Forstmeier 2009) of birth cohorts within mothers' ID. Sex and birth cohorts were manually dummy-coded and centered on the mean. Originally, we also included parameters for the correlations between random slopes and intercepts, but as the models did not converge, we had to exclude them again. For the models fitting the proportion of time spent on self-grooming and foraging, we also had to exclude the random slope of birth cohorts within mothers' ID because the models did not converge.

Since grooming and independent locomotion emerged only at the end of our study periods, the sample size for these behavioral activities was relatively small. Therefore, we used an exact Mann-Whitney U-test implemented in the package exactRankTests to examine sex differences and a Kruskal Wallis test to examine differences in the proportion of time spent grooming and foraging between years. Finally, we used Spearman rank correlations to examine the relationship between food availability and mother's age, respectively, on these behavioral activities.

Models (LMM, GlmmTMB) were fitted in R (R Core Team 2020). All covariates in the models were z-transformed in order to obtain easier interpretable models (Schielzeth 2010) and to facilitate model convergence. For LMMs, we checked the assumptions of normality distributions and homogeneity by visual inspection of a QQ-plot (Field 2009) of residuals and residuals plotted against fitted values (Queen *et al*. 2002). For GlmmTMBs, we checked for overdispersion. For both types of models, we assessed model stability through the level of estimated coefficients and standard deviations. Furthermore, we checked collinearity issues by deriving variance inflation factors (VIF) (Field 2009) of the standard linear model lacking the random effects. To test the significance of the predictors as a whole, we compared the fit of the full model with that of the null model comprising only the intercept (Forstmeier and Schielzeth 2011).

We extracted data on infant growth rates and the average timing of developmental milestones in other species from the published literature (e.g. Kappeler and Pereira 2003, Young and Shapiro 2018) and plotted them against mean adult female body mass to assess the relative position of the values obtained for Verreaux's sifakas in a comparative context. Because of the small number of data points and their large intraspecific variation, we refrained from formal analytical tests and present these relationships for descriptive purposes only.

Ethical note

This study adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching (Animal Behaviour 2020) and the legal requirements of the country (Madagascar) in which the work was carried out. The protocol for this research was approved by the Malagasy Ministry of the Environment, Water, and Forests (245/17/MEFF/SG/DGF/DSAP/SCB.Re, 047, 215/18/MEFF/SG/DGF/DSAP/SCB.Re, 053/19/MEDD/SG/DGF/DSAP/SCB.Re). The authors declare they have no conflicts of interest.

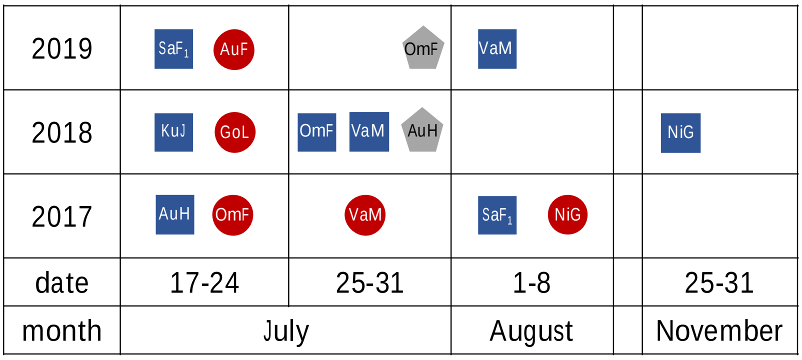
Data availability statement

The datasets generated and analysed during the current study are not publicly available due to further analyses but are available from the corresponding author on reasonable request.

RESULTS

Birth cohorts

Over the course of this study, 7 multiparous females, ranging in age between 5 to 20 years, from 7 different groups, gave birth to a total of 16 infants (Fig. 1). In 2017, three female, two male and one infant with unknown sex that died within a day after birth, were born within 3.5 weeks. In 2018, one female, three male and one infant with unknown sex that died at an age of 5 month were born within 1 week. One more male infant was born 2.5 months later (at the end of November); the latest birth recorded in 26 years in this population. Finally, one female, two male and one infant with unknown sex that died at an age of 5.5 month were born over a period of two weeks in 2019.



2019	SaF$_1$ AuF	OmF	VaM		
2018	KuJ GoL	OmF VaM AuH			NiG
2017	AuH OmF	VaM	SaF$_1$ NiG		
date	17-24	25-31	1-8		25-31
month	July		August		November

Fig:1: Distribution of births of Verreaux´s sifaka focal animals studied in Kirindy Forest, Madagascar from 2017-2019. Symbole include information about infant sex (blue squares = males; red circles=females; gray pentagons=unknown) and mother´s identity (first two letters)

Developmental milestones

Verreaux’s sifaka infants started to exhibit the first movements on their mother’s body (early locomotion) at an age of 1 to 6 weeks (median= 3 weeks). At about the same age (median= 3 weeks; range 1-13 weeks), infants began grooming themselves. At a median age of 5 weeks (range: 3-9 weeks), infants first began solitary motor play, object play (range: 1-17 weeks) as well as tasting solid food items eaten by their mothers (range: 3-7 weeks). Infants were first observed to switch from being carried on their mother’s ventrum to riding on their back when infants were at a median age of 6 weeks (range: 3-10 weeks). Social skills emerged slightly later and their emergence was highly variable across infants. Infants first played socially with other group members at a median age of 9 weeks (range: 3-17 weeks) and were first observed to actively groom others when they had a median age of 15 weeks (range: 2-23 weeks). Independent locomotion emerged last, at a median age of 16 weeks (range: 7-22 weeks), which was also highly variable across individuals. Overall, the model for the emergence of developmental milestones was significant (likelihood ratio test comparing full-null model comparison: χ^2=25.05, df=4, p<0.001). Social skills emerged at a later age than motor skills (Fig. 2, Table 2), but there were neither significant differences between birth cohorts and the sexes nor an influence of mother's age (Table 2).

Table 2: Influence of sex, birth year, mother's age and skill category (motor skills and social interactions[a]) on developmental milestones in Verreaux´s sifakas, studied in Kirindy Forest, Madagascar from 2017 to 2019

Term	Est	SE	*P*
Intercept	-2.94	0.24	[d]
Sex (male) [b]	0.31	0.29	0.315
Sex (unkown) [b]	0.15	0.44	0.738
Birth year: 2018 [b]	-0.04	0.24	0.911
Birth year: 2019 [b]	-0.60	0.34	0.117
Mother's age [c]	-0.04	0.13	0.771
Skill (social interactions)[b]	0.67	0.14	**<0.001**

[a] Motor skills: Early locomotion, self-grooming, locomotor and solitary object play, 1st time ingestion of solid food, ride on mother's back, independent locomotion. Social skills: grooming others and social play.

[b] Manually dummy-coded with females, birth cohort 2017 and motor skills being the reference categories

[c] z-transformed, mean and SD of the original values were: mothers age: 12.95 and 4.95 years

[d] Not shown as not having a meaningful interpretation

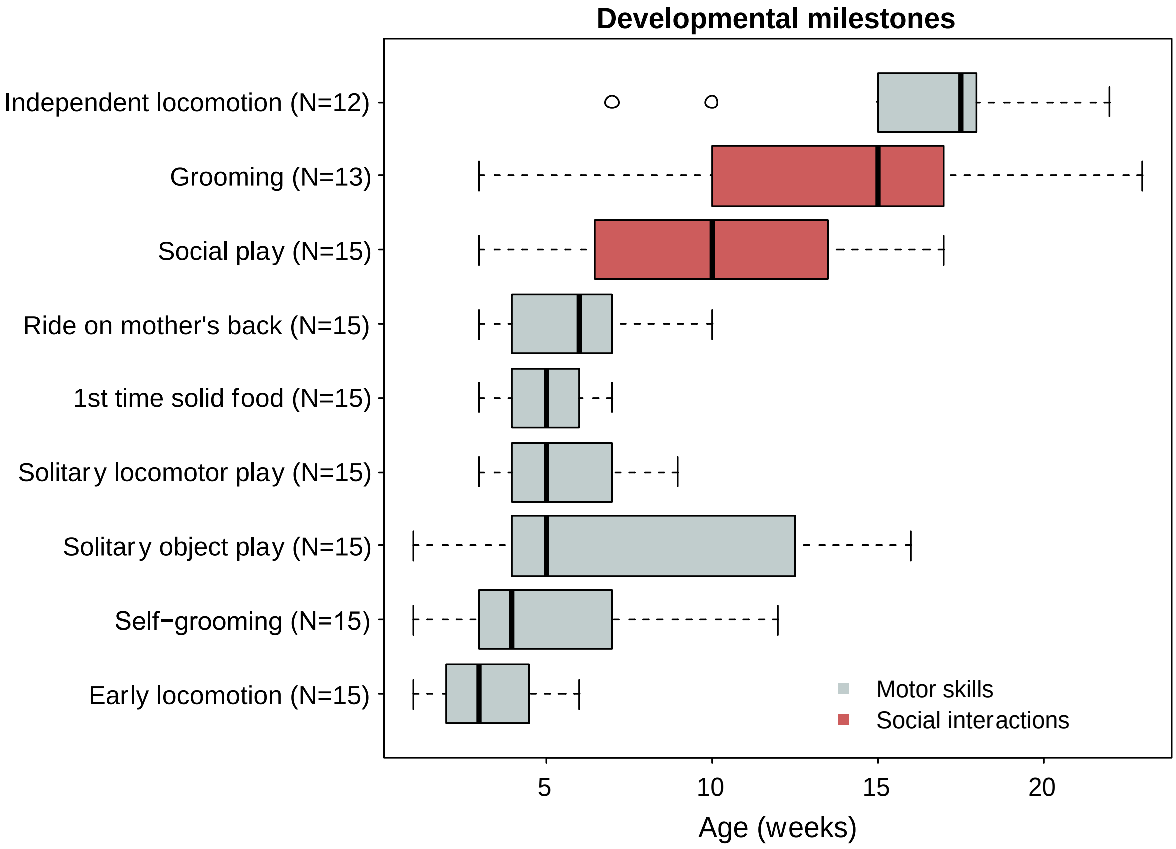


Fig. 2: Temporal patterning of developmental milestones of infant Verreaux’s sifakas, studied in Kirindy Forest, Madagascar from 2017 to 2019. Boxplots depicting medians (solid lines), inter-quartile range (boxes) and range (whiskers) of first observation (weeks) for 9 motor skills as well as for 2 types of social interactions

Physical development

Estimates of skeletal growth derived from photogrammetry indicated a linear increase of lower arm length in all infants and a very close correspondence to the fitted model in most cases (Fig.S1 SEM). Calibration with direct measures obtained during captures indicated a good fit with the estimates. Estimated arm length increased on average by 0.29±0.06 cm (mean ±SD) per day, and infants gained on average 6.16±0.95 g (mean ±SD) body mass per day.

The estimated linear skeletal growth rate correlated positively with somatic growth rate (Fig. 3; Spearman rank correlation, N=12, r=0.73, p=0.007). Both growth rates differed between the sexes, with females growing faster than males (exact Man Whitney U test: growth rate lower arm length: W=169, p<0.001, mean±SD: males: 0.26 ± 0.06 cm, females: 0.33 ± 0.06 cm; growth rate body mass: W= 0, p<0.001, mean±SD: males: 0. 63 ± 0.83 g, females: 0. 62 ± 1.34 g). Neither skeletal growth nor somatic growth correlated with time spent in nipple contact (Spearman rank correlation, N=12, r=0.04, p=0.908) or time spent foraging (Spearman rank correlation, N=12, r=0.23, p=0.442). Both growth rates also did not differ across years (Kruskal Wallis test: growth rate body mass: χ^2=0.78, df = 2, p= 0.680, mean±SD: 2017: 0. 32 ± 0.08 cm, 2018: 0. 25 ± 0.06 cm, 2019: 0. 31 ± 0.01 cm; growth rate lower arm length: χ^2=2.64, df = 2, p= 0.270, mean±SD: 2017: 6.68 ± 0.90 g, 2018: 6. 00 ± 1.34 g, 2019: 6.05 ± 0.33 g). Compared to other primate infants, young Verreaux's sifakas grow relatively quickly (Fig. 4; Table S1 SEM).

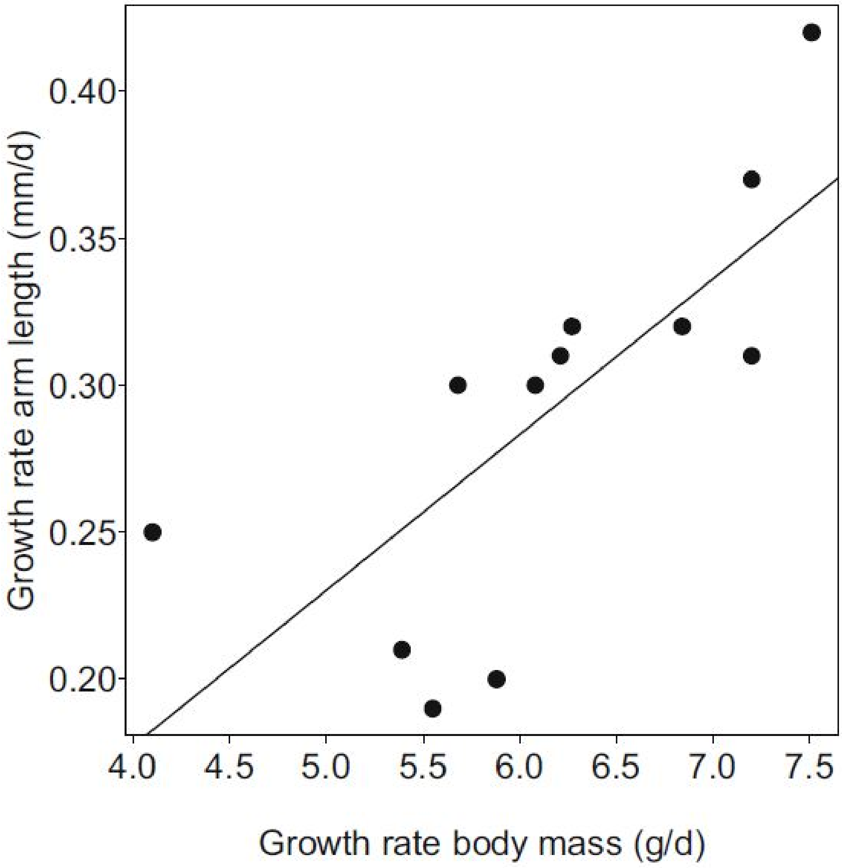


Fig. 3: Relationship between growth rates of lower arm length and body mass of infant Verreaux´s sifakas, studied in Kirindy Forest, Madagascar from 2017-2019. The black line indicates the regression line

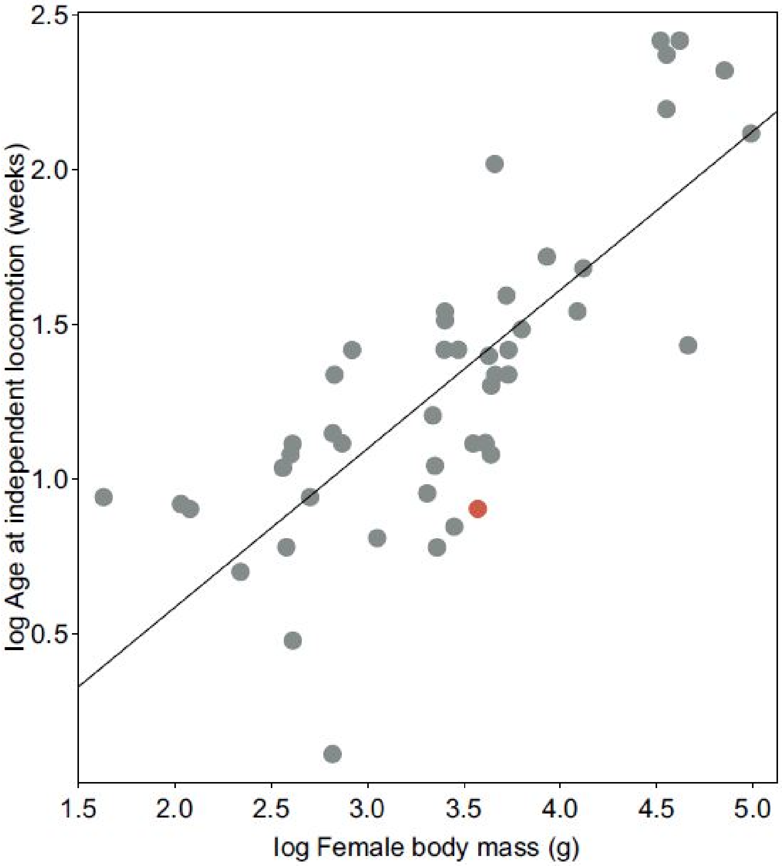


Fig 4: Age at independent locomotion (log) in relation to adult female body mass as proxy for relative growth rates in primates. Infant Verreaux´s sifaka (red) grow relatively fast until weaning. Data for other taxa (8 strepsirrhines 28 haplorhines) are from Young and Shapiro (2018) and data for Verreaux´s sifakas are from this study (ESM Table I)

Development of motor skills

We present models investigating factors potentially influencing the development of motor skills in the order of their relative emergence. The proportion of time infants spent with early locomotion decreased with age (likelihood ratio test comparing the full with the null model: χ^2=71.77, df=4, p<0.001, Table S2 SEM; age: p<0.001, Fig. 5a), and infants spent more time locomoting in 2017 (2017-2018: p<0.001, 2017-2019: p<0.001). Sex, mother's age and food availability did not influence the proportion of time spent on early locomotion (Table S2 SEM).

We found that infants groomed themselves for longer with increasing age (likelihood ratio test comparing the full with the null model: χ^2=57.79, df=4, p<0.001, Table S3 SEM; age: p<0.001; Fig. 5b), and that infants from the birth cohort of 2019 spent less time with self-grooming compared to infants born in 2017 (2017-2019: p=0.013).

Infants spent more time on solitary locomotor play with increasing age (likelihood ratio test comparing the full with the null model: χ^2=43.97, df=4, p<0.001, Table S4 SEM; age: p<0.001; Fig. 5c) and devoted less time to this activity in 2017 compared to infants born in 2018 and 2019 (2017-2018: p=0.009, 2017-2019: p=0.019). Compared to other species, infant Verreaux's sifakas begin to play by themselves relatively early (Fig. 6a, Table 1 SEM).

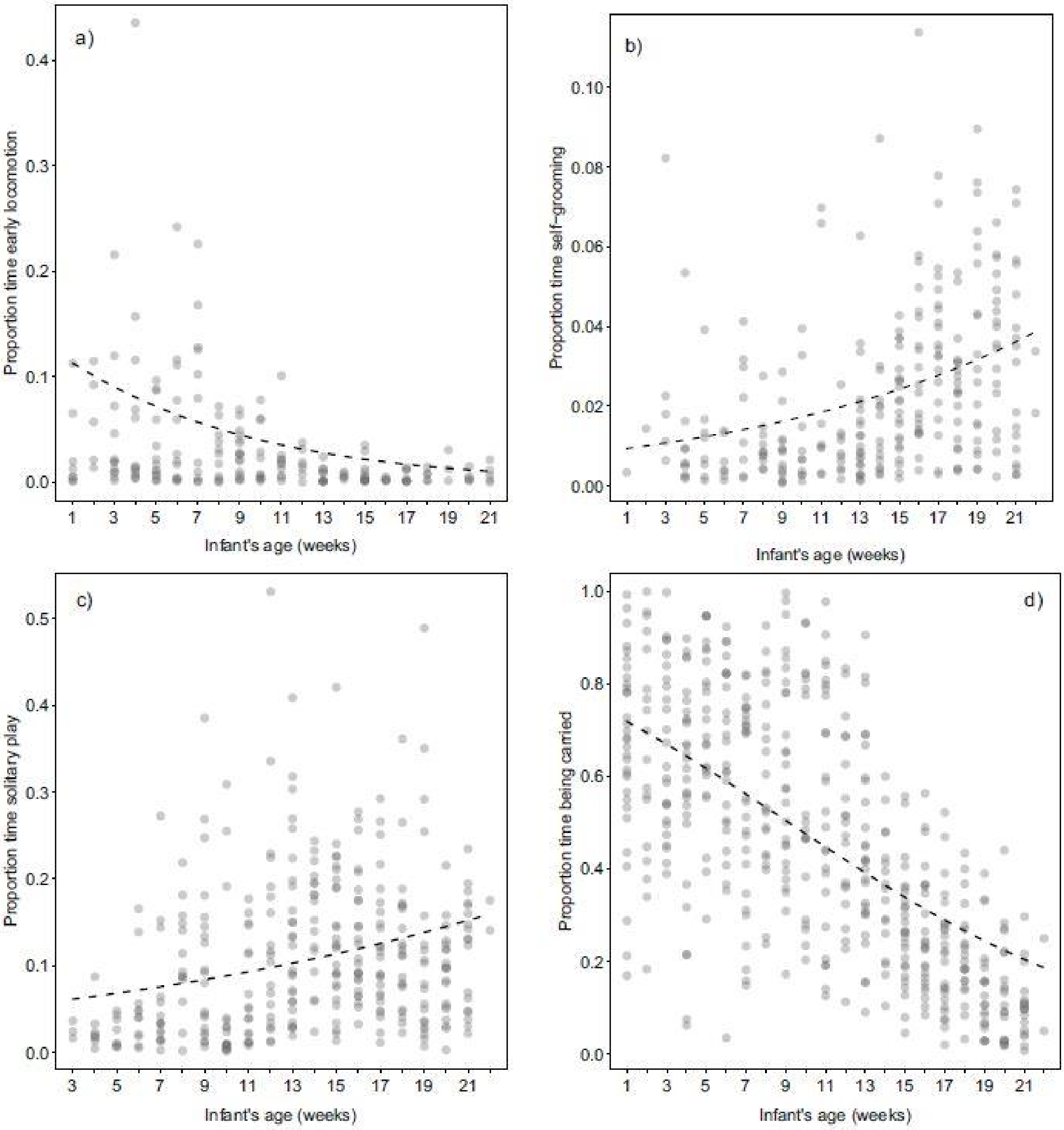


Fig 5: Development of motoer skills of infant Verreaux´s sifakas, studied in Kirindy Forest, Madagascar from 2017 to 2019. Proportion of time every infant spent exhibiting a particular behavior is plotted against their age (weeks). Dotted lines indicate the regression line. (a) Early locomotion. (b) Self-grooming. (c) Solitary locomotor play. (d) Carried by mother.

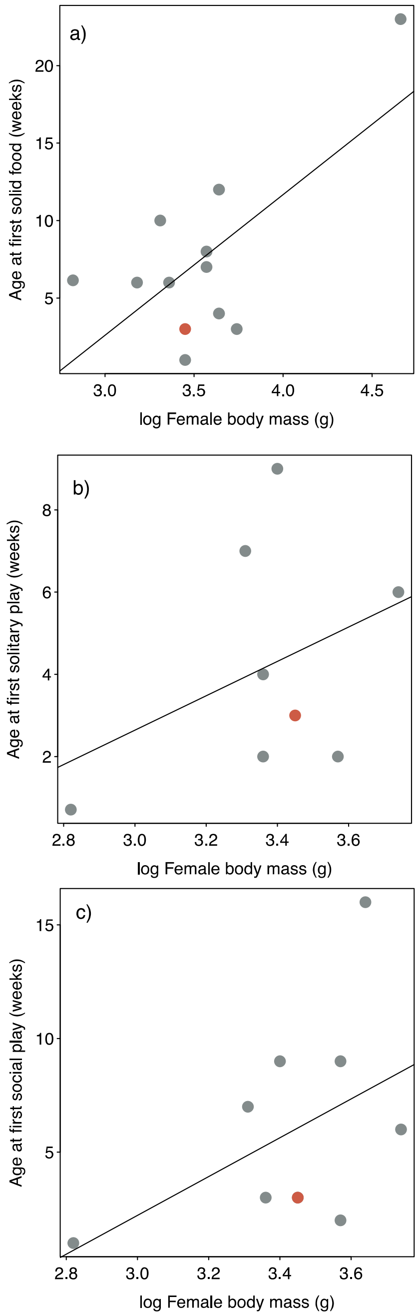


Fig. 6: Relative timing of developmental milestones in Verreaux´s sifakas (red) and other primates (gray). Age at (a) ingesting solid food for the first time, (b) solitary play, and (c) social play in relation to (log) adult female body mass. For sources see ESM Table I

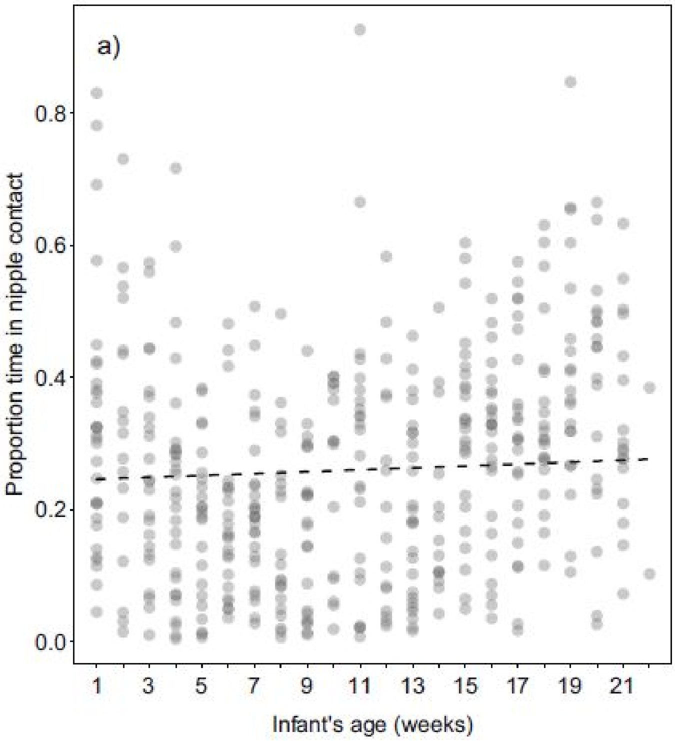
The proportion of time infants spent playing with objects did not change with age (likelihood ratio test comparing the full with the null model: χ^2=21.09, df=4, p<0.001, Table S5 SEM; age: p=0.050). However, infants of older mothers spent more time playing than those of younger mothers. Infants born in 2019 spent more time playing with objects than those born in 2017 (2017-2019: $p=0.002$). Sex and food availability did not influence variation in the proportion of time infants spent playing with objects (Table S5 SEM).

We found that infants were carried less with increasing age (likelihood ratio test comparing the full with the null model: $\chi^2=343.70$, df=4, $p<0.001$, Table S6 SEM; age:$p<0.001$; Fig. 5d) and that mothers carried infants less in 2019 compared to 2017 ($p=0.007$). Intra-annual variation in food availability influenced the proportion of time being carried negatively; infants were carried less as more food became available ($p<0.001$), but both of these variables covary with infant age – from the lowest food availability in September/October to the highest in December (Table S7 SEM; Fig. S2 SEM). Mother's age and sex of the infant did not explain variation in the proportion of time being carried by the mother (Table S6 SEM).

Finally, the mean time spent locomoting independently differed between the sexes (exact Mann-Whitney-U-test: W=0, $p<0.001$, mean±SD: males: 0. 008 ± 0.004; females: 0. 005 ± 0.008), with males spending more time locomoting independently than females. The mean time spent locomoting independently did not differ across birth cohorts (Kruskal Wallis: $\chi^2=0.35$, df=2, $p=0.840$, mean±SD: 2017: 0. 008 ± 0.005, 2018: 0. 006 ± 0.002, 2019: 0. 007 ± 0.002). It also neither correlated with mother's age (Spearman rank correlation: N=11, r=-0.05, $p=0.890$) nor with food availability (Spearman rank correlation: N=11, r=-0.17, $p=0.615$).

Nutritional access

The proportion of time infants spent in nipple contact did not vary with infants' age and sex (likelihood ratio test comparing the full with the null model: $\chi^2=37.47$, df=4, $p<0.001$, Table S8 SEM; age: $p=0.343$, sex (male): $p=0.906$, sex (unknown): $p= 0.880$; Fig. 7a), but with mother's age ($p=0.049$); infants of younger mothers spent more time in nipple contact than those of older mothers. Also, infants spent more time in nipple contact when more food was available ($p<0.001$) and infants born in 2018 and 2019 spent less time in nipple contact than infants born 2017 (2017-2018: $p=0.006$; 2017-2019: $p=0.001$).



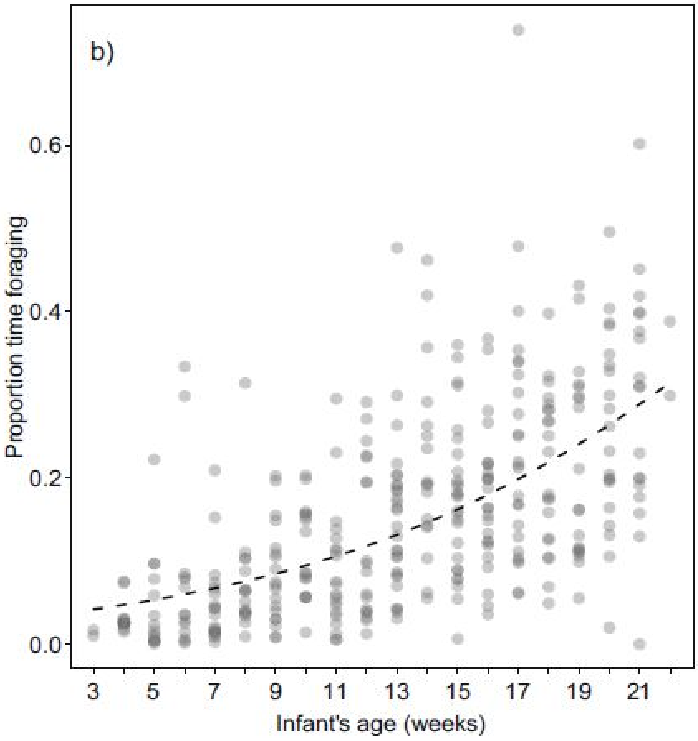


Fig 7: Proportion of (a) time spent in nipple contact and (b) time spent foraging as a function of age (weeks) in infant Verreaux´s sifakas, studied in Kirindy Forest, Madagascar from 2017 to 2019. Dashed lines indicate the regression line.

Compared to other species, infant Verreaux's sifakas first ingested solid food very early in life (Fig. 6b, Table S1 SEM). The proportion of time infants spent foraging increased with age (likelihood ratio test comparing the full with the null model: $\chi^2=195.56$, df=4, p<0.001, Table S9 SEM; age:p<0.001; Fig. 7b), and infants of the birth cohort 2019 spent less time foraging than infants born in 2017 (2017-2019: p=0.017). Sex, food availability and mother's age did not co-vary with the time spent foraging (Table S9 SEM).

Social development

Compared to other species, infant Verreaux's sifakas first played with other group members at a relatively early age (Fig. 6c). The model estimating the effect of sex, infant's and mother's age, birth year, and food availability on the proportion of time infants spent playing socially was not significant (likelihood ratio test comparing the full with the null model: $\chi^2=3.40$, df=4, p=0.493, Table S10, SEM). Grooming given during the first six months of life was observed in 13 infants. The mean time spent grooming differed between the sexes (exact Mann-Whitney-U-test: W=0, p<0.001), with males (mean± SD: 0.0043 ± 0.0024) spending more time grooming others than female infants (mean± SD: 0.0038 ± 0.0026). The time spent grooming differed across birth cohorts (Kruskal Wallis: $\chi^2=6.24$, df=2, p=0.044; Fig. S3 SEM), but did not correlate with mother's age (Spearman rank correlation: N=13, r=-0.18, p=0.558) or with food availability (Spearman rank correlation: N=13, r=0.28, p=0.353).

DISCUSSION

Our study, on early infant development in three cohorts of wild Verreaux's sifakas revealed that skeletal growth rates assessed via photogrammetry correlated positively with somatic growth estimates. Female infants grew faster than males according to both estimates. The temporal emergence of developmental milestones broadly reflected the infants' physical and social maturation, and our study provides a comprehensive data set that allows to pinpoint these events and to quantify inter-individual variation in their occurrence for this species. Despite pronounced variation in the timing and occurrence of infant activities, except that male infants were more engaged in grooming others. With respect to nutritional development, infants began to taste and ingest their first solid food items at an age of 3-5 weeks, which is extremely early for a primate of this body size and much earlier than in Lemuridae. Time spent in nipple contact as a rough proxy for potential energy intake did not change with age, even when infants spent about 20% of their time foraging independently at an age of about 15 weeks. However, time spent in nipple contact did correlated positively with food availability. The first occurrence of motor and social milestones occurred relatively early.

Determinants of individual variation in physical development

Regarding physical development, we found variation in infant growth rates, which differed between the sexes but these sex differences were not reflected by variation in feeding and nursing behavior. First, from a methodological perspective, we showed that growth estimates derived from photogrammetry correlated significantly with estimates based on changes in body mass between an age of two weeks and first capture. The latter estimate could not be based on the actual average birth mass because this datum is unavailable for this species, so our analyses exclude growth during the first two weeks of life. Because it is rarely possible to capture and weigh wild juvenile primates, photogrammetry therefore provides a non-invasive alternative to assess growth rates (Berghänel *et al*. 2015, 2016). Further, as indicated by the actual measurements of lower arm length at the time of capture, there is a reasonable correspondence with the estimated length because 6 out of 11 measures were within the fitted confidence intervals. In principle, one may prefer to compare the CIs of the actually measured arm length rather than those of the fitted model. However, we opted for the latter, as this approach is more conservative (revealed narrower Cl) and because it could be argued that the actual arm length measures can be determined without error. Thus, we advocate the use of photogrammetry in species where captures are not possible, but urge others who can use both methods to contribute more comparative data to better characterize their correspondence (cf. Cui *et al*. 2020; Galbany *et al*. 2016).

Regarding variation in growth rates, two points are noteworthy. First, the proximate mechanism giving rise to interindividual variation in growth rates remains obscure. Physical growth has to be supported by energy, which infants can derive either from milk or from solid food (Hinde and Milligan 2011). However, our behavioral measure of infant energy intake, i.e. time spent feeding, was not correlated with variation in growth rates, which might be due to our small sample size. In principle, mothers of faster-growing infants may have provided milk that is higher in energy content (Bernstein and Hinde 2016; Fairbanks and Hinde 2013; Hinde et al. 2009; Smith *et al*. 2017). However, time spent in nipple contact as a potential proxy for energy intake did not change with age, perhaps because the end of nipple contact, which can vary by more than 100% among infants (Borries *et al*. 2014), occurred after the end of our study. In addition, maternal energy transfer via lactation is challenging to assess with behavioral data alone because infants may also spend time in nipple contact for other reasons, such as comfort (Johnson *et al*. 1998).

Older infants spent more time foraging on solid food, as would be expected for increasing need and opportunity with age, but this behavioral change was not corelated with interindividual variation in growth rates. Because Kirindy sifakas are not strict capital breeders (Koch *et al*. 2017; Lewis and Kappeler 2005a; Lewis and Kappeler 2005b), mothers' ability to invest in lactation may depend on food availability, and infants spent more time in nipple contact when more food was available, indirectly supporting this notion. In addition, females at our study site and in other sifaka species adapt their glucocorticoids, and hence energy production to changes in food availability (*P. verreauxi*, Rudolph *et al*. 2020; *P. diadema*, Tecot *et al*. 2019) or energy demands (*P. coquereli*, Ross 2016; Ross 2020). Even though average food availability in the study area did not differ across the three study years, we may have missed local variation across home ranges (Rudolph *et al*. 2019) that may have allowed some mothers to provide more or more nutritious milk. In other species, a link between food availability and infant development has been established. For example, in mountain gorillas (*Gorilla beringei beringei*) infants in a more folivorous population reach adult size faster than infants in a more frugivorous population (Robbins and Robbins 2018). Thus, pinpointing the ecological and physiological drivers of variation in infant growth rates with non-invasive methods remains challenging (Hinde *et al*. 2009)

Second, we found a consistent sex difference in early infant growth rates. Independent of the estimate used, female infant sifakas grew faster than males. Sex differences in early growth have not been found in several lemur species studied in captivity (Leigh and Terranova 1998). Their adults generally lack sexual size dimorphism (Kappeler 1991), a pattern confirmed for wild sifakas (Gordon *et al*. 2013; Kappeler and Fichtel 2012; King et al. 2011; Lawler 2009; Tennenhouse 2005). In lorises and galagos, males grow faster or for longer to achieve moderately male-biased adult sexual size dimorphism (O'Mara *et al*. 2012). As discussed above, the proximate drivers of sex-biased infant growth remain elusive. However, sex-differences in infant growth might be related to future reproductive strategies. In Verreaux`s sifakas, heavier females have a higher probability of reproducing (Richard et al. 2002), whereas male reproductive success is correlated to leg shape, a trait that is functionally related to locomotor performances (Lawler et al. 2005; Lawler 2009). In savannah baboons (*Papio cyncocephalus*) and chimpanzees (*Pan troglodytes*), resource availability, maternal dominance rank and parity explained variation in infant and juvenile growth and maturation (Altmann and Alberts 2005; Lonsdorf *et al*. 2020), but none of these factors are known to have varied among the mothers included in this study. Sex-biased maternal investment in favor of daughters is an unlikely ultimate explanation, because Verreaux's sifakas have the highest male reproductive skew reported for any primate species (Kappeler and Schäffler 2008), indicating that mothers should invest more in sons, who have a much higher reproductive potential (Trivers and Willard 1973), but a comprehensive study that also takes variation in birth sex ratios as a function of maternal condition into account is required to explain this sex difference (Carranza 2002). Finally, we found a sex difference in physical, but not in behavioral development, but the relationship between these biases, if any, has not yet been systematically explored (see Lonsdorf 2017) and represent another interesting topic for future research.

Determinants of individual variation in behavioral development

The development of sifaka infants' behavior varied in two respects: the developmental timing and subsequent frequency of occurrence of behaviors and activities. First, within each of the behavioral categories, there was variation among infants on the order of several weeks in when a certain behavior or activity was first observed. Social interactions (grooming and play) exhibited the greatest inter-individual variation, perhaps because their first occurrence is co-dependent on the behavior of conspecifics. To evaluate the possibility that the observed magnitude of inter-individual variation is exceptional, comparative data are required. To date, however, detailed quantifications of primate developmental milestones have only been published for humans and chimpanzees (Bründl *et al*. 2020; Flensborg-Madsen and Mortensen 2018; but see Barthold *et al*. 2009). Compared to these species, the magnitude of the observed range of dates of first observation of various traits in Verreaux's sifakas does not appear to be exceptional; in chimpanzees, the ranges for some behaviors also span multiple months or even years, and variation in the reported estimates across several chimpanzee studies covers a similar range (Bründl *et al*. 2020). A comparable pattern of variation across studies can also be observed in sifakas, where the infants' transition from being carried ventrally to the dorsal jockey position provides an unambiguous exemplary behavioral marker. In our study, this transition occurred at about 6 weeks. Our observed range of 3–10 weeks covers the range of averages reported in previous studies (Grieser 1992; Jolly 1966; Richard 1976; Ross and Lehmann 2016). Thus, the observed inter-individual variation in the achievement of developmental milestones does like not represent a methodological artefact and requires explanation.

Consistent inter-individual differences in developmental sequences could explain the observed variation in the timing of first observations of the various behaviors. In this case, fast developing infants would set the lower limits of the observed ranges and consistently slower developing infants would define the upper bounds. If this was true, we would predict positive correlations among the individual occurrence dates of behavioral milestones, but only three out of 36 of these correlations were significant (Table S11 SEM). Thus, infants that were the first to exhibit a particular behavior were most often not among the earliest exhibitors of another behavior. This result contrasts with studies of wild chimpanzees and Eurasian lynx (*Lynx lynx*), where multiple motor and social milestones were positively correlated with each other and or with rates of physical growth (Antonevich *et al.* 2020; Heintz *et al.* 2017). In Assamese macaques (*Macaca assamensis*), play and growth were negatively correlated (Berghänel *et al.* 2015), however. Thus, there is interspecific variation in the interrelationships among physical, motor and social developmental milestones that deserves more systematic future studies.

Our analyses also revealed that neither infant sex, maternal age nor the year of study, which serves as a proxy for potential variation in food availability, had significant impacts on the average first occurrence of various behaviors. As in chimpanzees (Bründl *et al.* 2020), however, we found that social skills emerged at a later average age than various motor skills, and that later emerging milestones tended to exhibit greater interindividual variation in the timing of the emergence, but more detailed meaningful comparisons are precluded by the fact that the relevant haplorhine studies spanned multiple years (Lee *et al.* 2020). Thus, with the currently available information we are unable to explain the great inter-individual variation in the emergence of developmental behavioral milestones.

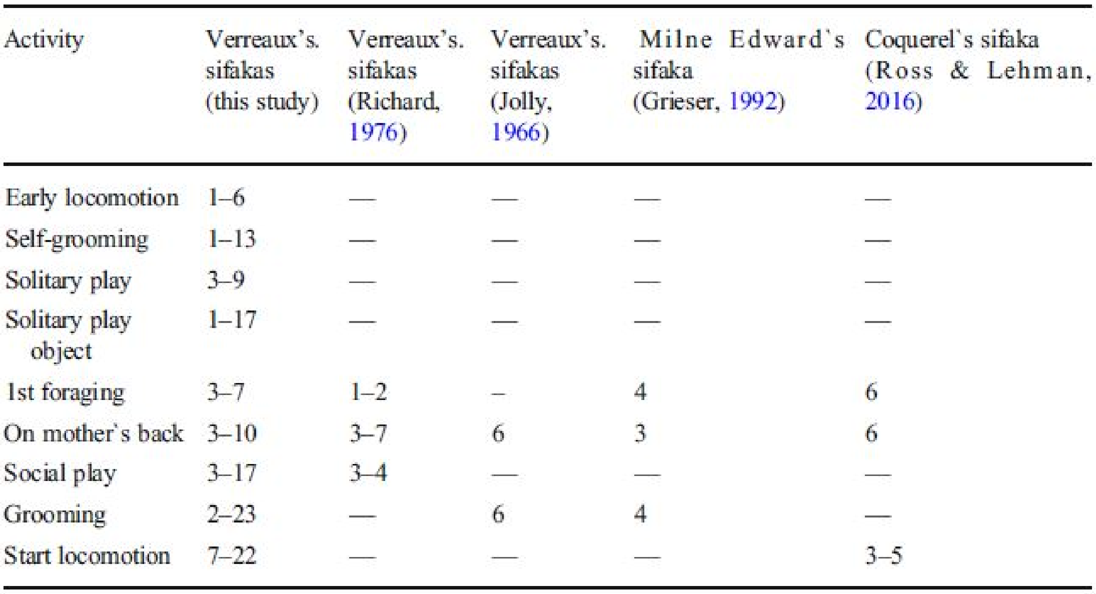
In addition, the occurrence and relative salience of various activities, here measured as the proportion of time devoted to an activity or behavior, also varied widely among individuals. Except for time spent in nipple contact, age was a significant predictor of this variation, with some behaviors, like solitary object play, decreasing in occurrence with time, and others, like time spent self-grooming increasing in prominence. Such temporal dynamics are the essence of behavioral development, and, thus, not surprising (Pereira and Altmann 1985). Independent of age, however, there was also a pervasive effect of the year of study on the mean frequency with which certain behaviors were exhibited. For example, infants born in 2017 exhibited higher rates of early locomotion and self-grooming, and they were carried more by their mothers, but they had lower rates of solitary locomotor and object play. Because mean food availability did not differ across study years, the ultimate reason behind this level of variation remains obscure. Nonetheless, this effect serves as a useful reminder that studies of limited duration or with a small sample size may yield results that are not representative of long-term averages or the population as a whole. Finally, of a large number of factors and behaviors examined in separate models, only intra-annual variation in food availability had an effect on being carried and duration in nipple contact, with the latter correlating negatively with maternal age. Even if they did not reflect Type I errors, these few effects do not point at a comprehensive explanation for this aspect of intra-individual variation in infant behavior. Thus, the comprehensive set of analyses examining the potential effects of various predictors of behavioral variation did not permit a conclusive explanation of the observed variation among infants.

Comparative perspective on sifaka infant development and life history

Regarding lemur life history evolution, we can now, in combination with data on life history traits from previous studies of this species, address potential intraspecific variation in developmental patterns and milestones across the range of Verreaux's sifakas in southern and western Madagascar (Table 3; Gordon et al. 2013; Jolly 1966; Richard 1976; Richard *et al.* 1991; Richard *et al.* 2000; Richard *et al.* 2002). Jolly (1966) first reported that infant Verreaux' sifakas at Berenty transferred onto other group members in week 2, and switched to the dorsal jockey position in week 6 when they also began grooming others. Richard (1976) reported that Verreaux's and Coquerel's sifakas (*P. coquereli)* infants, which were considered subspecies of the same species at the time, switched to the dorsal position when they were 3-7 weeks old; they initiated social play when they were 3-4 weeks old and they began tasting food as early as 1-2 weeks of age. Comparable data from long-term sifaka studies at Beza Mahafaly and Kirindy Mitea are not available yet. Since other conspecific lemurs (Lahann and Dausmann 2011) and vertebrates (Eckhardt *et al*. 2017) with a wide geographical distribution across southwestern Madagascar exhibit plasticity in life history traits, future comparisons of Verreaux's sifakas infant development across the four long-term study sites within their range are potentially interesting.

Moreover, sifaka infant development has only been studied in Milne Edward’s sifakas (*P. diadema edwardsi)* and Coquerel’s sifakas (Table 3; Grieser 1992; Ross and Lehmann, 2016). Ross and Lehmann (2016) reported that their infants were similar to Verreaux’s sifakas still carried by their mothers 26% of the time at 6.5 months. Interestingly, anti-predator behavior, i.e., the ability to act upon alarm calls with appropriate escape-responses, emerged when sifakas started to be physically independent from their mothers at an age of about 6 months (Fichtel 2008). Anthropoid primates, which differ greatly in body mass and developmental rates, also exhibit appropriate anti-predator responses when they become physically independent from their mothers, suggesting that the development of motor skills coincides with cognitive skills, i.e., the emergence of alarm call recognition (Fichtel 2008). The existing data on sifaka infant development are nonetheless sufficient to sketch a consistent pattern of motor, social and nutritional development, highlighting the relatively early interactions with solid food, but more detailed studies on additional species are required for more informative comparisons.

Table III Overview of the emergence (age in weeks) of developmental milestones in sifakas.



Activity	Verreaux’s. sifakas (this study)	Verreaux’s. sifakas (Richard, 1976)	Verreaux’s. sifakas (Jolly, 1966)	Milne Edward`s sifaka (Grieser, 1992)	Coquerel`s sifaka (Ross & Lehman, 2016)
Early locomotion	1–6	—	—	—	—
Self-grooming	1–13	—	—	—	—
Solitary play	3–9	—	—	—	—
Solitary play object	1–17	—	—	—	—
1st foraging	3–7	1–2	–	4	6
On mother`s back	3–10	3–7	6	3	6
Social play	3–17	3–4	—	—	—
Grooming	2–23	—	6	4	—
Start locomotion	7–22	—	—	—	3–5

Third, compared to other large-bodied lemurs, infant Verreaux’s sifaka started to eat solid food earlier, but developed locomotor independence relatively later. In brown lemurs (*Eulemur fulvus)*, black lemurs (*Eulemur macaco)*, blue-eyed black lemurs (*Eulemur flavifrons)*, redfronted lemurs (*Eulemur rufifrons)*, ring- tailed lemur (*Lemur catta), g*reater bamboo lemurs (*Prolemur simus)*, black-and white ruffed lemurs (*Varecia variegata*), greater lesser and golden bamboo lemurs (*Hapalemur aureus*, *H. griseus)*, infants first tasted solid food at an age of 1-2 months whereas greater bamboo lemurs started to feed on solid food at an age of 3 weeks (Table 4). Independent movements started in bamboo lemurs at an age of 2-3 months. Thus, the lemurids for which data on infant development exist concur in reporting later ingestion of solid foods and earlier motor development than in sifakas.

Table 4 : Overview of the emergence (Age in weeks) of developmental milestones in various lemurs

Activity	Ring-tailed lemur (Gould 1990)	Blue-eyed black lemur (Volampeno et al. 2011)	Brown lemurs (Tarnaud 2004)	Black lemurs (Harrington , 1978)	Ruffed lemurs (Moorland , 1990)	Redfronted lemurs (Bathold et al. 2009	Greater bamboo lemur (Tan, 2006; Fraisier et al 2015)	Eastern lesser bamboo lemur (Tan, 2006)	Golden bamboo lemur (Tan, 2006)
1s foraging	6	9-10	6-8	6	8	8	8	3-6	6
On mother´s back	1	3	-	6	-	-	-	3	-
Social play	3	7	-	-	-	-	-	-	-
Independent locomotion	4-6	9-10	-	-	8-12	-	12-16	-	-

Finally, the functional significance of the combination of dental precocity with relatively slow motor development remains elusive. As all other indrids, sifakas are born with their milk teeth fully erupted, and have slower postnatal growth rates than all lemurids (Godfrey *et al*. 2004). This contrast, which was mainly based on data from captive animals, has been attributed to lower maternal investment in indrids (Godfrey *et a*l. 2004), where the very early ingestion of solid foods by infants would further reduce the costs of maternal investment. Prudent allocation of limited energy during lemur reproduction has been identified as a key target of selection because reproduction takes place in a seasonal and unpredictable environment (Jolly 1984; Kappeler 1996; Young *et al*. 1990). After all, the second half of gestation and the first 3 months of lactation of Verreaux's sifakas coincide with the cool dry season that is characterized by reduced food availability (Koch *et al*. 2017; Lewis and Kappeler 2005a). In other sifakas, and across lemurs more generally, weaning is scheduled to coincide with the period of greatest food availability, however (Meyers and

Wright 1993; Tecot *et al*. 2013), suggesting that this timing provides a more important target of natural selection. Because of variable gestation lengths, different sympatric lemur species give birth at various times of the year where infants face a given forest in a very different situation (Wright *et al*. 2012), so that the absolute timing of birth and lactation provides no explanation as to why sifaka infants begin feeding on solid food so early.

Furthermore, sympatric lemurids are exposed to the same conditions and selective pressures; yet, their infants do not exhibit precocial dentition. Because neonate dentition does not appear to be expensive to produce (Mongle *et al*. 2020), there may simply not be enough costs associated with dental precocity, so that minor benefits contribute to the maintenance of this trait in this lineage. Our study has substantiated the timing and relative importance of independent foraging in early in life, and indicated that infant Verreaux's sifaka did not grow or develop faster than other lemurs despite the extra available energy, but that they appear to experience maternal care, especially in the form of carrying, for longer. This aspect of interspecific variation has been attributed to the unique demands of vertical clinging in a three-dimensional habitat in sifakas, compared to the more quadrupedal and terrestrial locomotion of lemurids (Klopfer and Boskoff 1974). Future studies of additional indrids and lepilemurs, should allow more formal tests of this notion. In conclusion, the function of this combination of life history traits of sifakas remains elusive until more detailed comparative data become available

Author contributions

HSM collected the data, HSM and CF analyzed the data, all authors wrote the manuscript.

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Supplementary Electronic Material

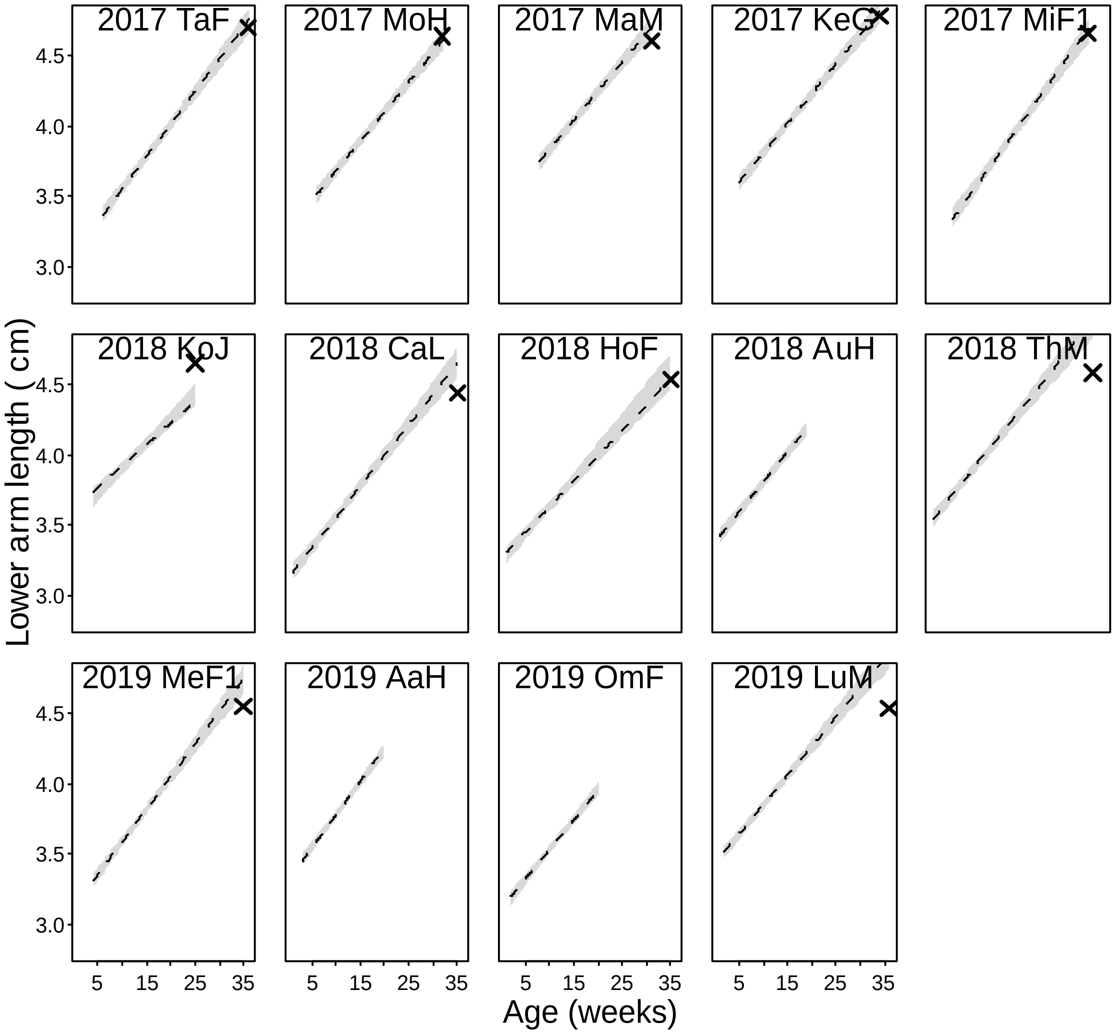

Figure S1: Estimates of lower arm growth for 14 infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019. Mean weekly estimates of lower arm length obtained by photogrammetry (dots) are plotted against age (weeks). In 11 infants, lower arm length was also measured during their first capture (crosses). Black dashed lines and grey polygons depict the individual specific model and its confidence limits over the age range for which we had measures for the respective individual. Acronyms depict the birth year, infant ID and group affiliation.

Table S1: Minimum age in weeks and adult female body mass for the developmental milestones: 1st time feeding on solid food, independent locomotion, and social play.

Species	**Developmental milestones**	**Female body mass (g)**	**Min age (weeks)**	**Reference**
Allouatta guariba	1st solid food	4350	4	Miranda et al. 2005
Allouatta guariba clamitans	1st solid food	4350	12	Podgaiski and de Assis Jardim 2009
Eulemur flavifrons	1st solid food	2042	10	Volampeno et al. 2011
Eulemur fulvus	1st solid food	1500	6	Tarnaud 2004
Lemur catta	1st solid food	2268	6	Gould 1990
Pan troglodytes	1st solid food	45800	23	Bründl et al. 2020
Propithecus edwardsi	1st solid food	5504	3	Grieser 1992
Propithecus verreauxi	1st solid food	2850	1	Richard 1976
Propithecus verreauxi	1st solid food	2850	3	this study
Propithecus coquereli	1st solid food	3700	7	Grieser 1992
Saimiri sciureus	1st solid food	662	6,14	King and King 1970
Varecia variegada	1st solid food	3748	8	Morland 1990
Allouatta guariba	independent locomotion	4350	20	Miranda et al.2005
Allouatta guariba clamitans	independent locomotion	4350	12	Podgaiski et al. 2009
Alouatta guariba	independent locomotion	4550	21,71	Young and Shapiro 2018
Alouatta palliata	independent locomotion	5320	26,14	Young and Shapiro 2018
Alouatta seniculus	independent locomotion	5300	39,14	Young and Shapiro 2018
Aotus trivirgatus	independent locomotion	740	13,00	Young and Shapiro 2018
Ateles paniscus	independent locomotion	8440	52,14	Young and Shapiro 2018
Callithrix flaviceps	independent locomotion	410	13,00	Young and Shapiro 2018
Callithrix jacchus	independent locomotion	380	6,00	Young and Shapiro 2018
Cebuella pygmaea	independent locomotion	120	8,00	Young and Shapiro 2018
Cebus capucinus	independent locomotion	2540	26,14	Young and Shapiro 2018
Cebus olivaceus	independent	2520	32,57	Young and Shapiro 2018

	locomotion			
Chlorocebus aethiops	independent locomotion	4090	13,00	Young and Shapiro 2018
Chlorocebus aethiops	independent locomotion	4090	13,00	Young and Shapiro 2018
Eulemur flavifrons	independent locomotion	2042	9	Volampeno et al. 2011
Galago senegalensis	independent locomotion	220	5,00	Young and Shapiro 2018
Gorilla beringei	independent locomotion	97500	130,43	Young and Shapiro 2018
Gorilla gorilla	independent locomotion	71500	208,71	Young and Shapiro 2018
Lagothrix poeppigii	independent locomotion	4530	104,29	Young and Shapiro 2018
Lemur catta	independent locomotion	2268	6	Gould 1990
Lemur catta	independent locomotion	2210	16,00	Young and Shapiro 2018
Macaca mulatta	independent locomotion	5370	21,71	Young and Shapiro 2018
Microcebus rufus	independent locomotion	43	8,71	Young and Shapiro 2018
Otolemur crassicaudatus	independent locomotion	1110	6,43	Young and Shapiro 2018
Pan paniscus	independent locomotion	33200	260,86	Young and Shapiro 2018
Pan troglodytes	independent locomotion	45800	27	Bründl et al.2020
Pan troglodytes	independent locomotion	41600	260,86	Young and Shapiro 2018
Papio anubis	independent locomotion	13300	47,86	Young and Shapiro 2018
Papio cynocephalus	independent locomotion	12300	34,71	Young and Shapiro 2018
Perodicticus potto	independent locomotion	840	26,14	Young and Shapiro 2018
Pongo abelii	independent locomotion	35600	156,57	Young and Shapiro 2018
Pongo pygmaeus	independent locomotion	35800	234,86	Young and Shapiro 2018
Prolemur simus	independent locomotion	2248	11	Frasier et al. 2015

Propithecus coquereli	independent locomotion	4280	25,00	Young and Shapiro 2018
Propithecus diadema	independent locomotion	6260	30,43	Young and Shapiro 2018
Propithecus verreauxi	Independent locomotion	2850	7	this study
Propithecus verreauxi	independent locomotion	2950	26,14	Young and Shapiro 2018
Saguinus fuscicollis	independent locomotion	360	10,86	Young and Shapiro 2018
Saguinus geoffroyi	independent locomotion	500	8,71	Young and Shapiro 2018
Saguinus oedipus	independent locomotion	400	12,00	Young and Shapiro 2018
Saimiri oerstedii	independent locomotion	680	21,71	Young and Shapiro 2018
Saimiri sciureus	independent locomotion	662	1,29	King and King 1970
Saimiri sciureus	independent locomotion	662	14	King and King 1970
Sapajus apella	independent locomotion	2520	34,71	Young and Shapiro 2018
Suguinus oedipus	independent locomotion	404	3	King et al. 1974
Tarsius tarsier	independent locomotion	106	8,29	Young and Shapiro 2018
Varecia variegata	independent locomotion	3748	8	Morlland 1990
Varecia variegata	independent locomotion	3520	13,00	Young and Shapiro 2018
Allouatta guariba	social play	4350	16	Miranda et al. 2005
Cebus apella	social play	2520	9	Fragaszy et al. 1991
Eulemur flavifrons	social play	2042	7	Volampeno et al. 2011
Lemur catta	social play	2268	3	Gould 1990
Propithecus edwardsi	social play	5504	6	Grieser 1992
Propithecus verreauxi	social play	2850	3	Richard 1976
Propithecus verreauxi	social play	2850	3	this study
Propithecus coquereli	social play	3700	2	Grieser 1992
Propithecus coquereli	social play	3700	9	Grieser 1992
Saimiri sciureus	social play	662	1	King and King 1970

Table S2: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 spent on **early locomotion** (GlmmTMB; N=186; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-3.06	0.11	[d]
Sex (male) [a]	-0.13	0.15	0.398
Sex (unkown) [a]	0.33	0.35	0.346
Infant's age [b]	-0.64	0.07	**<0.001**
Mother's age [b]	-0.06	0.07	0.403
Birth year: 2018 [c]	-1.33	0.20	**<0.001**
Birth year: 2019 [c]	-0.97	0.21	**<0.001**
Food availability [b]	0.12	0.07	0.087

[a] Manually dummy-coded with females being the reference category
[b] z-transformed, mean and SD of the original values were:
infant's age: 9,68 and 5.40 weeks, mother's age: 12.69 and 4.89 years
[c] Manually dummy-coded with 2017 being the reference category
[d] Not shown as has no meaningful interpretation

Table S3: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 spent **self-grooming** (GlmmTMB; N=269; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-3.81	0.11	[d]
Sex (male) [a]	0.18	0.11	0.112
Sex (unkown) [a]	0.28	0.17	0.099
Infant's age [b]	0.35	0.07	**<0.001**
Mother's age [b]	0.03	0.07	0.684
Birth year: 2018 [c]	0.01	0.13	0.099
Birth year: 2019 [c]	-0.33	0.13	**0.013**
Food availability [b]	-0.01	0.06	0.943

[a] Manually dummy-coded with females being the reference category
[b] z-transformed, mean and SD of the original values were:
infant's age: 13.76 and 5.15 weeks, mother's age: 12.56 and 4.73 years
[c] Manually dummy-coded with 2017 being the reference category
[d] Not shown as has no meaningful interpretation

Table S4: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 spent on **locomotor play** (GlmmTMB; N=335; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-2.33	0.09	[d]
Sex (male) [a]	0.09	0.10	0.378
Sex (unkown) [a]	-0.25	0.15	0.095
Infant's age [b]	0.27	0.05	**<0.001**
Mother's age [b]	0.05	0.05	0.293
Birth year: 2018 [c]	0.30	0.12	**0.009**
Birth year: 2019 [c]	0.26	0.11	**0.019**
Food availability [b]	-0.04	0.06	0.518

[a] Manually dummy-coded with females being the reference category

[b] z-transformed, mean and SD of the original values were:
infant's age: 9.68 and 5.40 weeks, mother's age: 12.69 and 4.89 years

[c] Manually dummy-coded with 2017 being the reference category

[d] Not shown as has no meaningful interpretation

Table S5: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 spent **playing with objects** (GlmmTMB; N=208; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-3.55	0.16	[d]
Sex (male) [a]	-0.21	0.12	0.078
Sex (unkown) [a]	-0.34	0.18	0.055
Infant's age [b]	-0.13	0.07	0.050
Mother's age [b]	0.10	0.05	0.045
Birth year: 2018 [c]	0.29	0.18	0.108
Birth year: 2019 [c]	0.54	0.17	**0.002**
Food availability [b]	-0.12	0.08	0.116

[a] Manually dummy-coded with females being the reference category

[b] z-transformed, mean and SD of the original values were:
infant's age: 12.32 and 5.04 weeks, mother's age: 12.89 and 4.80 years

[c] Manually dummy-coded with 2017 being the reference category

[d] Not shown as has no meaningful interpretation

Table S6: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 were **carried by their mothers** (GlmmTMB; N=494; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-0.40	0.13	[d]
Sex (male) [a]	-0.00	0.17	0.100
Sex (unkown) [a]	-0.12	0.28	0.665
Infant's age [b]	-0.69	0.05	**<0.001**
Mother's age [b]	0.07	0.07	0.299
Birth year: 2018 [c]	0.24	0.18	0.196
Birth year: 2019 [c]	0.51	0.18	**0.007**
Food availability [b]	-0.25	0.05	**<0.001**

[a] Manually dummy-coded with females being the reference category

[b] z-transformed, mean and SD of the original values were:
infant's age: 10.61 and 6.04 weeks, mother's age: 12.87 and 4.67 years

[c] Manually dummy-coded with 2017 being the reference category

[d] Not shown as has no meaningful interpretation

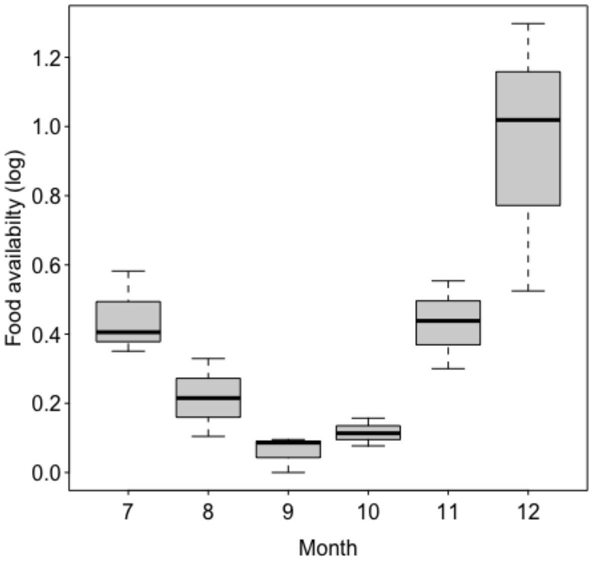

Figure S2: Seasonal fluctuation in food availability in Kirindy Forest, Madagascar from 2017-2019. The mean cumulative availability of fruits, leaves and flowers varies significantly across months (Table 6 SEM).

Table S7: Results of the linear model: effects of year and month on **food availability** in Kirindy Forest, Madagascar from 2017-2019 (LM: Full-null model comparison: $F=8.23_{7,10}$, p=0.002; N=48, estimates, together with standard errors)

Term	Est	SE	*P*
Intercept	0.48	0.11	[b]
Year (2018) [a]	-0.14	0.10	0.193
Year (2019) [a]	0.05	0.10	0.660
Month (August) [a]	-0.23	0.14	0.131
Month (September) [a]	-0.39	0.14	0.020
Month (October) [a]	-0.33	0.14	0.040
Month (November) [a]	-0.02	0.14	0.915
Month (December) [a]	0.50	0.14	0.001

[a] Reference category for year was 2017 and for month July.

[b] Not shown as has no a meaningful interpretation

Table S8: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 spent in **nipple contact** (GlmmTMB; N=459; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-0.82	0.08	[d]
Sex (male) [a]	-0.01	0.01	0.906
Sex (unkown) [a]	-0.03	0.17	0.880
Infant's age [b]	0.05	0.05	0.343
Mother's age [b]	-0.09	0.05	**0.049**
Birth year: 2018 [c]	-0.03	0.12	**0.006**
Birth year: 2019 [c]	-0.34	0.10	**0.001**
Food availability [b]	0.21	0.04	**<0.001**

[a] Manually dummy-coded with females being the reference category

[b] z-transformed, mean and SD of the original values were:
infant's age: 10.65 and 6.13 weeks, mother's age: 13.03 and 4.65 years

[c] Manually dummy-coded with 2017 being the reference category

[d] Not shown as has no meaningful interpretation

Table S9: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of **time infant** Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 **spent foraging** (GlmmTMB; N=350; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-1.81	0.13	[d]
Sex (male) [a]	0.11	0.10	0.304
Sex (unkown) [a]	-0.01	0.14	0.956
Infant's age [b]	0.61	0.05	**<0.001**
Mother's age [b]	-0.08	0.11	0.467
Birth year: 2018 [c]	-0.08	0.11	0.528
Birth year: 2019 [c]	-0.25	0.10	**0.017**
Food availability [b]	0.01	0.04	0.858

[a] Manually dummy-coded with females being the reference category
[b] z-transformed, mean and SD of the original values were:
infant's age: 13.19 and 4.94 weeks, mother's age: 12.89 and 4.69 years
[c] Manually dummy-coded with 2017 being the reference category
[d] Not shown as has no meaningful interpretation

Table S10: Influence of sex, infant's and mother's age, birth year, and food availability on the proportion of **time infant** Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 **spent playing socially** (GlmmTMB; N=165; N_{ID} = 15; estimates, together with standard errors).

Term	Est	SE	*P*
Intercept	-3.05	0.18	[d]
Sex (male) [a]	-0.16	0.18	0.373
Sex (unkown) [a]	0.15	0.26	0.562
Infant's age [b]	0.03	0.07	0.692
Mother's age [b]	0.18	0.08	**0.020**
Birth year: 2018 [c]	-0.09	0.36	0.798
Birth year: 2019 [c]	0.07	0.18	0.677
Food availability [b]	-0.10	0.08	0.205

[a] Manually dummy-coded with females being the reference category
[b] z-transformed, mean and SD of the original values were:
infant's age: 10.84 and 6.63 weeks, mother's age: 12.43 and 4.85 years
[c] Manually dummy-coded with 2017 being the reference category
[d] Not shown as has no meaningful interpretation

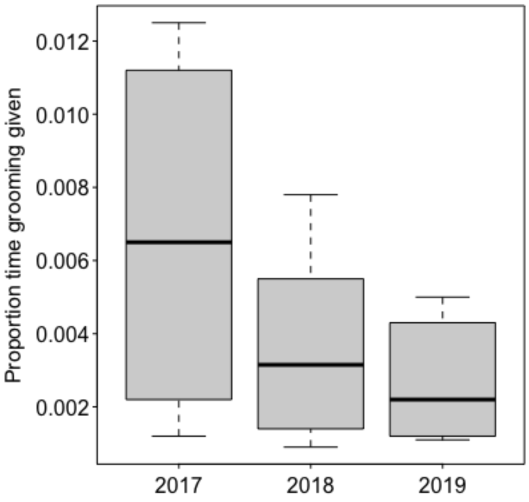

Figure S3 Proportion of time infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019 spent grooming across birth cohorts 2017-2019.

Table S11: Pearson correlations among age of emergence of the respective developmental milestones in infant Verreaux's sifakas, studied in Kirindy Forest, Madagascar from 2017-2019. In bold: significant correlations

	Social play (N=15)	Independent locomotion (N=12)	Grooming (N=13)	1st solid food (N=15)	Early locomotion (N=15)	Self-grooming (N=15)	Object play (N=15)	Ride on mother's back (N=15)	Locomotor play (N=15)
Social play	0								
Independent locomotion	R=0.19, p=0.18	0							
Grooming	R=0.24, p=0.29	R=0.53, p=0.096	0						
1st solid food	R=0.46, p=0.33	R=-0.028, p=0.25	R=0.29, p=0.23	0					
Early locomotion	R=0.0054, p=0.96	R=-0.24, p=0.66	R=-0.33, p=0.29	R=0.58, p=0.11	0				
Self-grooming	R=-0.3, p=0.17	R=0.2, p=0.22	R=-0.094, p=0.89	R=0.13, p=0.081	R=0.18, p=0.71	0			
Object play	R=-0.14, p=0.68	R=0.37, p=0.61	R=0.19, p=0.45	R=0.25, p=0.19	R=0.06, p= 0.81	**R=0.86, p=0.005**	0		
Ride on mother's back	R=-0.28, p=0.88	R=0.1, p=0.38	R=0.18, p=0.45	R=0.45, p=0.25	R=0.21, p=0.44	R=0.34, p=0.8	R=0.49, p=0.076	0	
Locomotor play	R=0.16, p=0.19	R=0.43, p=0.061	R=0.28, p=0.27	R=0.67, p=0.11	R=0.31, p=0.3	R=0.68, p=0.39	**R=0.77, p=0.013**	**R=0.69, p=0.003**	0

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Chapter II

Maternal stress effects on infant development in wild Verreaux's sifakas *(Propithecus verreauxi)*

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Abstract

Maternal effects mediated by nutrients or specific endocrine states of the mother can affect infant development. Specifically, pre- and postnatal maternal stress associated with elevated glucocorticoid (GC) output is known to influence the phenotype of the offspring, including their physical and behavioral development. These developmental processes, however, remain relatively poorly studied in wild vertebrates, including primates with their relatively slow life histories. Here, we investigated the effects of maternal stress, assessed by fecal glucocorticoid output, on infant development in wild Verreaux's sifakas (*Propithecus verreauxi*), a group-living Malagasy primate. In a first step, we investigated factors predicting maternal fecal glucocorticoid metabolite (fGCM) concentrations, how they impact infants' physical and behavioral development during the first 6 months of postnatal life as well as early survival during the first 1.5 years of postnatal life. We collected fecal samples of mothers for hormone assays and behavioral data of 12 infants from two birth cohorts, for which we also assessed growth rates. Maternal fGCM concentrations were higher during the late prenatal but lower during the postnatal period compared to the early/mid prenatal period, and were higher during periods of low rainfall. Infants of mothers with higher prenatal fGCM concentrations exhibited faster growth rates and were more explorative in terms of independent foraging and play. Infants of mothers with high pre- and postnatal fGCM concentrations were carried less and spent more time in nipple contact. Time mothers spent carrying infants predicted infant survival: infants that were more carried had lower survival, suggesting that they were likely in poorer condition and had to be cared for longer. Thus, the physical and behavioral development of these young primates were impacted by variation in maternal fGCM concentrations during the first six months of their lives, presumably as an adaptive response to living in a highly seasonal, but unpredictable environment.

Significance statement

The early development of infants can be impacted by variation in maternal condition. These maternal effects can be mediated by maternal stress (glucocorticoid hormones) and are known to have downstream consequences for behavior, physiology, survival and reproductive success well into adulthood. However, the direction of the effects of maternal physiological GC output on offspring development are highly variable, even within the same species. We contribute comparative data on maternal stress effects on infant development in a *Critically Endangered* primate from Madagascar. We describe variation in maternal glucocorticoid

output as a function of ecological and reproductive factors and show that patterns of infant growth, behavioral development and early survival are predicted by maternal glucocorticoids. Our study demonstrates how mothers can influence offspring fitness in response to challenging environmental conditions.

Keywords
Glucocorticoid concentrations, Maternal stress, Infant development, Environmental stressors, Verreaux’s sifaka

Introduction

The survival and reproductive success of animals are determined by adequate responses to challenges and opportunities in their physical and social environments (Alberts 2019). These responses are modulated by phenotypic differences among individuals, which in turn are shaped during development by additive genetic and maternal effects (Moore et al. 2019). While these developmental processes remain relatively poorly studied in wild vertebrate populations, it has been established that maternal effects are mediated by nutrients or specific endocrine states of the mother that affect offspring morphology, but also life history traits and behavior, and that they tend to influence juvenile traits more than adult traits (Bernardo 1996; Moore et al. 2019; Mouton and Duckworth 2021). In addition, it is now widely recognized that events experienced by individuals during early development and adolescence not only have instantaneous fitness effects, but that they can also have downstream consequences for behavior, physiology, survival and reproductive success well into adulthood, in taxa ranging from insects to humans (Lea et al. 2015; Tung et al. 2016; Morimoto et al. 2017; Langenhof and Komdeur 2018; Sachser et al. 2018; Schülke et al. 2019; Rosenbaum et al. 2020; Snyder-Mackler et al. 2020; Thompson and Cords 2020; Weibel et al. 2020). In fact, the environment individuals experience during early development can even impact the phenotypes and fitness of their own later offspring (Zipple et al. 2019, 2021).

Ultimate explanations for maternal effects focus on phenotypic adaptations to environmental factors, either instantly or in the future, but the effects themselves may also result from intrinsic factors, such as maternal age. These effects are based on the fact that, as a consequence of anisogamy, female fitness is primarily limited by mothers’ ability to provide pre- and postnatal maternal investment, which, in the end, is linked to maternal condition and access to resources. If a mother is exposed to favorable environmental conditions (e.g. in terms of climate, food, predators or parasite exposure), and if these conditions are stable and predictable, her offspring should enjoy relatively high fitness under similarly good conditions. However, if the environmental conditions are more variable and less predictable, there is a risk of a mismatch between the maternal environment and that of her then adult young (Nettle and Bateson 2015). If offspring that developed under good conditions achieve the highest fitness regardless of future environmental conditions, they enjoy a so-called silver-spoon effect (Grafen 1988). If maternal effects adapt offspring to the expected future environmental conditions, they exhibit an external predictive adaptive response (PAR). When infants develop instead under developmental constraints that affect their somatic state negatively, and they adjust to this unfavorable internal state (e.g. by accelerating reproduction), regardless of future environmental conditions, this represents an internal PAR (Gluckman et al. 2005; Sheriff and Love 2013; Hanson and Gluckman 2014; Schülke et al. 2019). Because the predictability of later-life environments decreases with increasing longevity, external PARs are not expected in long-lived species (Wells 2007a), such as most primates (van Noordwijk 2012; van Noordwijk et al. 2013; Berghänel et al. 2016; Snyder-Mackler et al. 2020). Here, an alternative model has been proposed, postulating that early-life effects promote immediate survival, independent of any costs this may incur later in life (Lea et al. 2015, 2018), though these costs may be partly compensated for by internal PARs (Nettle et al. 2013).

In addition to ecological crises, infants may experience stressful social events, like weaning-related rejection, maternal death or birth of a sibling (Tung et al. 2016; Maestripieri 2018), or they are impacted by maternal senescence (Ivimey-Cook and Moorad 2020), all of which tend to reduce the amount of maternal investment they receive. There is empirical evidence from studies of both humans and other vertebrates for rippling effects of early life adversity on offspring development and fitness (Lummaa and Clutton-Brock 2002; Weinstock 2008; Giesing et al. 2011; Berghänel et al. 2017; Crockford et al. 2020; McGhee et al. 2021), but the proximate mechanisms underlying this phenomenon remain poorly known, especially in wild animals (Edes and Crews 2017; Langenhof and Komdeur 2018; Lea et al. 2018; Hawkley and Capitanio 2020). However, one factor that has been identified as important mediator of the relationship between individuals' early experiences and health outcomes in several species and taxa is the exposure to maternal stress hormones, i.e. glucocorticoids (GC; Love et al. 2013), both pre- and postnatally.

In birds and other oviparous species, mothers can adjust offspring´s exposure to prenatal GC levels only during egg production (Love and Williams 2008). In mammals, however, maternal GCs are transferred through the placenta and later on through mother's milk and can therefore presumably be fine-tuned over longer periods of early offspring development (Hinde 2013). Maternal GC levels in free-living birds and mammals are predictably increased in response to unpredictable changes in food availability or quality (Love et al. 2005; Welcker et al. 2009), but also to other potential stressors, like reproduction or predation risk, that make an increase in mobilized energy beneficial (Beehner and Bergman 2017). Pre-, and in the case of mammals, also postnatal maternal stress is known to influence several aspects of offspring's phenotype, including their physical development (Berghänel et al. 2017), behavioral development (Maestripieri 2018), skill acquisition (Berghänel et al. 2015) or immune function (Veru et al. 2014). However, the direction of the effects of maternal physiological GC output on offspring development are highly variable, even within the same species (Hauser et al. 2007; Berghänel et al. 2017; Schülke et al. 2019; for intra-specific plasticity see Dantzer et al. 2013), leading to opposite conclusions about their ultimate function.

Accordingly, the observed offspring phenotypic responses to maternal GCs have either been interpreted as unavoidable negative outcomes, such as reduced offspring size or growth (Love et al. 2013), or as evidence for adaptive maternal programming that prepares offspring for their predictable future environment (Sheriff et al. 2017), or as adjustments of their internal somatic state (Nettle et al. 2013). In addition, there is also evidence for sex-specific intraspecific variation in the response to maternal stress. For example, infant male and female rhesus monkeys exhibited different temperament responses to variation in maternal milk cortisol. Infant males of mothers with higher milk GC concentrations showed a more confident temperament (more active, playful, and curious), whereas female infants did not (Sullivan et al. 2011). Similarly, in humans, higher milk cortisol levels were found to induce "negative affectivity" (fear, sadness, frustration) in daughters but not in sons (Grey et al. 2013). Consequently, there is a need for studies contributing comparative information from additional taxa to document patterns and drivers of maternal stress effects on infant development.

Here, we contribute new data on the effects of maternal stress as well as environmental and social adversaries on infant development in wild Verreaux's sifakas (*Propithecus verreauxi*), a group-living *Critically Endangered* (Louis et el. 2020) primate from the seasonal dry forests of southwestern Madagascar. Specifically, we first examine the effects of variation in local climate, food availability and previous reproduction on maternal GCs. In a second step, we explore how maternal GC output is linked to the physical and behavioral development as well as to the survival of two cohorts of infants.

Previous studies have explored the effects of environmental stressors on individual stress hormone levels in various lemur species (Lemuriformes). In both lemurids (Lemuridae) and indrids (Indriidae), GC output is influenced by seasonal variation, and average levels are higher during the dry season in Verreaux's sifakas (Rudolph et al. 2019) and ring-tailed lemurs (*Lemur catta*, Cavigelli 1999; Pride 2005). In ring-tailed lemurs, GCs are elevated during droughts and cyclones (Fardi et al. 2018). GCs were also found to be higher during periods of low food availability, especially during fruit scarcity, in collared lemurs (*Eulemur collaris*, Balestri et al. 2014), red-bellied lemurs (*E. rubriventer*, Tecot 2008; 2013), ring-tailed lemurs (Pride 2005), diademed sifakas (*P. diadema*, Tecot et al. 2019) and in Verreaux's sifakas (Rudolph et al. 2020).

Moreover, social variables were also found to induce changes in GC levels, albeit not consistently so. For example, members of larger groups exhibited elevated GC level in ring-tailed lemurs (Pride 2005; Fardi et al. 2018; Gabriel et al. 2018), but not in Verreaux's sifakas (Rudolph et al. 2019). Moreover, increased GC levels characterized top-ranking females in ring-tailed lemurs (Cavigelli 1999; Cavigelli et al. 2003), and dominant males in Verreaux's sifakas (Fichtel et al. 2007; Rudolph et al. 2020), but rank did not predict GC levels in male red-fronted lemurs (Ostner et al. 2008) and male ring-tailed lemurs (Gould et al. 2005). Further, fluctuations in group aggression rates associated with seasonal reproduction did not influence GC levels in male ring-tailed lemurs (Gould et al. 2005), but increases in male GC levels during the mating and/or birth season were reported for Verreaux's sifakas (Fichtel et al. 2007; Brockman et al. 2009; Rudolph et al. 2020), red-fronted lemurs (Ostner et al. 2008) and collared lemurs (Balestri et al. 2014). Finally, GC levels increased during late gestation and the birth season in female sifakas (Tecot et al. 2019; Ross 2020; Rudolph et al. 2020), collared (Balestri et al. 2014), and ring-tailed lemurs (Cavigelli 1999). Thus, lemurs apparently respond to challenging ecological and social factors with changes in GC levels, and some of these responses appear to be variable among species and between the sexes. Previous lemur studies have not linked these stress responses to infant development, however, even though this variability in GC responsiveness offers a promising opportunity for examining whether pre- and postnatal maternal GC output affects infant development and if so, in which way.

Here, we predicted that relatively harsh climatic conditions (i.e. low temperatures and rainfall) with low food availability will increase maternal average GC levels, both prenatally and postnatally. Further, focusing on developmental constraints, we predicted that elevated pre- and postnatal maternal GC concentrations will be associated with reduced maternal investment (e.g. in terms of infant carrying) and retarded infant physical and behavioral development (but see Dantzer et al. 2013). Specifically, we predicted that, as in some other species (Sullivan et al. 2011; Grey et al. 2013), infants from mothers with higher GCs will grow and develop more slowly and exhibit reduced levels of playing, foraging, locomotion, and grooming compared to mothers exhibiting lower GC concentrations. Finally, given the detrimental effects of prolonged exposure to high GC levels in adult primates (Campos et al. 2021), we predicted that high maternal GC levels are also associated with an increased mortality risk for infants.

Methods

Study site and subjects

Data on wild Verreaux's sifaka were collected during two successive breeding seasons (2017 and 2018) at the field station of the German Primate Center at Kirindy Forest/CNFEREF, located in central western Madagascar (Kappeler and Fichtel 2012). The area is dominated by dry deciduous forest and a climate characterized by a hot wet season from November to March and a cool dry season from April to October. A local population of Verreaux's sifakas has been studied in Kirindy Forest since 1995. These lemurs are habituated to human observers and are being individually marked with unique neck collars when they are about 8 months old or when they immigrate into the study population.

Verreaux's sifakas are 3 kg arboreal, foli-frugivorous primates that can live up to 30 years (Richard et al. 2002). They live in groups of about 6 individuals, and there is no sexual size dimorphism (Lawler 2009; Kappeler and Fichtel 2012). Females become mature at 5 years and give birth to a single infant at the height of the austral winter (July-August) after a gestation period of about 5 months. Weaning takes place at the height of the wet season (January-February), when food is most abundant. Infants are entirely dependent on their mother during their first three months of life (Jolly 1966), and mothers constitute their primary caregiver and invest more in transport than the other group members (Patel 2007; Malalaharivony et al. 2021). Infant mortality is very high, with about 62% of infants dying during their first year of life (Kappeler and Fichtel 2012).

Behavioral and morphometric data

A total of 12 infants, whose exact birth dates were known from daily group censuses, and their mothers from 7 study groups served as focal animals. All of the mothers included in this study were multiparous, and four of them had an infant in both study years. Infants were born between July and August, with most being born in July. We observed infants until February for the first cohort (N=6 infants, 2017) and until December for the second cohort (N=6 infants, 2018). An effort was made to record the behavior of mothers and infants simultaneously for 5 daily observation hours, balanced between 3 h in the morning (8:00 - 11:00h) and 2 h in the afternoon (14:00 -16:00h), using continuous focal animal sampling (Altmann 1974). Focal subjects were chosen in a randomized but counter-balanced manner throughout morning and afternoon observations. As our study involved focal animal observations, it was not possible to record data blind.

Operational definitions of all recorded behavioral elements are provided in SEM Table 1 (see also Malalaharivony et al. 2021). To quantify patterns of infant development, we specifically recorded the occurrence and duration of all infant activities, such as feeding on solid food and the time spent in nipple contact, which provides a proxy for the opportunity to obtain access to milk, solitary locomotor and object play as well as independent locomotion. We also recorded all interactions, including social play and grooming with other group members to characterize the social development of infants. Finally, to assess maternal investment, we recorded the proportion of time infants were carried by their mothers.

We used two independent methods to assess infant physical growth rates. One non-invasive estimate was based on changes in infants’ lower arm length, which was estimated once a month via photogrammetry (Breuer et al. 2007). A second estimate was based on records of body mass obtained during infants’ first capture when they were about 9 months old and related to this species’ estimated mass at birth (Kappeler and Fichtel 2012). Two infants died postnatally before either estimate could be obtained. Both measures were positively correlated with each other and described and discussed in detail elsewhere (Malalaharivony et al. 2021).

Phenology and climatic variables

Food availability, estimated as the relative abundance of leaves, flowers and fruits (i.e., the main constituents of sifakas' diet, Guevara et al. 2021), was assessed during bi-weekly phenology transects of 784 trees in the study area as detailed elsewhere (Koch et al. 2017). Briefly, we applied a semi-quantitative method in which the availability for each food item was scored on an ordinal scale ranging from 0 to 4, where 0 reflects the complete absence of the item and 4 represents its maximum abundance. Average monthly scores for leaves, fruits, and flowers were summed up to obtain one score for food availability per month. A fully automatic weather station (Lamprecht, Göttingen, Germany) recorded data on ambient temperature and rainfall at the field station.

Collection of fecal samples and GC analyses

We attempted to collect weekly fecal samples for glucocorticoid metabolite (fGCM) analyses from mothers (N=377) throughout gestation and lactation (SEM Table 2). Samples uncontaminated with urine were collected immediately after defecation in the morning between 07:00-11:00 h and transferred into a 15 ml tube containing 5 ml of 80% ethanol in water. FGCM extractions took place in our field laboratory using a validated field extraction method (Shutt et al., 2012) applied successfully in several other studies on wild primates (Rimbach et al. 2013; Hämäläinen et al. 2015; Kalbitzer et al. 2015), including Verreaux´s sifakas (Rudolph et al., 2019). In brief, samples were manually homogenized in their original ethanolic solvent, subsequently vortexed and then centrifuged manually (Rudolph et al., 2019). About 1.5ml of the supernatant were finally decanted into 2ml polypropylene safe-lock tubes (Eppendorf®, Hamburg, Germany) for storage at ambient temperatures in the dark. Within 1-6 months following sample collection, fecal extracts were shipped to the German Primate Center and stored at -20°C until fGCM analysis.

We assessed fGCM concentrations by using a validated enzyme immunoassay (EIA) for the measurement of immunoreactive 11ß-hydroxyetiocholanolone, which is a group-specific measure of 5ß-reduced cortisol metabolites that has been shown to reliably track adrenocortical activity from fecal samples in several primate and other mammal species (Braga Goncalves et al. 2016; Heistermann et al. 2006), including Verreaux's sifakas (Fichtel et al. 2007; Rudolph et al. 2019, 2020). For details of assay methodology see Heistermann et al. (2006). Inter-assay coefficients of variation (CVs) of high- and low-value quality controls were 11.2% (high) and 9.5% (low), while both intra-assay CVs were <10%. All hormone concentrations are expressed as ng/g wet weight of feces.

Statistical analyses

In general, we fitted statistical models (LMM, GlmmTMB) in R (version 4.0.3; R Core Team 2018). All covariates in the models were z-transformed in order to obtain models that are easier to interpret (Schielzeth 2010) and to facilitate model convergence. For LMMs, we checked the assumptions of normality distributions and homogeneity by visual inspection of a QQ-plot (Field 2009) of residuals and residuals plotted against fitted values (Queen et al. 2002). For GlmmTMBs, we checked for overdispersion. For both types of models, we assessed model stability through the level of estimated coefficients and standard deviations (Nieuwenhuis et al. 2012). Furthermore, we checked collinearity issues by deriving variance inflation factors (VIF; Field 2009) of the standard linear model lacking the random effects. To test the significance of the predictors as a whole, we compared the fit of the full model with that of the null model comprising the intercept and the random effects (Forstmeier and Schielzeth 2011). Statistics for these comparisons are given in the summary tables of the respective models.

According to when fecal samples were collected, we categorized log-transformed fGCM concentrations into a pre- or postnatal period. For analyses examining the effects of maternal fGCM levels on infant development, the 6 months of the prenatal period were further divided into three periods between the estimated date of conception (calculated back from the birth date of the infant) and the date of birth because maternal GCs are known to increase during late gestation (Rudolph et al. 2019), presumably also because of increasing fetal GC production (see below). We therefore distinguished between the early-mid prenatal period, which lasted from February – May, and the late prenatal period, which included data from June and July. The postnatal period was defined as the period between the birth date and the end of data collection, spanning the months from July/August – December for most infants of both birth cohorts.

Predictors of variation in fGCM concentrations and influence of FGCMs on maternal care

To assess variation in pre- and postnatal fGCM concentrations, we fitted a Linear Mixed Model using the package lme4 (Bates et al. 2014). Since one infant died on day 1 postnatally, we excluded postnatal samples collected from this female, resulting in a sample size of N=359. We fitted log-fGCM concentrations as response, period (early/mid, late prenatal and postnatal), monthly cumulative rainfall, cumulative rainfall during the preceding wet season until tentative conception (November – January), and mother's age (in years) as fixed factors. Mothers' identity was included as a random factor, and all mothers were either the only or the dominant adult female of their group. We included rainfall as a proxy for food availability in this model because fruit availability, which is associated with variation in fGCM concentrations (Rudolph et al. 2020), was colinear with increases in fGCM concentrations during early pregnancy. To avoid overconfident model estimates and to keep Type I error rate at the nominal level of 0.05, we included random slopes (Schielzeth and Forstmeier 2009; Barr et al. 2013) of mother's age, rainfall before conception, and rainfall within mothers' identity. Originally, we also included parameters for the correlations between random slopes and intercepts, but as the model did not converge, we had to exclude them again.

To examine whether maternal prenatal fGCM concentrations predict postnatal fGCM concentrations, we fitted another LMM. As response we fitted postnatal fGCM concentrations, average prenatal fGCM concentrations as fixed factor and mother's identity as random factor. To control for autocorrelation, we fitted two additional models, using the package "nlme" (Pinheiro and Bates 2000), by including sample date as correlation. Samples that were collected on the same day (N=18) were excluded in these models. Since the results did not deviate between these and the original models without controlling for autocorrelation, we present the original models and depict the results of the new models in the SEM (Table S3, S4).

To quantify inter-individual variation in maternal care, we calculated the proportion of time (minutes per hour) for each behavioral activity based on observational data collected between July and December of each study year. To estimate variation in the proportion of time mothers spent carrying infants, we fitted a Generalized Linear Mixed Model (GLMM; Baayen 2008) with a beta error distribution and logit link function (package glmmTMB; McCullagh and Nelder 1989; Bolker 2008). The proportion of time mothers spent carrying infants was fitted as response, and infants age in weeks, infant's sex, average early/mid prenatal and monthly postnatal fGCM concentrations, study year, fruit availability, as well as mother's age as fixed factors. Individual and maternal identities were fitted as random factors, including monthly postnatal fGCM concentrations and mothers age within maternal identity and fruit availability as well as monthly postnatal fGCM concentrations within individual identity as random slopes. Originally, we also included parameters for the correlations between random slopes and intercepts, but as the model did not converge, we had to exclude them again.

Influence of maternal fGCM concentrations on infant physical and behavioral development

To estimate the influence of maternal early/mid prenatal and postnatal fGCM concentrations on infants’ body mass and arm length growth rates, we calculated the mean maternal pre- and postnatal fGCM concentrations and correlated them with individual growth rates derived from a generalized least square regression (Malalaharivony et al. 2021) by using Spearman rank correlations.

To estimate variation in infant behavioral development (proportion of time spent in nipple contact, foraging and playing), we fitted three Generalized Linear Models (GLMM; Baayen 2008) with a beta error distribution and logit link function (package glmmTMB; McCullagh and Nelder 1989; Bolker 2008). The proportion of time spent in nipple contact, foraging or playing per observation hour was fitted as response, and infants´ age in weeks, average early/mid prenatal and monthly postnatal fGCM concentrations, study year, fruit availability, as well as mother’s age were included as fixed factors. For the model investigating variation in time spent playing, we included another fixed factor differentiating between play types (solitary locomotor, solitary object, and social play). In the models fitting the time spent in nipple contact and foraging, individual and maternal identities were fitted as random factors including mother’s age and fruit availability within mother’s identity and postnatal fGCM concentrations and fruit availability as random slopes within individual identity without correlations between random slopes and intercepts. In the model fitting time spent playing, we had to exclude the random slope of mother’s age with mother’s identity because the model did not converge.

The sample sizes for the proportion of time infants spent grooming or locomoting independently was relatively small because these behaviors were more regularly shown towards the end of the study period when infants were older. We therefore calculated the mean of the time spent grooming or locomoting independently and correlated them with mean average early/mid prenatal and postnatal fGCM concentrations by using Spearman rank correlations.

To assess factors predicting infants’ survival during the first 1.5 years, we calculated Cox proportional-hazards model (function ‘Coxph’, ‘survival’ package; Therneau et al. 2020) with the function Surv (age at 30.01.2020 | survived 1.5 years) as proportional hazard. One infant died a day after birth, which was excluded in these analyses. All other infants (n=5) died after the end observation period at a mean age of 11.8 ± SD 4.4 months. Since some mothers gave birth in both years, we included maternal identity as a cluster to control for repeated measures. As predictors, we included average early/mid prenatal and postnatal fGCM concentrations, time being carried by the mother, body mass and arm length growth rates, time spent in nipple contact and foraging, as well as year of the birth cohort. Because of the small sample size of 12 infants, we fitted a separate model for each predictor variable.

Results

Predictors of variation in prenatal fGCM concentrations and influence of fGCM levels on maternal care

FGCM concentrations differed across periods, with higher levels during the late prenatal period in comparison to the early/mid prenatal period. (Table 1, S3, Fig. 1a). Average postnatal fGCM concentrations were lower than early/mid concentrations, though absolute values appeared to be in between early/mid fGCM concentrations. Rainfall was negatively correlated with fGCM concentrations, with females having higher fGCM concentrations during periods with little rainfall (SEM, Fig. S1). Mothers that had given birth to an infant the year before experienced higher average fGCM concentrations (Fig. 1b). Rainfall during the wet season before conception and mother’s age did not co-vary with fGCM concentrations (Table 1, S3). Since rainfall is a proxy for food availability (Rudolph et al. 2020), food shortages might have resulted in reduced maternal condition and were associated with higher stress. Prenatal fGCM concentrations predicted postnatal fGCM concentrations (LMM: N=194, likelihood ratio test comparing the full with the null model: χ^2=7.61, df=1, p=0.006; estimate=0.28, SE=0.09, p=0.016, Table S4).

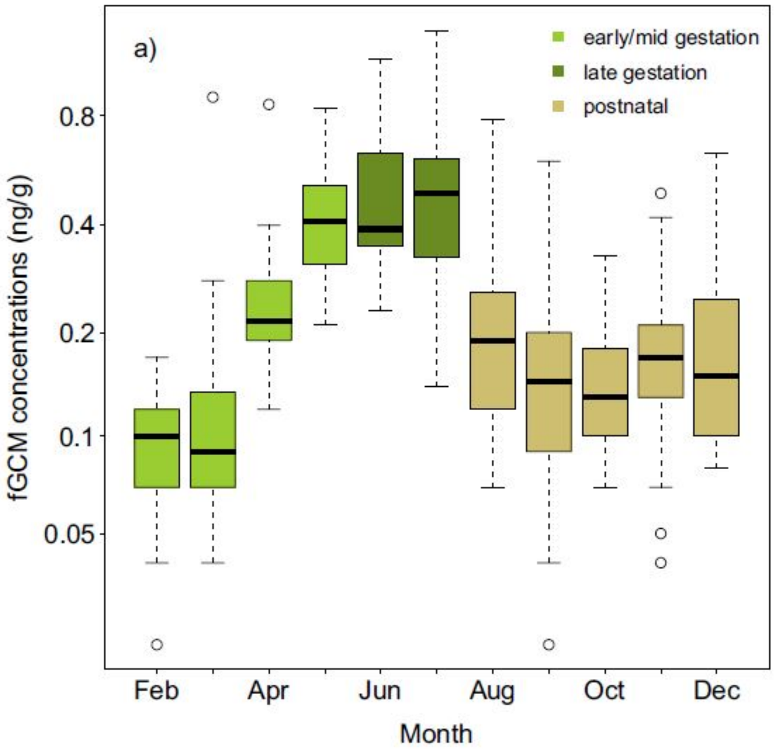
Table 1 Factors predicting variation in maternal fGCM concentrations (LMM; N=359; N_{ID} = 8; estimates, together with standard errors). Likelihood ratio test comparing the full with the null model: χ^2=95.76, df=7, p=0.001

Term	Est	SE	*P*
Intercept	-1.69	0.12	[c]
Late prenatal (early/mid prenatal) [a]	0.56	0.08	**<0.001**
Postnatal (early/mid prenatal) [a]	-0.24	0.06	**<0.001**
Rainfall before conception [b]	0.01	0.04	0.936
Rainfall [b]	-0.17	0.07	**0.047**
Age [b]	0.08	0.04	0.071
Infant in year before (yes) [a]	0.31	0.12	**0.038**

[a] Manually dummy-coded with early/mid prenatal period and no infant in the year before as reference categories

[b] z-transformed, mean ± SD of the original values are: rainfall before conception: 174.32 ± 23.25 mm, monthly rainfall: 19.02 ± 54.24 mm, maximum temperature: 35.73 ± 1.23 °C, age=12.86 ± 4.9 years

[c] Not shown as has no meaningful interpretation



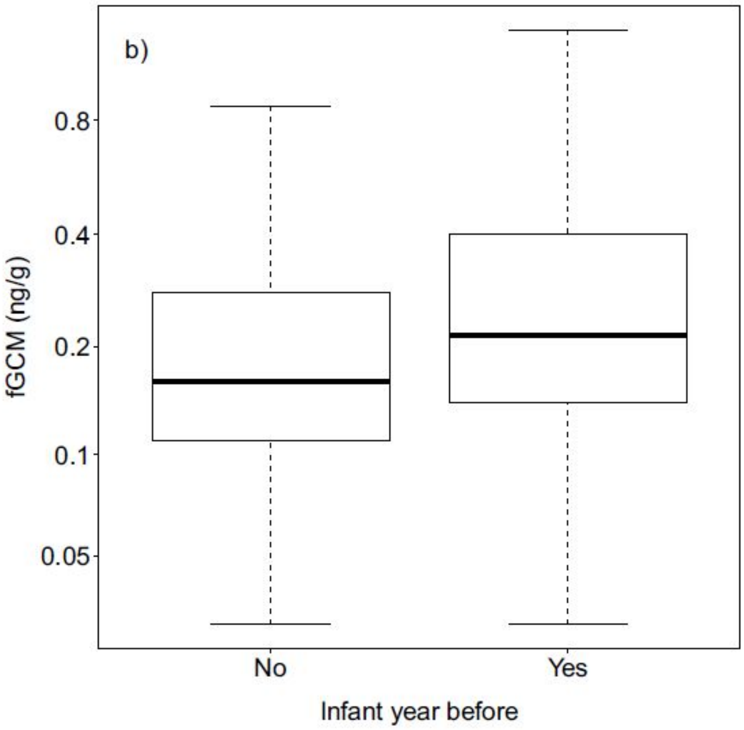


Fig. 1: Variation in fGCM concentrations across **a** the early/mid prenatal (light green), late prenatal (dark green) and postnatal period (beige) in Verreaux's sifaka mothers. **b** Comparison of fGCM levels between mothers that gave birth to an infant in the previous year or not. Depicted are boxplots showing medians (solid lines), inter-quartile ranges (boxes), ranges (whiskers) and outliers (> 1.5 x IQR; open circles) of fGCM concentrations. Note that the y-axis is depicted on a log scale but axis tick labels show the original fGCM values

The time spent carrying infants decreased with infants' age (Table 2). Both, early/mid and postnatal fGCM concentrations predicted carrying time, with mothers having lower fGCM concentrations spending more time carrying their infants (Fig. 2a, b). Fruit availability, birth cohort, and mother's age did not influence the time spent carrying infants (Table 2).

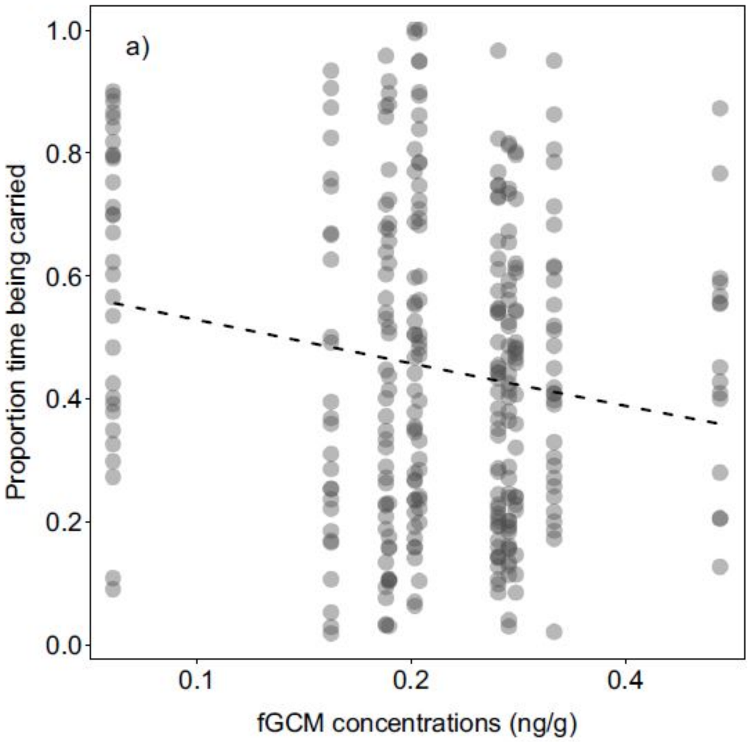
Table 2 Factors predicting variation in time mothers spent carrying their infants (GlmmTMB; N=317; N_{ID} = 11; estimates, together with standard errors). Likelihood ratio test comparing the full with the null model: χ^2=167.35, df=6, p<0.001

Term	Est	SE	*P*
Intercept	-0.20	0.07	[c]
Infant age [a]	-0.83	0.06	**<0.001**
Early/mid prenatal fGCM [a]	-0.18	0.06	**0.003**
Postnatal fGCM [a]	-0.15	0.06	**0.013**
Year (2018) [b]	-0.04	0.11	0.707
Fruit availability [a]	-0.13	0.07	0.077
Mother's age [a]	0.09	0.05	0.070

[a] z-transformed, mean ± SD of the original values are: infant age: 10.14 ± 6.2 weeks, postnatal fGCm: 0.21 ±0.1 (ng/g), early/mid prenatal fGCm: 0.24 ± 0.1 (ng/g), fruit availability: 0.11 ± 0.06, mother's age: 12.63 ± 4.63 years

[b] Manually dummy-coded with year 2017 as reference category

[c] Not shown as has no meaningful interpretation



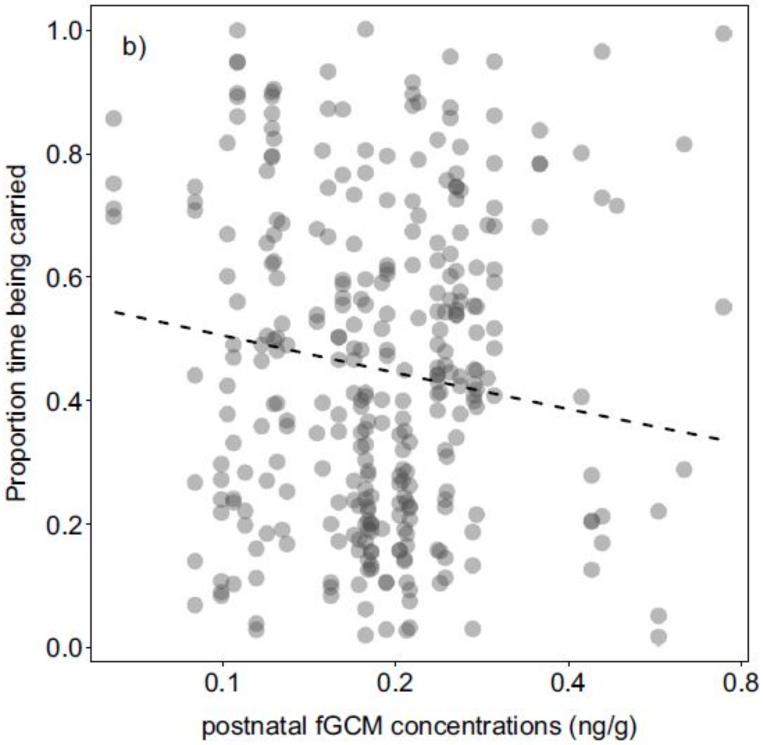


Fig. 2: Proportion of time (m/hr) mothers spent carrying infants as a function of **a** early to mid and **b** postnatal fGCM concentrations. Dashed line indicates the regression line. Note that the x-axis is depicted on a log scale but axis tick labels show the original fGCM values

Influence of maternal fGCM concentrations on infant physical and behavioral development

Neither early/mid prenatal nor postnatal fGCM concentrations correlated with average body mass growth rates (Spearman rank correlation: early/mid prenatal: N=10, r=0.51, p=0.137; postnatal: N=10, r=0.61, p=0.062). Similarly, arm length growth rates did not correlate with early/mid or postnatal fGCM concentrations (Spearman rank correlation: early/mid prenatal: N=10, r=0.25, p=0.492, postnatal: N=10, r=0.37, p=0.296). However, average prenatal fGCM concentrations correlated positively with both growth rates (Spearman rank correlation: body mass growth rate: N=10, r=0.74, p=0.014, arm-length growth rate: N=10, r=0.66, p=0.044, SEM Fig. S2, S3).

Postnatal fGCM concentrations and fruit availability predicted the time spent in nipple contact (Table 3, Fig 3). Infants of mothers with higher postnatal fGCM concentrations spent more time in nipple contact. In addition, infants spent more time in nipple contact when more fruits were available. Neither infant’s nor mother’s age, sex, birth cohort or early/mid prenatal fGCM concentrations covaried with time spent in nipple contact (Table 3).

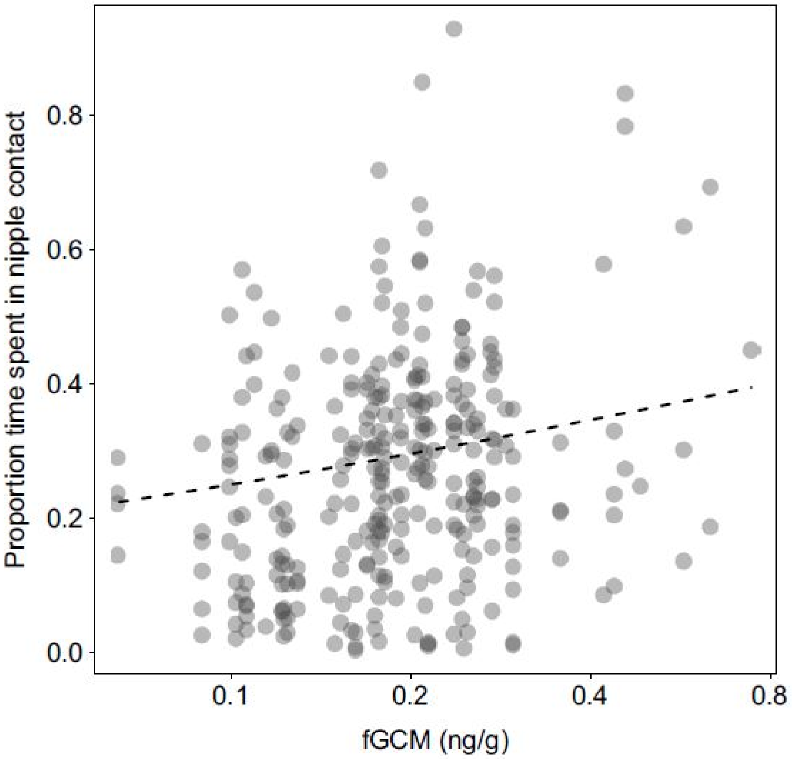


Fig. 3: Proportion of time (m/hr) infants spent in nipple contact as a function of postnatal fGCM concentrations. Dashed line indicates the regression line. Note that the x-axis is depicted on a log scale but axis tick labels show the original fGCM values

Table 3 Factors predicting variation in time spent in nipple contact (GlmmTMB; N=300; N_{ID} = 11; estimates, together with standard errors). Likelihood ratio test comparing the full with the null model: χ^2=19.17, df=6, p=0.004

Term	Est	SE	*P*
Intercept	-0.89	0.10	[c]
Infant age [a]	-0.05	0.07	0.466
Early/mid prenatal fGCM [a]	-0.09	0.08	0.270
Postnatal fGCM [a]	0.14	0.06	**0.023**
Year (2018) [b]	-0.20	0.12	0.096
Fruit availability [a]	0.24	0.09	**0.008**
Mother's age [a]	-0.12	0.08	0.145

[a] z-transformed, mean ± SD of the original values are: infant age: 10.13 ± 6.13 weeks, postnatal fGCm: 0.21 ±0.09 (ng/g), early/mid prenatal fGCm: 0.24 ± 0.1 (ng/g), fruit availability: 0.12 ± 0.06, mother's age: 12.98 ± 4.81 years

[b] Manually dummy-coded with year 2017 as reference category

[c] Not shown as has no meaningful interpretation

Infants spent more time foraging with increasing age. Early to mid fGCM concentrations predicted the proportion of time infants spent foraging; infants of mothers with higher fGCM concentrations spent more time foraging (Fig. 4, Table 4). Postnatal fGCM concentrations, birth cohort, mother's age and fruit availability did not co-vary with time spent foraging (Table 4).

Table 4 Factors predicting variation in time infants spent foraging (GlmmTMB; N=215; N_{ID} = 11; estimates, together with standard errors). Likelihood ratio test comparing the full with the null model: χ^2=85.29, df=6, p<0.001

Term	Est	SE	*P*
Intercept	-1.88	0.09	[c]
Infant age [a]	0.62	0.09	**<0.001**
Early/mid fGCM [a]	0.20	0.09	**0.032**
Postnatal fGCM [a]	-0.12	0.10	0.227
Year (2018) [b]	0.19	0.12	0.120
Fruit availability [a]	0.06	0.09	0.475
Mother's age [a]	-0.16	0.09	0.099

[a] z-transformed, mean ± SD of the original values are: infant age: 12.57 ± 5.11 weeks, postnatal fGCm: 0.19 ±0.08 (ng/g), early/mid prenatal fGCm: 0.24 ± 0.1 (ng/g), fruit availability: 0.12 ± 0.06, mother's age: 12.76 ± 4.70 years

[b] Manually dummy-coded with year 2017 as reference category

[c] Not shown as has no meaningful interpretation

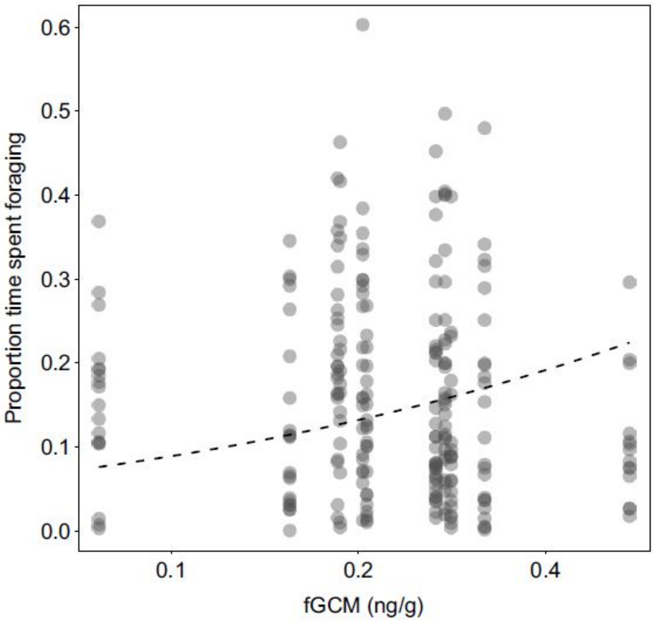


Fig. 4: Proportion of time (min/h) infants spent foraging as a function of early/mid prenatal fGCM concentrations. Dashed line indicates the regression line. Note that the x-axis is depicted on a log scale but axis tick labels show the original fGCM values

The time infants spent playing increased with age, and they spent more time with solitary locomotor than with solitary object or social play (Fig. 5, Table 5). Early/mid prenatal fGCM concentrations predicted time infants spent playing, with infants of mothers exhibiting higher prenatal fGCM concentrations spending more time playing (Fig. 5). Infants of the birth cohort 2018 spent more time playing than infants of the birth cohort 2017, but postnatal fGCM concentrations, fruit availability, and mother's age did not predict the time infants spent playing (Table 5).

Table 5 Factors predicting variation in time infants spent playing (GlmmTMB; N=415; N_{ID} = 11; estimates, together with standard errors). Likelihood ratio test comparing the full with the null model: χ^2=148.64, df=8, p<0.001

Term	Est	SE	*P*
Intercept	-2.48	0.08	[c]
Infant age [a]	0.19	0.08	**0.020**
Early/mid prenatal fGCM [a]	0.16	0.07	**0.015**
Postnatal fGCM [a]	0.05	0.05	0.403
Solitary object play[b]	-1.13	0.10	**<0.001**
Social play[b]	-0.77	0.09	**<0.001**
Year (2018) [b]	0.43	0.09	**<0.001**
Fruit availability [a]	-0.06	0.09	0.513
Mother's age [a]	0.03	0.05	0.562

[a] z-transformed, mean ± SD of the original values are: infant age: 13.89 ± 4.78 weeks, early/mid fGCM: 0.24 ±0.1 (ng/g), postnatal fGCM: 0.19 ±0.84 (ng/g), fruit availability: 0.13 ± 0.06, mother's age: 12.66 ± 4.75 years

[b] Manually dummy-coded with solitary locomotor play and year 2017 as reference categories

[c] Not shown as has no meaningful interpretation

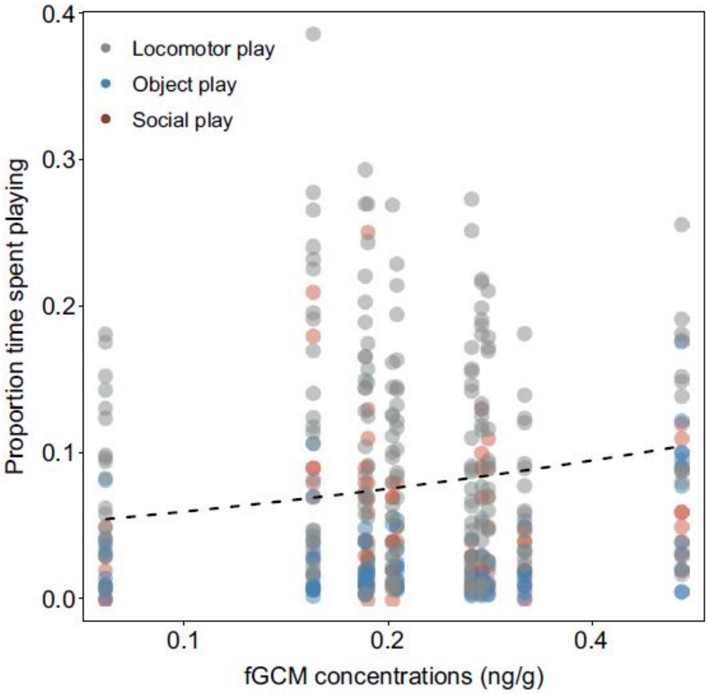


Fig. 5: Proportion of time (m/hr) infants spent playing (gray = solitary locomotor play, blue = solitary object play, red = social play) as a function of maternal prenatal fGCM concentrations. Dashed line indicates the regression line. Note that the x-axis is depicted on a log scale, but axis tick labels show the original fGCM values

The average proportion of time infants spent locomoting independently did neither correlate with early/mid prenatal nor postnatal fGCM concentrations (Spearman rank correlation, early/mid prenatal fGCM: N=7, r=0.07, p=0.906; postnatal fGCM: N=7, r=0, p=1). Similarly, the average proportion of time infants spent grooming did not correlate with either maternal pre- or postnatal fGCM concentrations (Spearman rank correlation, prenatal fGCM: N=11, r=0.36, p=0.313; postnatal fGCM: N=10, r=0.22, p=0.537).

Infant survival was neither predicted by mid-early prenatal nor postnatal fGCM concentrations, but by the proportion of time being carried by the mother and arm length growth rate. Infants that were carried more often died earlier (Fig. 6; Table 6). In addition, infants with higher arm length growth rates lived longer, but body mass growth rate did not predict survival. Mother’s age, year of the birth cohort as well as time spent foraging by the infants or being in nipple contact did not predict their survival either (Table 6).

Table 6 Results of the Cox proportional hazard models on factors predicting infant's survival past 1.5 years of life

				Wald test		
Factor	Coef	SE	P	χ^2	df	P
Early/mid fGCM	3.44	3.72	0.170	1.88	1	0.200
Postnatal fGCM	-9.27	9.07	0.109	2.57	1	0.100
Mother's age	0.09	0.09	0.261	1.26	1	0.300
Time carrying infants	8.42	5.30	**0.002**	9.37	1	**0.002**
Body mass growth rate	-0.64	0.47	0.156	2.01	1	0.200
Arm length growth rate	-13.11	8.99	**0.004**	8.26	1	**0.004**
Year	0.75	0.87	0.389	0.74	1	0.400
Foraging	-18.63	14.95	0.196	1.67	1	0.200
Nipple contact	-17.45	10.47	0.076	3.15	1	0.080

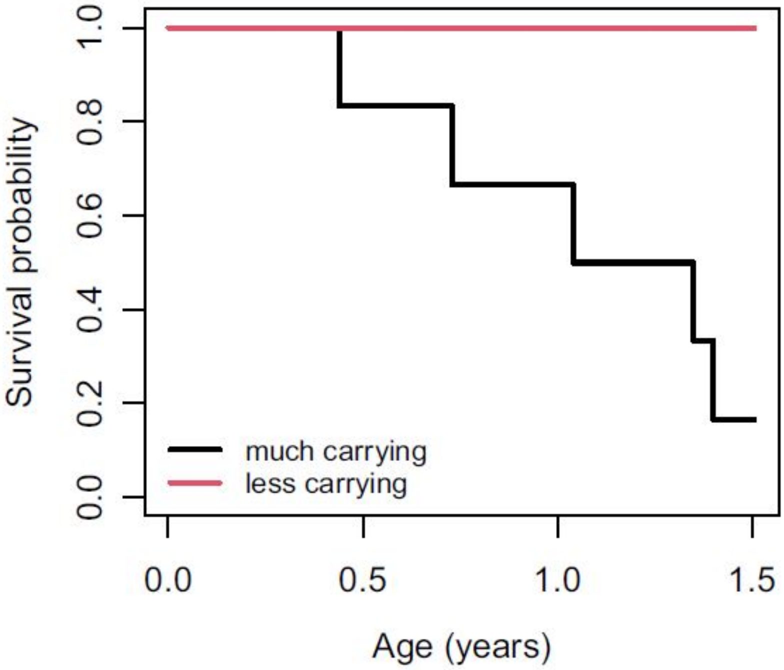


Fig. 6: Kaplan–Meier survival curve. Survival probability for infants surviving during the first 1.5 years depending on the time mother's spent carrying infants (*N* = 6 infants surviving and *N* = 6 infants that died). For illustrative purposes, we divided the time spent carrying into much carrying (black line; above median time spent carrying and low (red line); below median time spent carrying)

Discussion

In this study, we investigated factors predicting maternal fGCM concentrations and their impact on infant physical and behavioral development in a wild population of Verreaux's sifakas. We found that maternal fGCM concentrations were higher in the late prenatal period, compared to the early/mid prenatal period. Average postnatal fGCM concentrations were lower than early/mid concentrations, but absolute postnatal fGCM values appear to be in between early/mid concentrations. This dynamic might be due to the steep rise in fGCM concentrations from early to mid gestation, which might have also been influenced by changes in rainfall and food availability at the beginning of the dry season in April/May. fGCM concentrations were higher during months with little rainfall. Since rainfall is a proxy for food availability (Koch et al. 2017; Rudolph et al. 2019), mothers might have been in poorer condition during periods of lower food availability, a state typically associated with elevated fGCM concentrations. Mothers that gave birth to an infant the previous year had higher fGCM concentrations, indicating that these mothers had to mobilize more energy or higher HPA-activity and that generally higher GC-levels in the mother (potentially due to her own early life experience) lead to a faster pace of life.

Most importantly, infants physical and behavioral development were influenced by mothers' prenatal fGCM concentrations. Specifically, infants of mothers with higher prenatal fGCM concentrations exhibited higher growth rates. Infants of mothers with higher early/mid prenatal fGCM concentrations were more active by spending more time foraging independently and being more active in all categories of play. Even though solitary locomotor and object play emerged earlier than social play (Malalaharivony et al., 2021), fGCM concentrations did not affect play types differently. In contrast, infants of mothers with low early/mid and postnatal fGCM concentrations were carried more, and those of mothers with higher postnatal GC levels spent more time in nipple contact. Time spent carrying infants predicted infants' survival, suggesting that infants that were potentially in poorer condition had to be carried more. Hence, infants that were carried less often and were more independent were able to successfully navigate their first ecological bottleneck, i.e. the first dry season after weaning, a period in which about 62% of infants die (Kappeler and Fichtel 2012). Thus, infants' physical and behavioral development were presumably impacted by maternal fGCM concentrations, but it is equally possible that the demands of caring for an infant in relatively poor condition caused an increase in maternal fGCM.

While our study was not designed to formally test predictions of ultimate hypotheses about maternal effects, the observed patterns of growth and behavioral development during early infancy are possibly indicative of an internal PAR response. However, “the PAR and developmental constraints models can only be distinguished by comparing fitness-related traits in individuals from high- and low-quality early environments, when each of these sets of individuals experience both high- and low-quality adult conditions” (Lea et al. 2015), which was not possible in this study. Additional future research will be required to determine how prenatally stressed offspring manage to grow faster and play more, and whether the extra time spent foraging is sufficient to provide the necessary energetic support.

Variation in maternal fGCM concentrations

Maternal fGCM concentrations of Verreaux’s sifaka can be examined with respect to the costs of reproduction or seasonality, which are not independent in sifakas, and therefore challenging to disentangle (see also Charpentier et al. 2018). First, maternal GCs increased during the prenatal period and were higher than during the postnatal period, confirming results of previous studies in the same population (Rudolph et al. 2019, 2020). Even though lactation is the energetically most challenging reproductive activity for mammals (Hinde and Milligan 2011), several other studies also reported higher maternal GC levels during gestation (particularly late gestation) than during lactation (e.g. Rimbach et al. 2013; Berghänel et al. 2016; but see Starling et al. 2010). In fact, GC levels increase across gestation in most mammals (Edwards and Boonstra 2018; but see Scott et al. 2013 for artiodactyls).

These pregnancy-related elevation in GC output are likely caused by interactions of increased metabolic demands during pregnancy and activation of the HPA-axis with concomitant stimulation of cortico-steroid-binding globulin due to elevated levels of estrogens as well as placental production of cortisol (Edwards and Boonstra 2018). High levels of GCs may also prepare the body for the stressful period surrounding parturition (Edwards and Boonstra 2018) and probably trigger developmental changes that prepare the late fetus for the extra-uterine environment, particularly with respect to organ maturation (Fowden et al. 1998), and may therefore not reflect direct adaptations to females’ energetic costs of reproduction. Our finding of a positive link between pre- and postnatal maternal GCs, in contrast, points towards intrinsic factors related to individual energetic investments into reproduction. Our finding that mothers that had an infant the previous year had marginally higher GC levels than those that did not also indicates that some long-term costs of reproduction contributed to variation in maternal GC levels, suggesting that the physiological costs of reproduction go beyond direct and indirect costs previously characterized for mammals (Wells 2007b; Speakman 2008).

Second, maternal fGCM concentrations were higher during periods with low rainfall, which serves as a proxy for food availability in this seasonal habitat (Koch et al. 2017; Rudolph et al. 2019), but rainfall in the months before conception did not co-vary with fGCM concentrations. This may reflect the position of Verreaux's sifakas along the continuum from capital to income breeders (Lewis and Kappeler 2005). A reduction in the quantity or quality of food has been shown to increase GC levels in several other species, including lemurs (Behie and Pevelka 2013, Chapman et al. 2015; Berghänel et al. 2016; Tecot et al. 2019; Rudolph et al. 2020), and may therefore reflect a response to compensate for reduced energy intake. Reduced food availability is particularly challenging for gregarious species because of feeding competition, which can be stressful for reproducing low-ranking individuals (Creel et al. 2013); subordinate reproduction has been regularly observed in our study population in previous years (Kappeler and Fichtel 2012). Because these sifakas inhabit forests that are highly seasonal, but in which rainfall and food availability is highly unpredictable from year to year (Dewar and Richard 2007; Lawler et al. 2009; but see Federman et al. 2017), it is likely that physiological adaptations are fine-tuned and superimposed upon predictable seasonal cycles (Reeder and Kramer 2005; Creel et al. 2013).

Effects of maternal GC levels on maternal investment and infant development

Our study revealed that variation in maternal GC levels were associated with several aspects of maternal care and infant development. First, variation in maternal stress levels was associated with patterns of maternal care. High maternal GC levels during the prenatal phase correlated with more explorative infants and low carry effort because infants of these mothers spent more time foraging independently and more time playing. High maternal GC during the postnatal phase correlated with infants who have more nipple contact and forage more while resting and being carried less. While mothers with lower fGCM levels carried their infants more, maternal GC levels had no effect on independent infant locomotion, presumably because infants also moved when their mothers did not. It would therefore be interesting to estimate maternal carrying effort as the proportion of total maternal locomotion to assess different maternal strategies: infant carrying vs. nursing plus independent infant locomotion (Kramer 1998; Harel et al. 2021). Further, time spent carrying infants predicted infant survival in the first 1.5 years, suggesting that infants that were potentially in poorer condition had to be carried for longer, but more detailed analyses of mothering styles are required to substantiate this idea. Moreover, long-term effects of early maternal adversity on maternal effort should also be considered in this context (Patterson et al. 2021).

Second, infants exhibited faster growth rates when mothers had higher prenatal GC levels, echoing findings of previous studies reporting a positive correlation between postnatal infant growth rates and maternal GC levels (Swolin-Eide et al. 2002; Hauser et al. 2007; Dantzer et al. 2013; Hinde et al. 2015; Berghänel et al. 2016). However, other studies reported the opposite effect, prompting Berghänel et al. (2017) to propose a model that reconciled these conflicting findings by suggesting that the effects of maternal GC output on infant growth depend on the infant's specific developmental period. Because we have no data on fetal growth and our estimate of postnatal body mass growth is based on a single datum obtained after weaning, and arm length growth rates were measured only until an age of 6 months, we cannot assess the potential specific dynamics of infant growth patterns in this species. While it is likely that mothers elevate their GC levels during gestation as a result of reduced energetic intake and/or increased expenditure, this response has no detrimental effects on their current reproduction, i.e. their infants' growth rates. It has been argued that mothers, through increasing prenatal GCs, adjust their infant's life trajectory by accelerating infant's life history pace altogether (Nettle and Bateson 2015), but we lack data on the long-term consequences on other life history traits, such as sexual maturation and longevity to evaluate this possibility. Because the infants of mothers with high prenatal GC levels developed faster and began foraging independently earlier, these stressed mothers benefit from an overall reduction of maternal investment, thereby making the best of a bad start of the current reproductive cycle (Jones 2005).

Finally, we found that arm length growth and time spent carrying predicted infant survival during the first 1.5 years of life. In Verreaux's sifaka, survival during the first year of life has been found to represent the most challenging life stage, with more than half of infants dying (Richard et al. 2002; Lawler et al. 2009; Kappeler and Fichtel 2012). Thus, this relationship is important for the fitness of both mothers and infants, but it is difficult to evaluate because in our study infant survival was not consistently linked to the two different growth estimates. Moreover, survival was not predicted by maternal GC levels or our estimates of infant's energy input, i.e., time spent foraging or in nipple contact and therefore appears to be unrelated to how much energy infants obtained. Finally, mother's age also did not predict early survival, although mothers in these two birth cohorts were rather old, with a mean age of 12.6 ± 4.6 years, including an 18-, 19-, and 20-year-old female. Female sifakas have an average life expectancy of 5 years (Colchero et al. 2021), and the oldest female in our long-term records was 21 years old. Hence, maternal senescence as described for many other mammals (Ivimey-Cook and Moorad 2020) did not influence infant pre-adult survival. However, since our sample size with 12 infants is small, limiting our analyses to one factor per model, and we had not many young mothers during the study period, the relative importance of each effect remains difficult to assess without additional data.

Conclusions

This study of a wild primate population in a seasonal habitat revealed that ecological and intrinsic effects on maternal GC concentrations are difficult to disentangle because responses to current climatic conditions, reproductive history and current reproductive activities are superimposed. Maternal GC levels were profoundly linked to infant behavior and development, however. Maternal effects mediated by hormones are therefore prevalent in this species and appear to reveal a trade-off between maternal benefits and infant costs. As such, our study provides mixed evidence for beneficial effects of extended maternal GC levels and provides one of the first studies simultaneously examining the connections between environmental factors, maternal stress and fitness proxies (Beehner and Bergman 2017; Campos et al. 2021).

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Author contribution HSM was primarily responsible for data collection, HSM and CF analyzed data, MH performed hormone analysis, and PMK drafted the manuscript. All authors reviewed the manuscript.

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Data availability The datasets that were analyzed for this study are deposited under this link: https://osf.io/sgvxj/?view_only=7e306fa1a514422a938b982af88adc80

Code availability The computer code that was used to analyze the data is available from the corresponding author upon request.

Declarations

Ethics approval This study adhered to the Guidelines for the Treatment of Animals in Behavioral Research and Teaching (Animal Behaviour 2020) and the legal requirements of the country (Madagascar) in which the work was carried out. The protocol for this research was approved by the Malagasy Ministry of the Environment, Water, and Forests (245/17/MEFF/SG/DGF/DSAP/SCB.Re, 047, 215/18/MEFF/SG/DGF/DSAP/SCB.Re, 053/19/MEDD/SG/DGF/DSAP/SCB.Re).

Consent to participate Not applicable.

Consent for publication The authors consent to the publication of this manuscript in Behavioral Ecology and Sociobiology.

Conflict of interest The authors declare no competing interests.

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Supplementary Electronic Material

Table S1: Operational definitions of all recorded behaviors on infant Verreaux's sifakas

Behavior	**Definition**
Early locomotion	Crawling across the mother's body
Self-grooming	Infant strokes with the tooth-comb through its own fur
Carried by mother	Being carried by the mother; either ventrally or dorsally
Independent locomotion	Locomoting independently over more than 5m
Solitary object play	Infant manipulates an object
Solitary locomotor play	Infant moves alone (locomotes, jumps, climbs) on branches or tree.
Nipple contact	Infant is in nipple contact with its mother
Tasting food	Infant tastes, and licks solid food
Foraging	Infant ingests solid food
Social play	Infant plays (repetition of movements) with the mother or another group member
Grooming given	Infant strokes with the tooth-comb through the fur of another individual
Grooming received	Another individual strokes with the tooth-comb through the fur of the infant

Table S2: Distribution of fecal sample collection. The number of samples collected per month is depicted for each mother in both study years.

Year	**ID**	**early-midprenatal**	**lateprenatal**	**postnatal**
2017	Aug	12	9	19
2017	Nia	12	12	18
2017	Nov	12	11	6
2017	Oma	12	9	24
2017	Dav	8	5	16
2017	Val	10	11	19
2018	Aug	6	3	15
2018	Goa	6	1	19
2018	Knu	2	-	17
2018	Nia	6	3	8
2018	Oma	10	3	15
2018	Val	6	2	18

Table S3 Factors predicting variation in maternal fGCM concentrations (LMM; N=359; N_{ID} = 8; estimates, together with standard errors), including control for autocorrelation.

Term	Est	SE	*P*
Intercept	-1.65	0.10	[c]
Late prenatal (early-mid prenatal) [a]	0.55	0.08	**<0.001**
Postnatal (early-mid prenatal) [a]	-0.25	0.06	**<0.001**
Rainfall before conception [b]	0.02	0.06	0.723
Rainfall [b]	-0.19	0.06	**0.003**
Age [b]	0.06	0.11	0.611
Infant in year before (yes) [a]	0.24	0.08	**0.004**

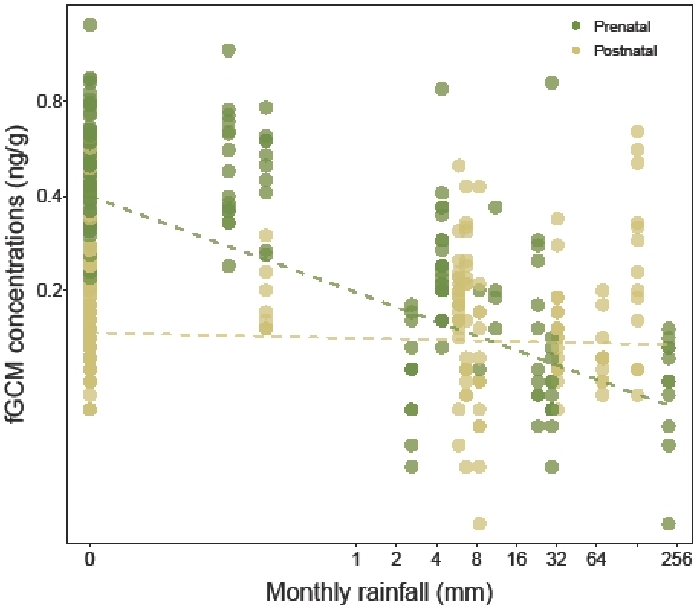
[a] Manually dummy-coded with early-mid prenatal period and no infant in the year before as reference categories

[b] z-transformed, mean ± SD of the original values are: rainfall before conception: 174.32 ± 23.25 mm, monthly rainfall: 19.02 ± 54.24 mm, maximum temperature: 35.73 ± 1.23 °C, age=12.86 ± 4.9 years

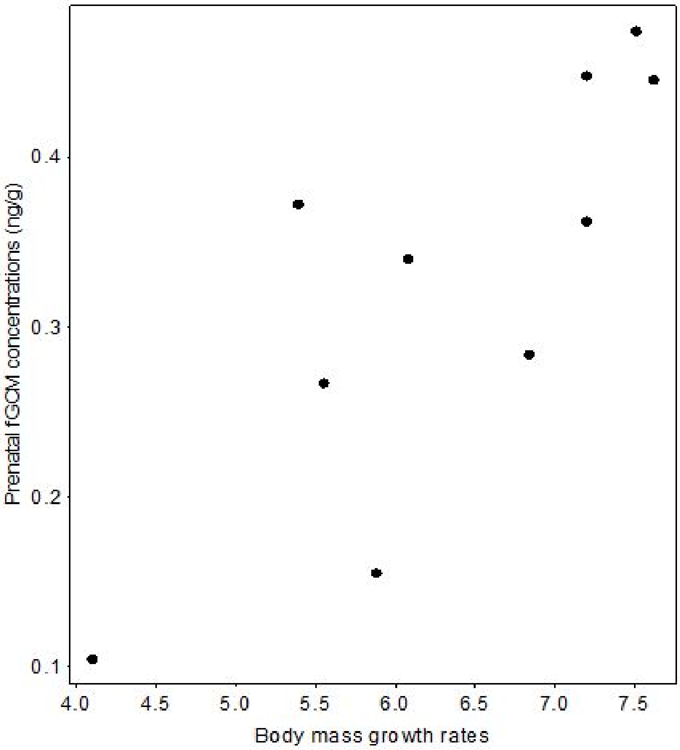
[c] Not shown as not having a meaningful interpretation

Table S4 Influence of prenatal fGCM concentrations on postnatal fGCM concentrations (LMM; N=194; N_{ID} = 7; estimates, together with standard errors), including control for autocorrelation

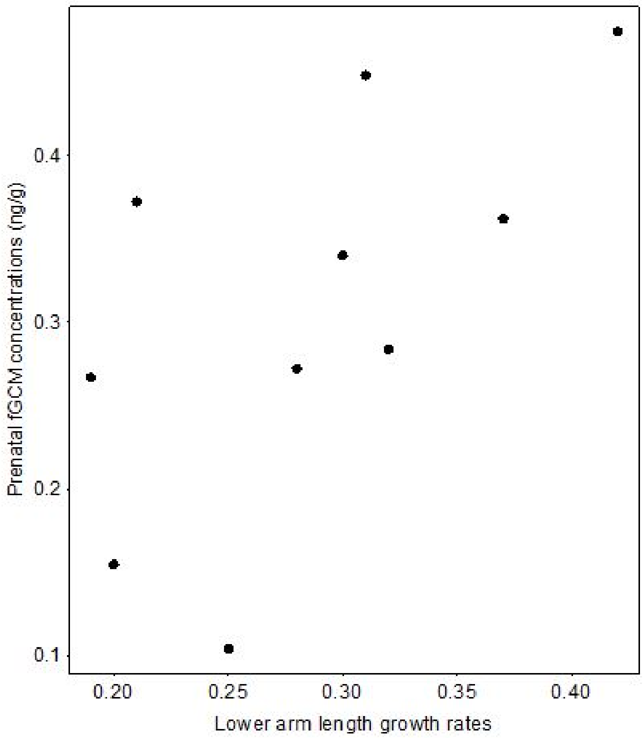
Term	Est	SE	*P*
Intercept	-1.39	0.09	[c]
Log-mean prenatal fGCM	0.26	0.07	**<0.001**



SEM Fig S1: Correlation between maternal fGCM concentrations and monthly cumulative rainfall. Dashed line indicates the regression line



SEM Fig S2: Correlation between average infant body mass growth rates (slopes of regression; see Methods) and prenatal fGCM concentrations in Verreaux's sifakas



SEM Fig S3: Correlation between average infant lower arm length growth rates (slopes of regression; see Methods) and prenatal fGCM concentrations in Verreaux’s sifakas

GENERAL DISCUSSION

Age and body size at maturation form the most important life-history characteristics and surprisingly vary even among conspecifics (Dmitriew, 2011; Kappeler& Pereira, 2003). Many studies reported evidence of the effects of environmental stressors and maternal stress on infant physical and behavioral development in many anthropoid species, including humans, but still, the directions of these effects remain highly variable. Here, I added new data to this field by investigating the environmental and maternal effects on infant development of wild Verreaux's sifakas. I examined various intrinsic and extrinsic factors, which could influence infant physical and behavioral development, such as infant's sex and age, mother's age, and food availability. I also explored the potential effects of environmental factors such as rainfall and food availability on maternal stress hormones (i.e., glucocorticoids concentration (GCc)) and maternal investment, and assessed the influence of elevated maternal GCc on infant physical and behavioral development including early survival. In the following, I will summarize the main results of each of my chapters and discuss the main findings.

Brief Summary

Chapter 1: Infant development and maternal care

In this first chapter, I examined growth patterns and the emergence of behavioral milestones during early infant development in three birth cohorts of wild Verreaux's sifakas.

First, I assessed physical growth using two measurement methods. I used photogrammetry for assessing the skeletal development of the infants by measuring their lower arm length. Second, I estimated their body mass growth by weighing them during individual capture. In contrast to my prediction, I found sex differences in infant growth rates in both methods; infant females have higher growth rates than males. Although the lack of sexual dimorphism in this species, these sex differences may reflect the sexual differences in Verreaux's sifakas' reproductive strategies and social organization.

Moreover, I found pronounced variation in the timing and occurrence of the activities of the infants, but none of them differed between the sexes, except for grooming and independent locomotion, where male infants engaged more than females. Also, I found that motor skills occurred earlier than social skills which occur late with a strong inter-individual variation. Foraging occurs at an early age in Verreaux's sifakas compared to other lemur species; however, independent locomotion is reached very late. These findings do not support my prediction. Although infant Verreaux's sifakas have fully erupted milk dentition at birth, they still have slow locomotor development compared to other lemur species.

Furthermore, I found that the time infants spent in nipple contact did not vary with the infants' age but was influenced by their mother's age, birth cohorts (years), and food availability. Infants of younger mothers spent more time in nipple contact compared to those of older mothers. Similarly, infants from the first cohort and had higher resources spent more time in nipple contact. These findings suggest the influence of environmental factors and mother's condition in maternal care and investment. Mothers that are in good conditions and have a good quality of environment may invest more in their infants than mothers under poor conditions, supporting my prediction. However, these results are still debatable, as spending more time in nipple contact does not always mean that the infants are suckling and receiving more care. More variables are needed to assess maternal care and investment into the offspring.

Chapter 2: Maternal stress and infant development

In this second chapter, I explored the effects of maternal glucocorticoid concentration (GCc) (in terms of elevated early to mid prenatal (PreGC) and postnatal (PostGC) glucocorticoid levels) in the physical and behavioral development of infant Verreaux's sifakas.

First, I examined the effects of variation in rainfall, food availability, and previous reproduction on maternal GCc. Consistent with my prediction, I found that harsh conditions, i.e., low rainfall increased maternal GCc (PreGC and PostGC). Although I did not find a significant effect of the variation on food availability on mothers GCc, rainfall is a good predictor of environmental conditions (Koch et al., 2017, Rudolph et al., 2019). These findings support the suggestion that ecological stressors influence maternal conditions. Similarly, I found that maternal PreGC levels were higher than PostGC but both were positively correlated. Related to that, I found that mothers that have infants the year before had higher GCc. These results indicate the cost of reproduction in mothers.

Second, I examined the effects of elevated maternal GCc on maternal investment into infants in terms of infant carrying. I found that mothers with higher GCc, both PreGC and PostGC, spent less time carrying their infants, which is consistent with my prediction. This result indicates the energy constraints faced by mothers and the impact of elevated maternal stress on maternal investment. Mothers may minimize time spent carrying infants to reduce energy expenditure. This finding supports the results from other studies that found that elevated maternal GCs reduce maternal investment in the offspring (Berghänel et al., 2016, 2017; Klaus et al., 2013; Bardi et al., 2003, 2004). However, I also found that infants of mothers with high GC levels spent more time in nipple contact, suggesting that mothers may reduce time carrying infants but enhance the lactation time. These results are still debatable, as having infants in nipple contact does not really explain maternal investment.

Lastly, I explored how maternal GCc influences the physical and behavioral development of infants. I tested whether increased maternal GCc can influence offspring development and in which directions. In contrast to my prediction, I found that elevated maternal PreGC positively influences the infants' physical and behavioral development. Infants of mothers with higher PreGC have higher growth rates and are more explorative by spending more time foraging and playing. Also, they are more independent and spend less time carried by their mothers. Infants that were less carried and had higher skeletal growth rates had higher survival during their first year of life, which is the most challenging period for Verreaux's sifaka infants. These findings reflect the adaptive responses of infant Verreaux's sifakas to early maternal stress.

In summary, I found inter-individual variation in infant physical and behavioral development. I also found sex differences in early growth rates and social interactions. This study shows that infant Verreaux's sifakas exhibit fast nutritional development but slow motor acquisition compared to other lemur species although they have dental precocity. I also found strong effects of maternal condition on infant physical and behavioral development. Reviewing the most extrinsic factors influencing infant development which are food availability and maternal condition (Janson & van Schaik, 1993, Berghänel et al., 2017), I found evidence of the second factor. Environmental stressors such as variation in food availability and seasonal changes, do not directly affect the early developmental process of infant Verreaux's sifakas;

however, these stressors affect maternal condition and investment, which in turn influence the development of their offspring.

I found evidence of the adverse effects of seasonal changes on maternal physiological conditions in terms of maternal GCc and the negative influence of this last on maternal investment. These findings are consistent with lemurs' life-history strategies, which minimize energy expenditure by limiting activities that are energetically costly (Wright, 1999). However, it is very interesting that infant Verreaux's sifakas show adaptive responses to elevated maternal GCc despite reduced maternal investment. My study results indicate the link between environmental stressors, maternal stress, and infant development, which appears to be adaptive during the first year of life of the infants. Below, I will give a detailed discussion of some of the main results of my study and will bring these findings to the perspective of the lemur's life history strategies, the so-called "lemur syndrome" (Kappeler & Fichtel, 2015; Kappeler & Schäffler, 2008).

Inter-individual variation in the physical and behavioral development of infant Verreaux's sifakas

Inter-individual variation: maybe related to the milk and ecological quality

First, the clear mechanism inducing inter-individual variation in infants' growth rates remain obscure. Normally, the infant's physical growth is supported by the energy intake that they received either from lactation or food intake (Hinde & Milligan, 2011). However, in this study, I did not find a correlation between individual growth rates and time spent foraging or in nipple contact. I found that time spent in nipple contact was influenced by mothers' age, food availability, and birth cohorts (year). Infants from younger mothers that have good condition spent more time in nipple contact. However, infants' growth rates were not significantly correlated to time spent in nipple contact. These results indicate the effect of mothers' conditions and environmental factors on maternal care and investment, but do not explain variation in infants' growth rates. Spending more time in nipple contact does not mean that infants received more energy (Johnson et al., 1998). Hence there are probably other factors inducing this inter-individual variation.

It has been argued that in mammalian species, including primates, the composition and the amount of milk produced differed between mothers (Hinde &Milligan, 2011). The lactation strategy and milk yield of the species depend on the quality of their ecological habitat (Oftedal, 1984, 2000; Riek, 2011).

For example, in the hooded seals (*Cystophora cristata*) live and raise their infants in the arctic environment, they lactate for a brief period (4 days), but their milk is very dense to provide enough energy for the offspring (Oftedal, 2000; Oftedal et al., 1993). However, for the species living in a dry habitat, their milk is more diluted to provide hydration, such as the case in many strepsirrhine species including lemurs (Hinde & Milligan, 2011; Tilden & Oftedal, 1997). Variation in the milk content between some lemur species has been reported due to the differences in their habitats (Tilden & Oftedal, 1997). Hence, there might be differences in each group's home ranges that may influence the milk nutrient of the mothers, which results in inter-individual differences in infants' growth rates.

Intraspecific variation in growth rates due to the differences in habitats has also been reported in diademed sifakas *(Propithecus diadema*), juveniles from fragmented areas exhibit slow growth than those from continuous areas (Irwin et al., 2010). In ring-tailed lemurs, immatures show variation in growth rates according to season, which is higher before the dry season (Pereira, 1993). Those findings indicate the influence of ecological conditions on immature growth rates. Similarly, in other primates, intraspecific variation in infants' growth rates is also found due to the differences in their ecological condition and diet. For instance, in mountain gorillas (*Gorilla beringei beringei*), infants in a more frugivorous population grew faster than those in a more frugivorous population (Galbany et al., 2017; Robbins & Robbins, 2018).

Maternal body mass can also influence the milk composition and thus affect offspring physical development in primates (Hinde & Milligan, 2011). It has been shown that milk quality is negatively correlated with maternal body mass, especially with species that do not park their offspring (Oftedal, 1984; Tilden & Oftedal, 1997), such as Verreaux's sifaka. Smaller-bodied mothers produce higher milk density than larger individuals (Hinde & Milligan, 2011) and thus may have bigger offspring. In this study, the mother's body mass was not included in the analysis, but this could also explain this inter-individual variation. Unfortunately, it was not possible to assess the maternal milk nutrient in this study. However, variation in milk quality might explain the variation in infant's growth rate.

Inter-individual variation: Probably influenced by the maternal condition

Maternal parity, such as multi or primiparous mothers but also maternal status have been reported to influence infant's growth rate in many taxa (Schai-braun et al., 2021; Love et al., 2005,2013; Samuni et al.,2020; Berghänel et al., 2016; Vercken et al., 2007; Emack et al., 2008). For instance, infants from primiparous mothers have lower body mass in hares (*Lepus europaeus*) (Schai-Braun et al., 2021). In chimpanzees, infants of low-ranking mothers have lower growth (Samuni et al., 2020). Unfortunately, mothers' rank and parity were not included in the analysis as all the mothers were dominant and multiparous. Hence, variation in milk quality, maternal physiological or physical condition but also differences in the home ranges quality might explain the inter-individual variation in infants growth rates found in this study, as Verreaux's sifakas are entirely dependent on their mothers during their early infancy period and allomaternal care is rare in this species (Ross & Lehman, 2016; Tecot et al., 2013). More studies about maternal care and variation in milk composition from wild lemur species are therefore needed.

Concerning the inter-individual variation found in infant behavioral development, it is also probably related to maternal "style" but also the behavior of the conspecifics. Richard (1976) also found differences in the age of the first occurrence of some behaviors in infant Verreaux's sifakas (Chapter I in this study). Maternal behavior and maternal "style" have been reported to influence infants' behavioral development (Bardi & Huffman, 2002; Schai-Braun et al., 2021; Thompson & Cords, 2020). For instance, in rhesus macaques, infants from protective mothers have reduced social interaction and explorative behavior (Bardi& Huffman, 2002). Similarly, in blue monkeys, female infants that received more grooming from their mothers exhibit reduced social interaction (Thompson & Cords, 2020). Inter-individual variation in infant behavioral development has also been found in chimpanzees and humans (Bründl et al., 2020; Siegler, 2006). It has been suggested that the acquisition of some skills, especially social interaction is related to external factors such as maternal condition and socio-environmental factors (Bründl et al., 2020; Murray et al., 2018; Samuni et al., 2020).

Sex differences in early physical and social development

Sex differences in growth rate: possibly related to future reproductive strategies

In mammals, sex differences in body size are related to their reproductive strategies (Kappeler & Fichtel, 2015; Leigh, 1992, 1995; Leigh & Terranova, 1998; Onyango et al.,

2013). However, most of the lemur species do not exhibit sexual size dimorphism, which is among the trait that distinguishes them from other primates (Kappeler & Fichtel, 2015).
Here I found sex differences in infants' early physical growth and social behavior such as grooming. Female infants show higher growth rates but are socially less active; whereas males have higher grooming activity but have lower growth rates. These early sex differences could be related to “lemur syndrome” (Kappeler&Fichtel, 2015) and reflect lemur reproductive strategies and social organization. In lemurs, females are dominant and exhibit high energetic burden than males due to reproduction costs(Young et al., 1990). Indeed, males and females have different life strategies.

Although Verreaux’s sifakas do not have any apparent sexual dimorphism, the sex differences found in early physical growth rates reflect their sex-specific future reproductive strategies. Females might invest more in physical growth because their fertility is influenced strongly by their body mass (Richard et al., 2000). In Verreaux’s sifakas, females with greater body mass are more likely to give birth than those with lower body mass (Richard et al., 2000). In this case, mothers might allocate more energy to their daughters that allows them to grow faster. However, male Verreaux’s sifakas’ reproductive strategies are based primarily on their physical strength rather than body size. It has been reported that, in this species, males with longer and stronger legs were more successful at reproduction because they have performed locomotion (Lawler et al., 2005). Hence, males may allocate their energy to enhance their physical strength rather than their body mass. For instance, in Assamese macaques, male infants engage more in locomotor play and acquired motor skills faster, whereas females invest more in foraging to increase body mass (Berghänel et al., 2015).

However, studies in captivity did not find sex differences in early growth rate in several Lemuridae species (Leigh & Terranova, 1998). In other primates, sex differences in growth rates have been found in many taxa due to the pronounced adult sexual size dimorphism (Leigh 1992, 1995; Leigh & Terranova, 1998). For instance, in lorises (e.g., *Nycticebus pygmaeus*) and galagos (e.g.,*Galago moholi*) males have higher growth rates than females (O’Mara et al., 2011). The same pattern has been found in baboons (Onyango et al., 2013). However, in some monomorphic primates, sex differences in early growth rates have also been observed. For instance, males have higher early growth rates than females in owl monkeys *(Aotus trivirgatus*), Goeldi’s marmosets (*Goeldi’s marmoset*), and golden lion tamarins (*Leontopithecus rosalia rosalia*) (Leigh, 1992; 1995). The reasons of these sex differences in early growth in monomorphic species remain obscure. It has been suggested that that early sex differences in morphology are related to the socio-ecological and behavioral parameters of the species (Leigh, 1995).

Sex differences in early social interaction: probably linked to the social organization

The sex differences in grooming reflect the social structure and organization of Verreaux's sifakas. In Verreaux's sifakas, females are less affiliative and have high intrasexual competition than males (Kappeler & Fichtel, 2015). Males and females have different social behavior and structure. Females rarely form a bond between them, whereas males can often form affiliative bonds with other males (Kappeler & Fichtel, 2015). Further, female competition is often high in lemur groups. Even though females are philopatric; some of them leave their natal groups because of the high cost of competition and have been evicted by dominant females (Kappeler & Fichtel, 2015). However, males are more affiliative, and male-male competition is less expressed. Males often form bonds with other males in the same groups through mutual grooming (Kappeler & Fichtel, 2015; Kappeler & Schäffler, 2008). Hence, this could explain the sex differences found in the early grooming activity of infant Verreaux's sifakas.

Moreover, in Verreaux's sifakas, males leave their natal groups when they reach maturity (Kappeler & Fichtel, 2012; Richard et al., 1993). Males have to find another group where they have to fight or adopt affiliative interactions to integrate into the new group. Physical strength but also highly affiliative behavior are needed during this process. Hence, infant males might invest more in grooming because they need to learn how to establish and maintain relationships. Social interactions such as grooming are essential to establishing and maintaining relationships. Hence, males and females have different approaches to prepare for those future life strategies. However, in ring-tailed lemurs, sex differences in early social interaction were not observed (Gould, 1990). This is probably due to the differences in the social organization of Verreaux's sifakas and ring-tailed lemurs.

Similarly, in other primates, sex differences in early social interaction have also been reported. For instance, males show more interest and involvement in play than females in gorillas (Watts & Pusey, 1993), chimpanzees (Pusey, 1990), and orangutans (Rijeksen, 1978).

In Assamese macaques (Berghänel et al., 2015) and geladas (*Theropithecus gelada*) (Barale et al., 2015), males play more and have more play partners. However, concerning grooming, immature male baboons interact and groom at lower rates than females (Cheney, 1978). It has been argued that interaction allows young individuals to predict their future social status and their role inside the group (Campan & Scapini, 2002). Hence, early social behavioral development may vary between sexes according to the social organization of the species.

“Slow-fast” development in Verreaux’s sifakas: mismatch between dental precocity and skill acquisition

“Slow-fast” development: probably related to the lifestyle of Verreaux’s sifakas

Variation in many life-history traits has been explained in various studies (Stearns, 1992; Pontzer et al., 2014; Kappeler & Pereira, 2003). Similarly, variation in life history is also found among lemurs. Indriidae lemurs have a slower life history in comparison to Lemuridae (Richard et al., 1976; Godfrey et al., 2004). The reasons for this difference between the two sympatric lemurs are well discussed by previous studies and reported to be related to the differences in their lifestyle and strategies but also associated with the maternal investment (Godfrey et al., 2004; Kappeler & Fichtel, 2015). Consistent with the previous findings, I found that Verreaux’s sifaka infants exhibit fast nutritional development but slow motor acquisition compared to lemurid species. My study supports the results of Richard (1976) that infant Verreaux’s sifakas start to forage earlier than do infants in lemurid species. However, their development of locomotor is slow. They reach independence later than infant lemurids.

The reasons for the variation in other developmental traits have been less discussed, for example, variation in the timing of acquisition of different developmental skills such as locomotion independence. Few studies only focused on the ontogeny of locomotion and explained the variation between and within species or the factors which influence locomotion development (Boulinguez-Ambroise et al., 2020; Wells & Turnquist, 2001; Workman & Covert, 2005; Wunderlich et al., 2011; Young & Shapiro, 2018).

It has been argued that the timing of independent locomotion is influenced by the locomotion mode (Sussman, 1977; Wunderlich et al., 2011; Young & Shapiro, 2018). Arboreal species need a more extended time because of the complexities of their habitat and substrate, which is more challenging than those for terrestrial species (Young & Shapiro, 2018; Wunderlich et al., 2011). However, a study by Young and Shapiro (2018) did not find a correlation between locomotion mode (arboreal or terrestrial) and age at independent locomotion. This study is in line with the argument that locomotion independence is shaped by locomotion mode and lifestyle. Verreaux's sifakas are highly arboreal and have a complex locomotion mode characterized by vertical leaping and bipedal galloping, which requires high performance and energetic demands (Wunderlich, 2011). Besides, it has been shown that the Indriidae shows slow skeletal development compared to Lemuridae (Wunderlich et al., 2011). This can explain the slow locomotion development and long developmental period in Verreaux's sifakas compared to other lemurid species.

In contrast to the development of some anthropoid species, where folivorous species exhibit faster development than frugivorous, which follows the Ecological Risk Aversion Hypothesis (ERAH) (Janson & van Schaik, 1993), lemurs development looks different. Verreaux's sifaka infants, which are more folivorous, start to eat solid food earlier but grow more slowly than do other Lemuridae species that are more frugivorous. Hence, in contrast to the ERAH hypothesis, in lemurs, folivorous species have slow development compared to frugivorous species although they have early dentition. The reasons for the mismatch between dental precocity and slow development have been discussed by previous research. It has been reported that this might be related to life-history strategies, the diet of indriid species, and maternal investment (Godfrey et al., 2004). The advanced dental development in Verreaux's sifakas may allow them to begin foraging earlier (Godfrey et al., 2004). According to the food processing hypothesis, the precocity of dental development depends on the diet and the food preparation (Eaglen, 1985; Godfrey et al., 2001). A study by Godfrey and colleagues (2004) showed evidence of this hypothesis; folivorous species have precocial dentition as they have more fibrous in their diet, and also they need to masticate seeds in the fruits (Godfrey et al., 2004). Besides, according to the foraging independence hypothesis, small brain species that have fewer or no helpers during foraging should have dental precocity as survival depends on themselves (Godfrey et al., 2001; Ross & Jones, 1999). The two theories could explain the dental precocity and early foraging development of infant Verreaux's sifakas compared to the other lemurid species. Verreaux's sifakas are highly folivorous and fed on fruits also when these are available. Infants do not receive any direct support during foraging. Hence, having advanced dental development helps infants to adapt to their lifestyle and to survive.

Therefore, dental precocity and slow development of infant Verreaux’s sifakas are part of an adaptation to their complex socio-ecological environment.

Concerning the developmental milestones of Verreaux’s sifakas, the results of this study are not different from the pattern of development found in other primates, such as chimpanzees (Bründl et al., 2020) and humans (Flensborg-Madsen & Mortensen, 2018). Similar to the results of this study, social skills emerged very late also in both chimpanzees and humans with high inter-individual variation (Bründl et al., 2020; Flensborg-Madsen & Mortensen, 2018). More complex skills such as food manipulation emerged at the latest in chimpanzees (Bründl et al., 2020). In Verreaux’s sifakas, independent locomotion appears to be the more difficult skill (Sussman, 1977, Wunderlich et al., 2011), which also emerged very late. Although Verreaux’s sifakas are not comparable to chimpanzees and humans in terms of body size, the comparisons of the emergence of various milestones illustrate that infants acquire all necessary skills at different ages and times which is influenced by the lifestyle of the species.

“Slow-fast” development: maybe related to the lack of allomaternal care

Allomaternal care can also influence infant developmental speed. Some studies found that allomaternal care correlates with faster growth rate, weaning, and shorter inter-birth interval (Ross, 2003; Ross & MacLarnon, 2000). Thus, this could also explain the rapid development of lemurid infants, such as ring-tailed lemurs, as they show more allomaternal care, all group members, even the non-father adult males, carry the infants (Gould, 1992) and allomaternal nursing has been observed (Gould, 1992; Gould et al., 2011). During our study, allomaternal care was rarely seen; males and females transported the infants only during exceptional situations. For example, when an infant was left with the male during social play, then the male had to transport it back to its mother. Richard (1976) also did not find any allomaternal care in infant Verreaux’s sifakas. However, Ross and colleagues (2016) found a weak allomaternal transport by adult males and other females in infant Coquerel’s sifakas. Hence, species that have less or no allomaternal care exhibit slow development, such as in Verreaux’s sifakas, supporting the suggestion that mother lemurs exhibit a high energetic burden. Raising an infant is very costly for mother lemurs, and allomaternal care can reduce the energetic costs.

How do mothers Verreaux's sifakas face the environmental stressors and the reproduction costs?

Increased maternal GCc during low rainfall: Energy mobilization

One of the largest factors inducing energy constraints in lemurs is seasonal changes. Due to the high variability and unpredictability of Madagascar's climate and environment, the "lemur syndrome" evolved (Kappeler & Fichtel, 2015) and leading the priority to females. Female lemurs have high energetic demands due to the high costs of reproduction(Young et al., 1990); hence they are more vulnerable to environmental variation. In this study, we found strong effects of the changes of precipitation in maternal GC levels. Prenatal and Postnatal maternal GC levels were higher during the low rainfall period, suggesting a mobilization of the energy metabolic. It has been reported that lemurs have a low basal metabolic rate (Genoud, 2002; Simmen et al., 2010). They use many strategies to cope with the seasonal changes in weather, such as hibernation in the small nocturnal lemurs (Dausmann, 2014) or the sun-bask in the larger diurnal lemurs (Eppley et al., 2017). A recent study with the same population also found that GC levels are increased during high temperatures (Rudolph et al., 2019). Increased stress hormone levels due to seasonal variation in weather have been also reported in many species, including lemurs. For instance, cortisol increased during the cold season in red deer *(Cervus elaphus)* (Huber et al., 2003) and chacma baboons (*Papio ursinus*) (Weingrill et al., 2004). GC levels were also increased during the dry season in Verreaux's sifakas and ring-tailed lemurs (Cavigelli, 1999; Pride, 2005; Rudolph et al., 2019).

Although we did not find a significant effect of food availability on maternal GC levels, rainfall is a good predictor of the quantity and quality of resources (Koch et al., 2017; Rudolph et al., 2019). During low rainfall, food availability and quality are also deficient, thus energy intake is decreased. Hence, organisms mobilize energy to compensate for this low energy intake. Besides, during low rainfall, finding food with high nutrients might be difficult, especially for mothers. They may need to increase traveling and foraging time. All of those activities require more energy, resulting in increased GC levels. High-stress hormone levels during seasonal changes in food availability and quality have been reported in many taxa, including lemurs. For instance, cortisol increased during a period of lower food availability in African elephants *(Loxodonta africana)* (Foley et al. 2001), baboons (Sapolsky, 1986), and red colobus monkeys (*Procolobus rufomitratus*) (Chapman et al., 2015).GC levels are increased during the low fruit period in collared brown lemurs (*Eulemur collaris*) (Balestri et al., 2014), red-bellied lemurs (*Eulemur rubriventer*) (Tecot, 2013), ring-tailed lemurs (Pride, 2005), diademed sifakas (Tecot et al., 2019) and also Verreaux's sifakas (Rudolph et al., 2020).

Higher GCc during gestation than lactation: gestation is energetically expensive

This study found that maternal GCc during pregnancy (PreGC) is higher than GCc during lactation (PostGC), suggesting that the gestation period requires more energy than the lactation period. Hence, postnatal maternal investment is maybe less costly in lemurs. However, it has been reported that lactation and infant transport are the most energetically expensive for all mammals (Hinde & Milligan, 2011, Tilden & Oftedal, 1997), and especially for lemur mothers because of the high environmental changes in their habitat (Young et al., 1990). Hence, maternal GC levels should be higher during the lactation period rather than gestation.

In contrast to those predictions, many studies have found that maternal GC levels are higher during gestation than lactation(Berghänel et al., 2016; Carnegie et al., 2011; Setchell et al.,2008; Rodrigues et al., 2015), which is consistent with my results. For instance, GC levels are higher during the gestation period in Assamese macaques (Berghänel et al., 2016), white-faced capuchins (*Cebus capucinus*) (Carnegie et al., 2011), mandrills (*Mandrillus sphinx*) (Setchell et al., 2008), Geoffroy's spider monkey (*Ateles geoffroyi*) (Rodrigues et al., 2015), and also in humans (Heinrichs et al., 2002).GC levels are also higher during gestation than the lactation period in many other lemur species such as in collared brown lemurs (Balestri et al., 2014) and ring-tailed lemurs (Cavigelli,1999). Recent studies in the same populations (Rudolph et al., 2020) and other sifaka species, i.e., Coquerel's sifakas, and diademed sifakas (Ross et al., 2020, Tecot et al., 2019), found a similar pattern. Hence, gestation requires high energetic demands for most of the primate species, including lemurs. During the gestation period, mothers ensure their survival but also have to ensure the development and maturation of the various organs of the fetus such as the brain (Heinrichs et al., 2003).

Furthermore, mothers may have reduced GC levels during the lactation than the gestation period because they might not mobilize more energy. Mothers may conserve their stored energy for the next reproduction period, consistent with the energy conservation hypothesis in lemurs (Wright, 1999). Lemurs have high energetic constraints due to the low and unpredictable resources available in their habitat. Hence, they adopt an energy conservation strategy to store energy and use it later. For female sifakas, their reproductive success is highly influenced by their energy intake. Only females with higher body mass have higher chances to give birth (Richard et al., 2000). Hence, mothers may already prepare for their subsequent reproduction and try to conserve their energy for this event. This might also explain the fact that Indriidae lemurs have a lower maternal investment (Godfrey et al., 2004). Besides, sifaka infants are born with a fully erupted milk dentition (Godfrey et al., 2004), which allows the infant to start foraging earlier than other lemur species (Chapter I in this study). This is maybe part of mother sifakas strategies to reduce energetic cost in lactation and enhance their future reproductive output by conserving more energy.

Alternatively, during the lactation period, the mother's body produces other hormones, such as oxytocin and prolactin, responsible for milk production. It has been reported that oxytocin can regulate the HPA axis activities and an organism's stress responses (Heinrichs et al., 2003; Ross, 2020). Oxytocin helps the organism to reduce stress to avoid adverse effects on offspring(Heinrichs et al., 2003). Elevated maternal stress has been shown to induce adverse outcomes in children that last during adulthood in humans (Cao et al., 2014; Grey et al., 2013). Hence, probably to avoid the negative effects of stress in infant development, mother GC levels are reduced during lactation than during gestation in many taxa (Berghänel et al., 2016; Carnegie et al., 2011; Setchell et al., 2008; Rodrigues et al., 2015; Ross & Lehman, 2016). Notably, for Verreaux's sifakas, they have low reproductive output compared to other lemur species. They have delayed sexual maturity, long inter-birth interval, and give birth to a single infant with a long infancy period and high infant mortality (Richard et al., 2002; Kappeler & Fichtel, 2012). Thus, reducing stress levels during the lactation period may help mothers increase their fitness and reproductive success and enhance infants' development and probably survival. Further, for Verreaux's sifakas, allomaternal care is rare; mothers have to ensure all activities, including carrying infants (Ross & Lehman, 2016). Infant carrying is very energetically expensive. Thus, mothers may reduce their stress responses to cope and concentrate on the various investments to the offspring.

How do maternal condition and stress affect infant development in Verreaux's sifakas?

Adaptive responses of infant Verreaux's sifakas to early adversity?

In this study, I found evidence of adaptive responses of the offspring to early to mid maternal prenatal GCc (PreGC). Increased maternal PreGC enhances the infants' growth rates and activities. Our results reflect the Predictive Adaptive Responses (PAR) hypothesis suggested that early adversities such as increased maternal PreGC accelerates infant development (Gluckman et al., 2005; Nettle et al., 2013). Unfortunately, I could not test offspring adult fitness and reproductive success yet, thus this study cannot confirm the existence of PAR in this species. However, the increased postnatal growth rate and explorative behaviors of the Verreaux's sifaka infants in response to increased maternal PreGC may reflect their predictive adaptive responses. Besides, for short-lived species, PAR suggested that mothers can inform infants about their future environment, which enables infants to predict their future environmental conditions and will be able to regulate their phenotype to match these conditions (Gluckman et al., 2005; Nettle et al., 2013). However, the evidence of PAR has not been supported for long-lived species living in an unpredictable environment. Verreaux's sifakas have a long gestation period (165 days), and their longevity is around 30 years (Kappeler & Fichtel, 2012). Hence, it remains hard to classify the responses of the offspring under PAR.

On the other hand, my finding is in line with the suggestion of Masson (1968) concerning maternal style effects on offspring development. Masson argued that infants from less supportive mothers are more developed. In this study, I assessed maternal investment in infant carrying which is among the expensive investment provided by mothers apart from lactation. I found that mothers with higher GC levels, both PreGC and PostGC, carry their infants less, suggesting that they are less supportive. Hence, due to reduced maternal investment, infants with less supportive mothers may be obliged to explore their environment, enhance independent foraging and interact with other group members; thus, they are more developed.

Furthermore, increased physical growth and activities in infants from mothers with higher GC levels and reduced carrying may occur due to their milk quality. It has been reported that mothers that carry their offspring all the time have more diluted milk than those that park their infants (Hinde & Milligan, 2011). There is evidence of milk nutrient differences in black and white ruffed lemur mothers (*Varecia variegata*) and brown lemur mothers (*Eulemur fulvus*) (Tilden & Oftedal, 1997). Hence, Verreaux's sifaka mothers may also reduce infant carrying to enhance the quality of their milk, increasing the infants' growth rates and exploration. Milk with higher content in protein has more energy thus increased infants' growth rates (Oftedal, 1984; Power et al., 2002) and infants' exploration behavior and competence (i.e., in *Macaca mulatta*, Hinde & Capitanio, 2010).

Besides, mother Verreaux's sifakas with higher GC levels probably minimize energy expenditure by reducing infant carrying but probably allocating more energy to the infants' growth and development. The results of this study show that infants of mothers with higher PostGC spent more time in nipple contact. This finding supports the suggestion that mothers might allocated more energy to infants' growth. However, spending more time in nipple contact does not always mean that the infants received more energy (Johnson et al., 1998). More information on infants' energy intake is needed. On the other hand, I found that infants that were less carried survived more likely the first year of their life. Hence, reducing infant carrying but allocating more energy in infants' growth is probably part of mother sifakas strategies to enhance infant survival but also their future reproductive success.

In other primate species, the effects of increased maternal GC levels in maternal investment, and infant development have also been found. High maternal GC levels induce reduced maternal investment and increased maternal rejections in many species, such as the case in baboons (Bardi et al., 2004), Japanese macaques (Bardi et al., 2003), and Assamese macaques (Berghänel et al., 2016). Increased prenatal maternal GC levels were also associated with an increased infants' growth rate in Assamese macaques (Berghänel et al., 2016), common marmosets (*Callithrix jacchus*) (Hauser et al., 2007), and red squirrels (Dantzer et al. 2013). Concerning infants' behavioral development, high maternal PreGC increased play activity in common marmosets but reduced skill acquisition in Assamese macaques (Hauser et al., 2007; Berghänel et al., 2016). Similarly, elevated prenatal maternal GC reduced motor skills and induced “negative temperament” in daughters in humans (Grey et al., 2013, Cao et al., 2014) and rhesus macaques (Sullivan et al., 2011). The effects of increased maternal GC levels on maternal investment and infant development depend on the timing of exposure and remain variable even between sexes (Sheriff et al. 2017, Berghänel et al. 2017). Positive effects of elevated prenatal maternal GC levels on infants physical growth have been found in many species (Berghänel et al., 2016, Hauser et al., 2007, Emack et al., 2008, Emgard et al. 2007; Dantzer et al. 2013), whereas the effects on infant survival are less documented. In this study, I did not find significant effects of maternal GCc on the early survival of infant Verreaux's sifakas. However, maternal investment in terms of carrying predicted infant survival. Mothers that have higher GCc spent less time carrying their infants, however, those infants were more likely to survive the first year of their life. Besides, the early survival of infants was also predicted by their skeletal growth rates which are, in turn, positively influenced by maternal PreGC. Hence, in this study, both PreGC and PostGC strongly influence maternal investment. Variation in maternal GCc affects, directly and indirectly, infant physical and behavioral development and early survival.

Overall, I found that infant Verreaux's sifakas exhibit slow development compared to other lemurid species with a high inter-individual variation. Infant development is shaped by maternal conditions that are in turn strongly influenced by environmental stressors. My study supports the findings of previous studies concerning lemur's development. Indriids have a slower development compared to lemurids because they have different life-history strategies and lower maternal investment (Godfrey et al., 2004). This study supports the idea that reproduction is energetically costly for female lemurs, particularly for Verreaux's sifakas. I found evidence of the energy conservation strategies in my research. Mother Verreaux's sifakas with high GC levels have reduced maternal investment in terms of infant carrying, suggesting that they may minimize energy expenditure. However, elevated maternal GC levels appear to be beneficial for infants during their first year of life. This study also reflects that infants' early physical and behavioral development are already adjusted to their future lifestyle and social organization, suggesting that this study may support the hypothesis that "lemur syndrome" is a result of maternal stress (Kappeler & Fichtel, 2015). My study added new information concerning the early physical and behavioral development of Verreaux's sifaka infants and provides evidence of the link between environmental stressors, maternal stress, and infant development. However, my study also has limitations. For example, it should be considered that my findings are based on small sample size. Moreover, I used non-invasive methods to assess some parameters such as photogrammetry and glucocorticoid derived from fecal samples, which will be discussed below.

Use of photogrammetry to assess infants' physical growth

Photogrammetry is an interesting and efficient method to measure physical traits of wild populations as it is not possible or very challenging to capture the animals every month or week to measure them directly**.** The photogrammetry method has been validated and commonly used to measure various physical traits in many taxa (Berghänel et al., 2017; Breuer et al., 2007; Deschner et al., 2004; Perryman & Westlake, 1998; Shrader et al., 2006).

Although the efficiency of photogrammetry has been shown, there are some limitations. For instance, the object should be relatively close to the observer to avoid wrong distances and fuzzy images when pointing the laser range finder on the subject. However, for Verreaux’s sifakas, which are highly arboreal, obtaining a closer distance and a clear view was quite challenging. Moreover, taking pictures of infants’ lower arms during their early ages was also a bit difficult as they were always in the ventrum of the mothers. Thus, we only had small sample sizes

Use of fecal glucocorticoids to assess maternal conditions

Several studies have used glucocorticoid metabolites to assess an organism’s state, such as health or stress (Love et al., 2013; Rudolph et al., 2020; Fichtel et al., 2007; Berghänel et al., 2016; Ostner et al., 2008). However, concerning maternal condition, elevated GC levels do not always mean that mothers are in poor or good condition. Many endocrine hormones are secreted during pregnancy and lactation which have specific roles and effects in maternal condition and behavior and should be considered (Bardi et al., 2004). For instance, estrogen and progesterone are essential for the maintenance of pregnancy (Challis et al., 2000). High levels of both hormones have been reported to increase mothers’ “responsibilities” (Bardi, 2001a,b).

Furthermore, some behaviors have been reported to reflect stress in mothers such as self-scratching (Brent et al., 2002) and infant rejection (Berghänel et al., 2016) that should also be considered to assess maternal condition. Lastly, because the maternal condition is highly related to its socio-environmental factors, considering other parameters can explain more maternal condition, such as maternal energy intake, maternal body mass, the quality and quantity of the food in each home range including mothers' milk nutrients.

Conclusions

Regarding the lack of studies assessing the link between environmental stressors, maternal stress, and infant development in wild populations, especially in lemur species, in this study, I added detailed information on the physical and behavioral development of an endangered lemur species and the effects of maternal condition and investment on this developmental process.

This study supports previous findings suggesting that in contrast to other primates, folivorous lemurs exhibit slow development compared to frugivores. I found that infant Verreaux’s sifakas show high inter-individual variation in physical and behavioral development. Infant males and females developed differently according to their future social organization and reproductive strategies. These findings suggest that mothers probably already adjust infant physical and behavioral development to their future lifestyle. Infant physical and behavioral development are strongly influenced by maternal conditions which are in turn affected by environmental stressors. Various environmental factors affect the maternal condition resulting in increased maternal glucocorticoids and reduced maternal investment. I found evidence of the energy conservation hypothesis. Mothers exhibit a high energetic burden and adjust their investment to the infants according to their conditions. Consistent with lemurs' life-history strategies, Verreaux’s sifaka mothers minimize energy expenditure by reducing infant carrying. Despite the reduced maternal investment, I found evidence of maternal stress effects on infant development, which appears to be adaptive for Verreaux’s sifaka infants during their first year of life. These adaptive responses of infants may be related to their adaptation to the harsh environment in their natural habitat.

Despite the adaptive responses of infant Verreaux’s sifakas, it is still debated whether the responses reflect PAR. Assessing infants' fitness and reproductive success in their future adult life can help understand these responses. Moreover, evaluating the responses of infant males and females to maternal stress is an interesting topic for future research to explore the hypothesis that maternal stress may induce “masculinization in daughters” leading to the evolution of the “lemur syndrome” (Kappeler & Fichtel, 2015). More studies assessing the link between environmental stressors, maternal stress, and infant development are needed, especially from other wild lemur species.

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DECLARATION

I hereby declare that I have written this thesis entitled "Environmental and maternal effects on infant development in Verreaux's sifakas (*Propithecus verreauxi*)" independently, without any other aids or sources than quoted.

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