Mother-infant relationships in wild Guinea baboons (*Papio papio*)

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I hereby declare that I have written this thesis independently and with no other aids or sources than those quoted.

Göttingen, 5th of November 2022

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Anaïs Avilés de Diego

To my parents, for always protecting me while, at the same time,
encouraging me to become a strong, independent woman

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Summary

During infancy, primates are heavily dependent on their mothers for nursing, transport, and thermoregulation, but also benefit from associating with their mothers for protection and social support. Furthermore, the mother acts as a role model for social learning, facilitates the interaction with the physical environment and the integration into a broader social network. The repeated interactions and reciprocity between mother and infant, along with the time that they spend together, lead to the formation of the mother-infant bond, which is typically recognised as the strongest social bond in the life of primates. The relationship between mothers and infants is dynamic, and they typically spend most of the time in contact and in close proximity just after infants have been born, and mothers frequently nurse and carry their infants, but soon enough time in contact, carrying, and nursing progressively decreases, and proximity increases as mother and infant move along infancy. Weaning is a period typically marked by behaviours of maternal rejection and increase of distance between mother and infant promoted by the mother. By the end of infancy, individuals will be independent from their mothers, and will therefore be able to move and feed by themselves. Even though the mother-infant dependency decreases as infancy progresses, not all mothers behave in the same way towards their infants. The individual variation in maternal care is known as mothering style, and it can have marked differences in the fate of infants' development and survival. Generally, mothers that are more protective produce infants that have higher survival rates and grow faster, and infants of rejecting mothers have lower survival and grow slower, but reach independence earlier.

The aim of this thesis was to investigate the mother-infant relationships in wild Guinea baboons living in the Niokolo-Koba National Park in Senegal. Guinea baboons live in a multi-level social organisation, with "units" at their base, several units forming "parties", and several parties grouping to form "gangs". Guinea baboons form strong social bonds with other males, have low levels of aggression, and show high spatial tolerance. Dispersal is female-biased, and even though females form linear and steep dominance hierarchies at the unit level, rank does not depend on kin. As a consequence of females transferring to other units, parties, or gangs, offspring might be left behind if a mother decides to disperse. Altogether, along with the fact that Guinea baboons live in a tolerant social system with regards to their social relationships, make Guinea baboons an interesting species to study mother-infant relationships.

In chapter 2 I provide a description of the behaviours between mothers and infants throughout infancy. I show that, similar to all primates, mothers and infants spend most of their time in contact and proximity in the early stages of infancy, and these behaviours, along with carry and nipple contact, decrease over time. Other behaviours, however, are very rare in Guinea baboons, such as protection and rejection, including nipple contact and carry rejections. I characterise mothering style in Guinea baboons, which can be considered as permissive, since the protective-rejecting range is not pronounced, and overall reflects their tolerant social style. I calculate infant growth from Parallel Laser Photogrammetry data, and I show that, contrary to other studies, mothering style and parity has no obvious effect on infant growth and survival. I then put in perspective the findings obtained by comparing them with yellow baboons, a species living in a multi-male multi-female society with female philopatry, clear matrilines and much more pronounced mothering styles. I further critically examine the results by pointing out possible effects of data sparsity and methodological issues derived from Parallel Laser Photogrammetry. In chapter 2, I develop a new statistical framework to account for lack of homogeneity in the data, which is not uncommon when studying wild animals, and of which my project was severely affected due to COVID-19 pandemic. Moreover, this statistical approach allows to control for infant age, which is paramount when studying ontogeny.

In chapter 3, I report 13 cases of post-mortem behaviours that have been observed towards infants in our population of Guinea baboons over nine years. Most of these behaviours were performed by the mothers of the infants, but occasionally also by other females. In line with reports from other studies, behaviours of carry, protection, and grooming were observed, but also cannibalism. I discuss our observations considering hypotheses that have been proposed until present to explain the occurrence of post-mortem behaviours, and I critically evaluate these hypotheses. I state that the *grief-management hypothesis* is non-testable, and I propose that selection has favoured post-mortem over-care-taking behaviours to avoid a type-II error in abandoning a non-responsive infant. I further suggest that the fading of the mother-infant bond leads to eventually discarding the corpse, and that the cannibalism observed indicates that the dead infant is eventually seen as food.

This thesis provides the first study on mother-infant relationships in wild Guinea baboons until present. In this thesis I shed light into the dynamics of behaviours between mothers and infants, characterised mothering styles, and evaluated the effect that differential mothering styles on the fate of the infants. I further contributed to disentangle the underlying mechanisms behind the occurrence of post-mortem behaviours and cannibalism in Guinea baboons, and in non-human primates in general.

Zusammenfassung

Primaten sind im Säuglingsalter absolut abhängig von ihren Müttern, wenn es um das Stillen, den Transport und die Wärmeregulierung geht, aber sie profitieren auch davon, dass sie sich zum Schutz und zur sozialen Unterstützung mit ihren Müttern assoziiieren. Darüber hinaus fungiert die Mutter als Vorbild für soziales Lernen, erleichtert die Interaktion mit der physischen Umwelt und die Integration in ein breiteres soziales Netzwerk. Die wiederholten Interaktionen und die Gegenseitigkeit zwischen Mutter und Säugling sowie die Zeit, die sie miteinander verbringen, führen zur Bildung der Mutter-Säuglings-Bindung, die in der Regel als die stärkste soziale Bindung im Leben von Primaten anerkannt wird. Die Beziehung zwischen Müttern und Säuglingen ist dynamisch, und kurz nach der Geburt verbringen sie die meiste Zeit in Kontakt und in unmittelbarer Nähe zueinander, und die Mütter stillen und tragen ihre Säuglinge häufig. Das Abstillen ist eine Phase, die typischerweise durch ablehnende Verhaltensweisen der Mutter und eine von der Mutter geförderte Zunahme der Distanz zwischen Mutter und Kind gekennzeichnet ist. Am Ende des Säuglingsalters sind die Tiere unabhängig von ihren Müttern und können sich selbständig bewegen und ernähren. Obwohl die Abhängigkeit zwischen Mutter und Kind im Laufe des Säuglingsalters abnimmt, verhalten sich nicht alle Mütter ihren Säuglingen gegenüber in gleicher Weise. Die individuellen Unterschiede in der mütterlichen Fürsorge werden als Bemutterungsstil bezeichnet und können sich deutlich auf die Entwicklung und das Überleben des Säuglings auswirken. Typischerweise bringen Mütter, die sich eher beschützend verhalten, Säuglinge hervor, die eine höhere Überlebensrate haben und schneller wachsen, während Säuglinge von abweisenden Müttern eine geringere Überlebensrate haben und langsamer wachsen, aber früher die Unabhängigkeit erreichen.

Ziel dieser Arbeit war es, die Mutter-Kind-Beziehungen bei wild lebenden Guineapavianen im Niokolo-Koba-Nationalpark in Senegal zu untersuchen. Guineapaviane leben in einer mehrstufigen sozialen Organisation, mit "Units" an der Basis, mehreren Einheiten, die "Parties" bilden, und mehreren Parteien, die sich zu "Gangs" zusammenschließen. Guineapaviane gehen starke soziale Bindungen mit anderen Männchen ein, haben ein geringes Aggressionsniveau und zeigen eine hohe räumliche Toleranz. Die Ausbreitung erfolgt überwiegend durch die Weibchen, und obwohl die Weibchen auf der Ebene der Units lineare und steile Dominanzhierarchien bilden, ist ihr Rang nicht von Verwandtschaft abhängig. Infolge des Wechsels der Weibchen zu anderen Units, Parties oder Gangs kann der Nachwuchs zurückbleiben, wenn die Mutter beschließt, abzuwandern. Dadurch, und auch da Guinea-Paviane in einem toleranten Sozialsystem leben, was ihre sozialen Beziehungen betrifft, sind Guinea-Paviane eine interessante Spezies für die Untersuchung von Mutter-Kind-Beziehungen.

In Kapitel 2 beschreibe ich die Verhaltensweisen zwischen Müttern und Säuglingen während der gesamten Säuglingszeit. Ich zeige, dass, ähnlich wie bei allen Primaten, Mütter und Säuglinge in den frühen Stadien der Kindheit, die meiste Zeit in Kontakt und Nähe verbringen, und dass diese Verhaltensweisen, zusammen mit dem Tragen und dem Kontakt mit der Brustwarze, über die Zeit abnehmen. Einige andere Verhaltensweisen sind bei Guineapavianen sehr selten, wie Schutz und Zurückweisung, sowohl des Kontakts mit der Brustwarze als auch des Tragens. Ich charakterisiere den Erziehungsstil von Guinea-Pavianen, der im Allgemeinen einen entspannten und toleranten Sozialstil widerspiegelt, da schützende und zurückweisende Verhaltensweisen nicht stark ausgeprägt sind. Ich berechne das Wachstum der Säuglinge anhand von Daten der Parallelen Laserphotogrammetrie und zeige, dass, im Gegensatz zu anderen Studien, der Erziehungsstil und die Parität keinen offensichtlichen Einfluss auf das Wachstum und die Überlebensrate der Säuglinge haben. Anschließend vergleiche ich die Ergebnisse mit Studien von Steppenpavianen, einer Spezies, die in einer Gesellschaft mit mehreren Männchen und Weibchen lebt, mit weiblicher Philopatrie, klaren Matrilinien und einem viel stärker ausgeprägten Erziehungsstil. Darüber hinaus untersuche ich die Ergebnisse kritisch, indem ich auf mögliche Auswirkungen der Datenknappheit und auf methodische Probleme hinweise, die sich aus der parallelen Laserphotogrammetrie ergeben. In Kapitel 2 entwickle ich einen neuen statistischen Rahmen, um die mangelnde Homogenität der Daten zu berücksichtigen, die bei der Untersuchung von Wildtieren nicht ungewöhnlich ist und von der mein Projekt aufgrund der COVID-19-Pandemie stark betroffen war. Darüber hinaus ermöglicht dieser statistische Ansatz die Kontrolle des Alters der Säuglinge, was bei der Untersuchung der Ontogenese von entscheidender Bedeutung ist.

In Kapitel 3 berichte ich über die 13 Fälle von postmortalen Verhaltensweisen, die in unserer Population von Guinea-Pavianen seit 9 Jahren gegenüber Säuglingen beobachtet wurden. Die meisten dieser Verhaltensweisen wurden von den Müttern der Säuglinge ausgeführt, gelegentlich aber auch von anderen Weibchen. In Übereinstimmung mit Berichten aus anderen Studien wurden Trage-, Schutz- und Pflegeverhalten, aber auch Kannibalismus beobachtet. Ich diskutiere unsere Beobachtungen unter Berücksichtigung der Hypothesen, die bisher zur Erklärung des postmortalen Verhaltens vorgeschlagen wurden, und bewerte diese kritisch. Ich behaupte, dass die Hypothese der Trauerbewältigung nicht überprüfbar ist, und schlage vor, dass die Selektion überfürsorgliches postmortales Verhalten begünstigt hat, um einen Typ-II-Fehler beim Verlassen eines nicht reagierenden Säuglings zu vermeiden. Ich schlage weiter vor, dass das Abschwächen der Mutter-Kind-Bindung dazu führt, dass der Leichnam schließlich liegengelassen wird, und dass der beobachtete Kannibalismus darauf hindeutet, dass der tote Säugling schließlich als Nahrung angesehen wird.

Diese Arbeit ist die erste zu Mutter-Kind-Beziehungen bei wildlebenden Guineapavianen, die bis heute vorliegt. In dieser Arbeit habe ich die Dynamik des Verhaltens zwischen Müttern und Säuglingen beleuchtet, die Erziehungsstile charakterisiert und die Auswirkungen der unterschiedlichen Erziehungsstile auf das Schicksal der Säuglinge untersucht. Darüber hinaus habe ich dazu beigetragen, die zugrundeliegenden Mechanismen hinter dem Auftreten von postmortalem Verhalten und Kannibalismus bei Guineapavianen und bei nichtmenschlichen Primaten im Allgemeinen zu entschlüsseln.

Résumé

Pendant l’enfance, les primates sont absolument dépendants de leur mère pour l'allaitement, le transport et la thermorégulation, mais ils bénéficient également de l'association avec leur mère pour la protection et le soutien social. De plus, la mère sert de modèle pour l'apprentissage social, facilite l'interaction avec l'environnement physique et l'intégration dans un réseau social plus large. Les interactions répétées et la réciprocité entre la mère et l’enfant, ainsi que le temps qu'ils passent ensemble, conduisent à la formation du lien mère-enfant, qui est généralement reconnu comme le lien social le plus fort dans la vie des primates. La relation entre les mères et les enfants est dynamique, et ils passent généralement la plupart du temps en contact et en proximité immédiate juste après la naissance des enfants, et les mères allaitent et portent fréquemment leurs enfants, mais assez rapidement, le temps de contact, de portage et d'allaitement diminue progressivement, et la proximité augmente à mesure que la mère et l’enfant avancent dans l’enfance. Le sevrage est une période typiquement marquée par des comportements de rejet maternel et d'augmentation de la distance entre la mère et l’enfant favorisés par la mère. À la fin de l’enfance, les individus sont indépendants de leur mère et sont donc capables de se déplacer et de se nourrir seuls. Même si la dépendance entre la mère et l’enfant diminue au fur et à mesure que l’enfance avance, toutes les mères ne se comportent pas de la même manière envers leurs enfants. La variation individuelle des soins maternels est connue sous le nom de style de maternage, et elle peut avoir des différences marquées dans le sort du développement et de la survie des enfants. En général, les mères qui sont plus protectrices produisent des enfants qui ont un taux de survie plus élevé et qui grandissent plus vite, tandis que les enfants de mères qui rejettent ont un taux de survie plus faible et grandissent plus lentement, mais atteignent l'indépendance plus tôt.

L'objectif de cette thèse était d'étudier les relations mère-enfant chez les babouins de Guinée sauvages vivant dans le parc national du Niokolo-Koba au Sénégal. Les babouins de Guinée vivent dans une organisation sociale à plusieurs niveaux, avec des "unités" à leur base, plusieurs unités formant des "partis", et plusieurs partis se regroupant pour former des "gangs". Les babouins de Guinée forment des liens sociaux forts avec les autres mâles, ont de faibles niveaux d'agressivité et montrent une grande tolérance spatiale. La dispersion se fait par les femelles, et même si les femelles forment des hiérarchies de dominance linéaires et abruptes au niveau de l'unité, le rang ne dépend pas de la parenté. En raison du transfert des femelles vers d'autres unités, partis ou gangs, la progéniture peut

être abandonnée si la mère décide de se disperser. Tous ces éléments, ainsi que le fait que les babouins de Guinée vivent dans un système social tolérant en ce qui concerne leurs relations sociales, font des babouins de Guinée une espèce intéressante pour étudier les relations mère-enfant.

Dans le chapitre 2, je fournis une description des comportements entre les mères et les enfants tout au long de l'enfance. Je montre que, comme chez tous les primates, les mères et les enfants passent la plupart de leur temps en contact et en proximité dans les premiers stades de l'enfance, et que ces comportements, ainsi que le portage et le contact des tétines, diminuent avec le temps. D'autres comportements, en revanche, sont très rares chez les babouins de Guinée, comme la protection et le rejet, y compris le contact avec la tétine et le rejet du portage. Je caractérise le style de maternage des babouins de Guinée, qui peut être considéré comme permissif, puisque la gamme protection-rejet n'est pas prononcée, et reflète globalement leur style social tolérant. Je calcule la croissance des enfants à partir des données de la photogrammétrie laser parallèle, et je montre que, contrairement à d'autres études, le style de maternage et la parité n'ont pas d'effet évident sur la croissance et la survie des enfants. Je mets ensuite en perspective les résultats obtenus en les comparant avec ceux des babouins jaunes, une espèce vivant dans une société multi-mâle et multi-femelle avec une philopatrie féminine, des matrilignes claires et des styles de maternage beaucoup plus prononcés. J'examine ensuite les résultats de manière critique en soulignant les effets possibles de la rareté des données et les problèmes méthodologiques dérivés de la photogrammétrie laser parallèle. Dans le chapitre 2, je développe un nouveau cadre statistique pour tenir compte du manque d'homogénéité dans les données, ce qui n'est pas rare lors de l'étude des animaux sauvages, et dont mon projet a été sévèrement affecté par la pandémie de COVID-19. De plus, cette approche statistique permet de contrôler l'âge de l'enfant, ce qui est primordial lorsqu'on étudie l'ontogenèse.

Dans le chapitre 3, je rapporte les 13 cas de comportements post-mortem qui ont été observés envers des enfants dans notre population de babouins de Guinée pendant 9 ans. La plupart de ces comportements ont été réalisés par les mères des enfants, mais aussi occasionnellement par d'autres femelles. Conformément aux rapports d'autres études, des comportements de portage, de protection et de toilettage ont été observés, mais aussi de cannibalisme. Je discute nos observations en considérant les hypothèses qui ont été proposées jusqu'à présent pour expliquer l'occurrence des comportements post-mortem, et j'évalue ces hypothèses de manière critique. J'affirme que l'hypothèse de la gestion du deuil n'est pas testable et je propose que la sélection a favorisé les comportements post-mortem de prise en charge excessive afin d'éviter une erreur de type II dans l'abandon d'un enfant qui ne réagit pas. Je suggère également que l'affaiblissement du lien mère-

enfant conduit à l'abandon du cadavre, et que le cannibalisme observé indique que l’enfant mort est finalement considéré comme de la nourriture.

Cette thèse fournit la première étude sur les relations mère-enfant chez les babouins de Guinée sauvages jusqu'à présent. Dans cette thèse, j'ai mis en lumière la dynamique des comportements entre les mères et les enfants, caractérisé les styles de maternage, et évalué l'effet des styles de maternage différentiels sur le sort des enfants. J'ai également contribué à démêler les mécanismes sous-jacents derrière l'apparition de comportements post-mortem et de cannibalisme chez les babouins de Guinée, et chez les primates non-humains en général.

Chapter 1

General Introduction

> "motherhood and infancy are only two stages, albeit particularly important ones, in the life histories of individuals whose lives extend before and, one hopes, after these periods. Females enter motherhood with their pasts and they and their infants carry into their futures the marks of their experiences during the life stage they so intimately share."
>
> Jeanne Altmann. *Baboon Mothers and Infants*, 1980 p. 6

1.1 The study of the mother-infant relationships in primates: a historical perspective

For the last century, the study of the mother-infant relationship has captivated the attention of many scientists, and over the decades, numerous disciplines such as ethology, evolutionary biology, psychology, anthropology, sociology, thanatology, genetics, and medicine have attempted to elucidate its underlying proximate and ultimate causes, its effects throughout the lifespan, and its biological and cultural variation. Research in human and non-human primates with regards to infants and mothers has been substantial, albeit fresh and exciting open questions remain yet to be addressed. The ubiquity of the mother-infant bond across species but, at the same time, the high intra- and inter-specific variability in the mother-infant relationships, are some of the most explored topics until present.

In non-human primates, the beginning of the research on mother-infant relationships dates back to the late 20s and early 30s of the 20th century, in captive conditions. Some of the first publications are the ones of Tinklepaugh and Hartmann (1932) and their "Behavior and maternal care of the newborn monkey (*Macaca mulatta* – "M. Rhesus")", along with Yerkes and Tomilin (1935) and their article on "Mother and infant relations in chimpanzee".

Years later, Harry Harlow set up a new framework regarding the development of mother-infant relationships, in which he investigated the interaction between behavioural development and maternal attributes. He made experiments with cloth and wire mother surrogates and found, to his surprise, that infant rhesus macaques preferred a non-feeding cloth mother to a feeding wire mother, revealing the importance of the mother's contact comfort for the infants (Harlow, 1958). Harlow's paper on "The nature of love" (1958) along with his experiments, have become classics in the disciplines of psychology and ethology. Some years later, the contribution of Robert Hinde was significant, both with his research on infant development in captive rhesus macaques and in setting up quantitative methods for the study of mother-infant relationships, such as the well-known "Hinde's index", a measure to assess which of two individuals are more responsible for keeping contact and proximity between them (R. A. Hinde, 1976; R. A. Hinde et al., 1964; R. A. Hinde & Atkinson, 1970; R. A. Hinde & Spencer-Booth, 1967, 1971).

Harlow, Hinde, Lorenz, and Tinbergen influenced John Bowlby's work to a great extent, who focused mainly on humans, but also considered non-human primates. In his *Theory of Attachment* (1969), Bowlby envisioned the healthy socio-emotional infant development as a result of the continuous responsiveness of the mothers (or main caregivers) to the infants, which produces positive attachment relationships. A lack of such positive relationships, in contrast, has direct consequences that may last throughout the life of individuals. Then, a new surge in the evolutionary theories of parental investment and parent-offspring theories arose, of which Trivers (1972, 1974) is one of the most prominent exponents (see sections 1.2 and 1.7.1). Since then, an increasing interest in elucidating social, demographic, ecological and life-history primate characteristics has led to an increase in field studies that investigate wild populations, and with this, a rise in the study of primate mother-infant relationships in natural conditions. Of these, one of the most paramount works has been the one of Jeanne Altmann, who studied yellow baboons (*Papio cynocephalus*) in the Amboseli National Park. The work of Jeanne Altmann, embodied in her book "Baboon Mothers and Infants" (1980), has become a cornerstone in the study of mother-infant relationships in wild primates.

1.2 Life-history strategies and parental investment

Parental investment is defined as the characteristics or actions of parents directed to their offspring that increase the fitness of their offspring, at the cost of any component of the parent's fitness, such as reduced parental care in terms of subsequent mating success, survival or fecundity (Trivers, 1972). Patterns of parental investment are ultimately shaped by life-history strategies (Stearns, 1992) and can be located along the semelparous-iteroparous spectrum. In semelparous species, individuals are short-lived, grow fast, reproduce early, and produce large amounts of small-sized offspring that experience high infant mortality. Individuals invest their energetic resources into reproduction instead of survival, which translates into a high reproductive effort followed by short post-reproductive lifespans and little or no parental care. This pattern can be found in the case of males and females of sockeye salmon (*Oncorhynchus nerka* [Truscott et al., 1986]), for instance, or the males of the Australian marsupial northern quoll (*Dasyurus hallucatus* [Oakwood et al., 2001]), which die shortly after mating. Iteroparous species, in contrast, typically have long lifespans, reproduce late, and as a result, they produce fewer offspring with higher survival rates. Individuals invest considerable energy into long-term survival, have late maturation and a prolonged post-reproductive lifespan, usually reproduce several times in a lifetime, and their offspring requires high parental investment. This pattern occurs in most birds (e.g., Japanese quail, *Coturnix coturnix japonica* [Ottinger et al., 1983]) and in many mammals (e.g., rat, *Rattus norvegicus* [McShane, 1996]; elephant, *Loxodonta africana* [Hanks, 1972]; chimpanzees [Nishida et al., 2003]). In mammals, a female's reproductive success depends on the quality of care and on ensuring the survival of individuals beyond weaning (Broad et al., 2006).

1.3 Animal taxa and parental care

Parental care is any form of parental behaviour that is likely to increase the fitness of a parent's offspring (Clutton-Brock, 1991); this definition does not imply any fitness consequences for the parents. Parental care is not uniform among animal taxa (Clutton-Brock, 1991). In fish and amphibians, parental care is mostly absent (Reynolds et al., 2002), although in teleost fish, male-only care is more common than in any other taxa (see Goldberg et al., 2020 for a meta-analysis of 48 teleost species). Seahorses and pipefishes (family Syngnathidae) have extraordinary adaptations for paternal care: males have a specialized brooding area or pouch under the tail or abdomen where the female deposits eggs (A. B. Wilson et al., 2003).

In birds and mammals, offspring care is widespread; endotherms need to keep their offspring warm and feed them. Parents might be close to their highest metabolic expenditure when feeding their offspring by collecting and supplying food to the chicks in the case of birds or by processing and providing milk in mammals (Clutton-Brock, 1991). Biparental care occurs in 75% of the known species of birds, and it is inferred in 81% of all species (Cockburn, 2006), allowing for both parents to increase their reproductive success by remaining together and sharing the costs of parental care (Davies et al., 2012). Eutherian mammals are characterized by placentation, internal development *in utero*, and extended care of the offspring after birth. Although paternal care to assist or aid mothers might occur in some animals, such as in carnivores and primates (Kleiman & Malcolm, 1981), mothers are the ones mainly responsible for providing parental care from conception to weaning, as they are the only ones able to gestate, give birth, and lactate (Broad et al., 2006; Clutton-Brock, 2016; Davies et al., 2012).

1.4 The immature period of development

The immature period of development (also referred to as "pre-reproductive period") comprises *infancy*, which is the period in which animals are dependent on their mothers to survive, and a longer period in which they do not depend on their mothers but are still not reproductively mature, which encompasses *youth* and *adolescence*, the latter beginning at the onset of puberty. In primates, infancy has been defined as the period in which infants cannot survive their mother's death, as they depend on their mothers mainly for nutrition and transport, but also for thermoregulation, protection from ectoparasites through grooming, and protection from elements, predation, and infanticide (Altmann, 1980; Pereira & Altmann, 1985). As infants move along infancy, they progressively decrease contact and proximity time with the mother, and start interacting with other members of the group, mostly peers (Walters, 1987). This shift in preferential interactions from their mother to other conspecifics intensifies after independence (Walters, 1987). The end of infancy and the subsequent achievement of independence does not occur abruptly when reaching a certain age (Altmann, 1980; Martin, 1984); it is generally accepted that infancy culminates at the end of the weaning process (Altmann, 1980; Lee, 1996; Martin, 1984) (see section 1.7 for more details on weaning), although tooth eruption, interbirth interval and percentages of maternal mass have also been used to define the transition from infant to juvenile (Setchell & Lee, 2004).

Primates are characterized by a lengthy period of immature development, even when compared to animals of similar size (Walters, 1987). It is in these early stages of life when individuals learn the behavioural repertoire typical of their species, develop sex-specific behaviours, establish relationships with conspecifics, acquire skills for adulthood, and gain an understanding of their physical and social environment (Altmann, 1980; Bekoff, 1984; Martin & Caro, 1985; Pereira & Altmann, 1985; Poirier & Smith, 1974; Walters, 1987). Three main hypotheses have been put forward to explain the protracted periods of immature development. The "needing-to-learn" hypothesis assumes that animals with large brains need longer learning periods to be able to successfully navigate complex physical and social environments. The prolonged immature period and subsequent late age of reproductive maturation are therefore an adaptation to optimize lifetime reproductive success (Stearns, 1977). The "brain growth constraint" hypothesis holds that animals with relatively large brains cannot grow as fast as those with relatively small brains due to sustained somatic growth; in other words, trade-offs in production (i.e., growth and reproduction) are expected in animals with large brains (Isler & Van Schaik, 2009; Isler & van Schaik, 2009; Ponce de León et al., 2008). Finally, the "juvenile risk" hypothesis (Janson & van Schaik, 1993) states that immature primates spend less time foraging to avoid competition with conspecifics and dedicate more energy to predator avoidance, at the cost of slow growth rates. Using a comparative approach, Ross and Jones (1999) found the best support for the "brain growth constraint" hypothesis, since age of maturation was related to brain size after controlling for body size.

This thesis focuses on mother-infant relationships in Guinea baboons. In the next pages, I will present some of the generalities of infants and mothers characteristic in primates, along with several theories that have been put forward to elucidate processes related to the first stages of ontogeny.

1.5 The mother-infant bond

Primates are social animals, and they form social bonds throughout their life. Social bonds, also referred to as relationships, are formed by affiliative interactions repeated over time with preferred individuals (R. A. Hinde, 1976). The first social bond in the life of infants is the one with their mothers, which is known as the mother-infant bond. The mother-infant bond is typically ubiquitous, strong, unique, and considered to be a prototype (Nicolson, 1987). Mothers provide their infants with an extensive variety of behaviours, such as nursing, transport, social support, protection, a role for social learning (e.g., to acquire foraging skills) and a pathway for exploring the physical environment and for integration into a broader social network (Altmann, 1980; Clutton-Brock, 2016; R. A. Hinde et al., 1964; R. A. Hinde & Spencer-Booth, 1967; Lonsdorf, 2013; Martin, 1984; Nicolson, 1987; Pereira & Altmann, 1985; Suomi, 2005). Although primates reach nutritional and transport independence at the end of infancy, the role of the mother might continue to have an influence beyond weaning, and offspring may obtain the benefits derived from the prolonged association with the mother (Altmann, 1980; Pereira & Altmann, 1985; Pusey, 1983), which has been termed "post-weaning dependency"(e.g., Samuni et al., 2020). The continued association will also promote a reinforcement of the mother-infant bond. Moreover, depending on the philopatric sex, mothers and offspring may continue to associate for their whole life (Maestripieri, 2018). The mother-infant bond is, above all, an attachment bond. Therefore, some insight into the Attachment Theory deserves mention (see section just below).

1.5.1 The Attachment Theory

The *Attachment Theory* (1969), formulated by John Bowlby, was the starting point for decades of unified research on human and non-human primates' development and parenting that is still ongoing. Bowlby's *Attachment Theory* (1969), to which Mary Ainsworth also greatly contributed (e.g., Ainsworth & Bell, 1970), brought together several scientific disciplines such as ethology, evolutionary biology, psychoanalysis and systems theory. Bowlby's work focused mainly on mother-child relationships in humans, but also extended to non-human primates. With his concept of attachment, Bowlby attempted to describe mother-infant relationships, claimed that the mother-infant bond is necessary for the healthy physiological and psychological development of children, and that infants use their mothers as a safe base for their explorations. For Bowlby, the mother-infant bond was the result of instinctual responses that both mother and infant possessed. He adopted an ethological approach and used the definition of "behavioural system" for his theory. Following Baerends (1976), behavioural systems are defined as a higher organisation of behavioural repertoires that are causally and functionally interrelated, and that can be activated by internal (e.g., hormones, central nervous system) and external cues (e.g., vocalisations of distress). Different behavioural systems interact and can arouse or inhibit one another. They might involve a goal-oriented behaviour and are at the service of biological functions and adaptive functions. On the one hand, the attachment system of the infant has behaviours aimed to seek contact and proximity. On the other hand, the caregiving system of the mother is reciprocal to the attachment system (Bowlby, 1969). According to Bowlby (1969), both systems evolved through natural selection to ensure infants' survival.

Bowlby's concept of attachment was, in many aspects, wrong and incomplete. For instance, he did not consider human cultural variation; he focused only on WEIRD infants (Western, Educated, Industrialized, Rich, Democratic), and even ignored caregiving variation in western societies (Keller et al., 2017; Morelli et al., 2017; Vicedo, 2017). He mainly focused on captive rhesus macaques and disregarded primate intra- and interspecific variation (Hawkes et al., 2017; Myowa & Butler, 2017). Bowlby had a limited understanding of evolutionary processes (Hawkes et al., 2017; Vicedo, 2017). Furthermore, he assumed that there is a preferential attachment relationship, and that this is the one with the mother, a concept that he called *monotropy*.

Many insights and clarifications have been made on behalf of understanding attachment since Bowlby's initial conception of the *Attachment Theory*, some of which I summarise here. First, infant care can be shared among several individuals, and the mother does not necessarily have to be the primary attachment figure, since in humans and in some non-human primate species the father can assume this role; further, infants are able to form multiple and varied styles of attachment. A broad social network might, in fact, imply more safety than a unique attachment figure (Hawkes et al., 2017; Maestripieri, 2003; Morelli et al., 2017, 2017; Myowa & Butler, 2017; Vicedo, 2017) (see section 4.4). Second, several sensory modalities are related to attachment and seem to play a role in recognising, forming and amplifying caregiver-infant relationships, such as visual and tactile cues. For instance, gibbons (*Hylobates agilis*) were able to distinguish the faces of their caregivers from others (Myowa-Yamakoshi & Tomonaga, 2001), and crab-eating monkeys (*Macaca fascicularis*) could recognise their mother's nipples (Negayama & Honjo, 1986). In humans, infants are attracted to gazing and to facial expressions from their caregivers (Myowa & Butler, 2017). Finally, because of the high variation in human cultures and non-human primate social systems, dominance relationships, dispersal patterns, competition, kin relationships, and general social and ecological environment, several patterns of mother-infant attachments and attachments beyond the mother are expected (Hawkes et al., 2017; Morelli et al., 2017).

1.5.2 Early-life adversity

The first stages of life are periods of high sensitivity to adversity both in human and non-human primates (Snyder-Mackler et al., 2020). Early-life adversity is a strong predictor of health, survival and fertility, and can occur at the social (e.g., maternal social isolation, low maternal rank, high population density) and environmental level (e.g., drought) (Snyder-Mackler et al., 2020). Several studies show evidence that early-life adversity can have immediate (i.e., infant, or juvenile death) and profound long-lasting consequences that can extend up to adulthood. Research in non-human primates shows that mothers that had experienced early life adversity themselves showed shortened lifespans, adult reduced social integration, elevated glucocorticoids, lower social status than expected, and higher offspring mortality in the first and second filial generation (French & Carp, 2016; Lea et al., 2014; Patterson et al., 2021, 2022; Rosenbaum et al., 2020; Tung et al., 2016; Weibel et al., 2020; Zipple et al., 2019, 2021). Among the types of early-life adversity that individuals can experience, the most severe ones are maternal loss, and reduced maternal investment due to the presence of a younger sibling close in age, which demonstrates the importance of the mother during the first stages of life.

1.6 Post-natal maternal investment: nursing and carrying

In mammals, maternal behaviours promote infant growth, development, and survival. The most crucial maternal behaviours for infant primates are nursing and carrying (Altmann, 1980; Clutton-Brock, 2016; Noordwijk et al., 2012), which happen at high frequencies just after infants have been born, and their occurrence steadily decreases as they move along infancy and until weaning is completed (Altmann, 1980). In primates, both carrying and nursing are behaviours performed mostly by the mothers, although in some species other individuals carry the infants frequently, of which the most known cases are found in the Callitrichidae family (reviewed in Sussman & Kinzey, 1984), and allonursing may occur rarely (e.g., wedge-capped capuchins, *Cebus olivaceus* [Robinson & O'Brien, 1991]) or frequently (e.g., tufted capuchin, *Cebus nigritus* [Baldovino & Di Bitetti, 2007], golden snub-nosed monkeys, *Rhinopithecus roxellana* [Xiang et al., 2019]). This phase of post-natal maternal investment is the most energetically demanding for mothers, exceeding the costs of gestation in many mammal species (K. Hinde et al., 2009; Martin, 1984; Speakman, 2008; Trivers, 1974). The milk of the mother by itself has to supply enough energy for the offspring's basal metabolism, growth, thermoregulation, and locomotor activity, at least until the infant starts eating solid food (Martin, 1984). Maternal energy intake is from two and a half to five times higher in lactating females compared to pregnant or not breeding females (Clutton-Brock, 2016). To supply this cost, lactating mothers increase foraging time or feed on higher-quality foods (Clutton-Brock, 2016; Murray et al., 2009). After nursing, carrying is the second most costly behaviour for mothers (Altmann & Samuels, 1992). As infants grow old, both lactation and carrying become increasingly costly for the mothers (Altmann & Samuels, 1992; Trivers, 1974). The increased food requirement for mothers to maintain prolonged nursing and carrying makes them more susceptible to predation, illness, and death (Martin, 1984). At a certain point, the maternal costs for nursing and carrying exceed the infant's benefits, and maternal net reproductive success would decrease if these behaviours would not cease: mothers must balance the needs of their current offspring and their future ability to reproduce (Trivers, 1972). Thus, it is in the mother's interest to promote the infant's independence in order to stop nursing and carrying the infant, a process that will initiate a conflict of interest between a mother and her infant (see sections 1.7 and 1.7.1) and will culminate at the end of weaning.

1.7 Weaning

The weaning period is the gradual process of transition from dependency to nutritional and transport self-sufficiency (Martin, 1984). During weaning, infants gradually reduce their mother's milk intake and increase solid food, until the only food source is solid aliments (Martin, 1984). However, weaning does not only imply a shift in nutrition, but is also strongly marked by behavioural changes in the mother-infant relationship: for instance, contact and proximity between the dyad decreases, and infants will be rejected, and can be mildly aggressed by their mothers (Altmann, 1980; Martin, 1984). The weaning brings along a conflict between mothers and infants, defined as the “parent-offspring conflict”.

1.7.1 Parent-offspring conflict

A broadly recognised period for parent-offspring conflict in primates is the weaning process. Early theories on the evolution of parental care assumed that parents were free to distribute their available investment as they pleased in order to maximise their own fitness, and that offspring were just passive entities, receivers of parental investment. However, this is not the case in diploid animals. The initial parent-offspring conflict theory was put forward by Trivers, who considered a model in which parent costs remain stable or increase with increasing offspring age, while the benefits of parental care to the current offspring decline (Trivers, 1974). In the initial model of Trivers, mothers would produce an offspring every year, the next offspring would be a full sibling with the current offspring (*inter-brood conflict*), and the fathers would not invest in offspring after the moment of conception. Because the coefficient of relatedness between a current offspring and its possible future siblings is 0.5, whereas it is 1.0 with itself, current offspring should bias the maternal investment towards its own benefit and away from the mother’s optimum, either by directly raiding parental resources or through deceit (e.g., begging for food), until the maternal fitness costs of care would be twice the benefit to itself. Therefore, a conflict of interest or a disagreement should be present between a mother and her current offspring from the moment in which the parental care benefit/cost ratio is 1.0 to when it equals 0.5. (Trivers, 1974). The timing in which this conflict will arise will depend on how fast the benefit/cost ratio reaches these values, but in general, they carry overt behavioural conflicts. During these conflicts, it is common that offspring produce exaggerated signals (e.g., moaning, tantrums) to manifest their need for care, and parents should be able to counteract their offspring’s manipulations but also should be able to assess when their infants are in real need for care. Nowadays, the principles that Trivers proposed are broadly accepted.

1.8 Variability in mother-infant relationships in non-human primates

Considerable intra- and interspecific variation is apparent in the relationships between mothers and infants, regardless of the inherent change in the relationship due to the decrease in infant dependency over time. This variation is defined as mothering style (e.g., Altmann, 1980; Fairbanks, 1996). Several factors influence the degree to which mothers have a more protective or a more rejecting style, such as social and ecological risks, environmental conditions (e.g., food availability), particularities of the social system, and characteristics of the mother (i.e., maternal age, parity, condition, reproductive value, and personality) (reviewed in Fairbanks, 1996; Maestripieri, 1994). Mothering styles produce differences in weaning timing and have consequences on the infant's development, with offspring of protective mothers typically experiencing higher survival rates but reaching independence later, whereas offspring of rejecting mothers are usually bolder, become independent earlier, but have higher mortality rates (e.g., Altmann, 1980). Detailed information about mothering styles and mothering style hypotheses related to maternal characteristics (i.e., parental investment theory and maternal experience hypothesis) can be found in chapter 2.

Concerning characteristics of the infants related to variation in mother-infant relationships, infant sex has historically been considered a contributing factor to variation in mothering style. However, the effect of infant sex remains unclear. Although some studies have shown evidence for an effect of sex on mothering style, for instance, primiparous mothers were more protective towards their daughters and multiparous mothers towards their sons in rhesus macaques (Holley & Simpson, 1981), many other studies have failed to show an effect (e.g., yellow baboons [Altmann, 1980]; vervet monkeys, *Cercopithecus aethiops* [Fairbanks & McGuire, 1987]; rhesus macaques [Holley & Simpson, 1981]). Moreover, other factors might influence the results of sex differences, for example, infant sex ratio (Gomendio, 1990), or rank-related patterns of infant mortality (Altmann & Samuels, 1992).

1.9 Guinea baboons: a model species

In the previous sections, I have presented a theoretical framework for the understanding of mother-infant relationships. I have first exposed the patterns of parental investment of organisms as a consequence of different life-history strategies, and the types of parental care that occur in vertebrates. I have presented the immature period of development, and I have stressed the importance of the mother for the offspring’s development, growth, and survival during infancy, along with the significance of the mother-infant bond during, potentially, the whole lifespan of individuals.

I have outlined the conflict that occurs when infants enter weaning, and the variation in mother-infant relationships. Now, I turn to present the study species of this thesis: the Guinea baboon. Currently, six species form the genus *Papio* (Zinner et al., 2009, 2013): olive (*Papio anubis*), hamadryas (*P. hamadryas*), yellow (*P. cynocephalus*), chacma (*P. ursinus*), Kinda (*P. kindae*), and Guinea baboons (*P. papio*). The genus *Papio* is diverse in its social systems, with species that form multi-male multi-female groups with male dispersal and female philopatry (i.e., olive, yellow, Kinda, and chacma baboons) to multilevel societies with one-male units in its base, male philopatry and female dispersal (i.e., hamadryas and Guinea baboons) (reviewed in Fischer et al., 2017). This variety in social systems, along with differences in dominance relationships, with species that are despotic and nepotistic and others that are tolerant, make *Papio* an interesting genus to study mother-infant relationships and the potential importance of the mothering style depending on the society type. Guinea baboons represent an ideal model to study these questions, since they are a tolerant species in which inter-individual familiarity across sub-groups and potentially low prominence of social risks constitute a relatively safe social environment for infants. Further, their female-biased dispersal may result in mothers that leave their offspring behind, who might be faced to carry on without the benefits derived from maternal association. In this thesis, I examine mother-infant relationships in Guinea baboons, with a special focus on the effects of mothering style on growth and survival during the infancy period, and the effect that the mother-infant bond might have in mothers even after infants die for eliciting caretaking behaviours towards their dead infants.

Guinea baboons live in nested multi-level societies (Patzelt et al., 2014). “Units” are at the base of the society, which are composed of one “primary” male, one to seven females and their immatures (Fischer et al., 2017; Goffe et al., 2016). Units frequently have at least one bachelor male associated, although bachelor males usually associate with several primary males at the same time (Dal Pesco et al., 2021). In a unit, female mating is almost exclusively restricted to the primary male (98.6% copulations), although occasionally occurs with other males (Dal Pesco et al., 2022; Goffe et al., 2016). Paternity for the primary male is high (91.7%; Dal Pesco et al., 2022). Several units associate into a “party”, and two or more “parties” group temporarily together into “gangs” (Patzelt et al., 2014). There is genetic and behavioural evidence of female-biased dispersal in Guinea baboons, with females dispersing relatively freely to other units, parties, and gangs (Kopp et al., 2015). Because of female-biased dispersal, mothers might transfer and leave behind their weaned and unweaned offspring. Females in a unit exhibit a linear and relatively steep hierarchy (Faraut et al., 2019; Fischer et al., 2017), although there are no matriclans in Guinea baboons and rank is not conditional on patterns of female relatedness. Female tenure might last from weeks to several years (Fischer et al., 2017). Males maintain affiliative relationships, engage in coalitions, are spatially tolerant, and form strong social bonds (Patzelt et al., 2014) even outside the unit level (Dal Pesco et al., 2021). Since aggressions between males are infrequent and decided outcomes are not always clear, it is not possible to evaluate male dominance hierarchy with certainty (Dal Pesco et al., 2021; Kalbitzer et al., 2015). On average, strongly bonded males are more closely related, which suggests that relatedness plays a role in forming and maintaining relationships, although males with low degrees of relatedness may also form strong bonds (Dal Pesco et al., 2021). Male Guinea baboons engage frequently in ritualized greetings (i.e., exchanges of non-aggressive signals), which seem to function as a signal commitment between party members, to enhance relationship strength between strongly bonded males, and to test the relationship between spatially tolerant partners (Dal Pesco & Fischer, 2018). Females enjoy certain spatial freedom since they spend considerable amounts of time away from their male. Further, females counter-attack males in aggressive episodes and take an active role in intersexual bond formation and maintenance, which suggests that female choice might play a role in Guinea baboons (Goffe et al., 2016).

1.10 Study aims

In study 1 (**chapter 2**) I characterise mothering styles in wild Guinea baboons and investigate their effect on infant growth and survival. Because of lack of homogeneity in the data, I develop a new statistical framework in which I age-correct mothering style (main predictor variable) and growth (one of the outcome variables), since it is paramount to consider the time scale when variables change with ontogeny. I ultimately define mothering style using only the behaviours that show enough maternal variability. For growth determination, I use measures obtained with Parallel Laser Photogrammetry. I then test the effect of mothering style on infant growth and survival. Finally, I provide a comparative approach with yellow baboons, in which I discuss the differences in mother-infant relationships related to infant general development, mothering style, and infant survival.

In study 2 (**chapter 3**) I present data on Guinea baboons collected during nine years of field observations on post-mortem caretaking behaviours and cannibalism directed towards dead infants. I discuss our observations and I critically evaluate hypotheses that have been put forward until present to explain the occurrence of these behaviours in primates.

With study 1 and study 2, I provide the first study on mother-infant relationships in wild Guinea baboons.

Chapter 2

Growth and survival in wild infant Guinea baboons (*Papio papio*)

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Anaïs Avilés de Diego, **Federica Dal Pesco** and **Julia Fischer** designed the study. **Anaïs Avilés de Diego** collected the data. **Anaïs Avilés de Diego** and **Federica Dal Pesco** prepared the data for analysis. **Anaïs Avilés de Diego** and **Roger Mundry** analysed the data and prepared the figures. **Anaïs Avilés de Diego** drafted the manuscript. **Anaïs Avilés de Diego**, **Roger Mundry, Federica Dal Pesco,** and **Julia Fischer** discussed the results and edited the manuscript.

2.1 Abstract

Primate infants depend on their mothers for nursing, transport and survival but also benefit from other behaviours such as contact, protection, and the mother being a model for social learning. During infancy, variation in maternal care, defined as mothering style, can have profound consequences for the development and survival of their infants. Mothering style has been shown to vary with maternal age (parity and experience) but also with the social system characteristics of the species. Guinea baboons, *Papio papio*, are a promising case to examine this conjecture since comparative data for another member of the genus *Papio*, namely yellow baboons, exist. While yellow baboons live in female philopatric societies, Guinea baboons live in a tolerant social system with female-biased dispersal. We investigated the effect of mothering style on the growth and survival of wild infant Guinea baboons, using a dataset of *N* = 79 infants (2016-2021) for survival and *N* = 50 infants (2018-2021) for growth. Growth data were obtained using Parallel Laser Photogrammetry (PLP). To account for the lack of homogeneity in the data, we developed a new statistical framework for analysing ontogenetic processes. Contrary to our predictions, mothering style did not have any noticeable effect on infant growth and survival. The results obtained might be due to a real lack of effect but can also potentially be explained by data sparsity or methodological issues associated with the PLP method. However, our qualitative comparisons between the species indicate substantial differences in mothering style between yellow and Guinea baboons, with Guinea baboon mothers being more lenient and providing care for longer than yellow baboons.

Keywords: mother-infant relationship, mothering style, *Papio papio*, growth, survival, Parallel Laser Photogrammetry

2.2 Introduction

Primates are the order with the slowest life histories compared to other mammals of similar size, since they have delayed neural development, lengthy periods of immature development, and late reproductive maturation. Further, behavioural maturation continues until the moment they die (Charnov & Berrigan, 1993; Maestripieri & Mateo, 2009; Pereira & Altmann, 1985). Although primates are at the precocial end of the altricial-precocial spectrum, they are born in a relative altricial state and need their mothers for more than just nursing. Primate infants are mostly helpless, relatively immobile, and until weaning is completed, they depend strongly on their mothers for transport, who carry them on their bodies (Nicolson, 1987). Besides, infants receive a wide range of significant maternal behaviours beyond nutrition and transport, such as social support and protection against predators or conspecifics. Moreover, mothers are the primary model for social learning, particularly for acquiring foraging skills (R. A. Hinde & Spencer-Booth, 1967; Suomi, 2005). Mothers also play an essential role in facilitating the early interactions of their infants with their physical and social environment (Altmann, 1980; R. A. Hinde et al., 1964; Lonsdorf, 2013).

The strong dependency of infants on mothers for growth and survival, the energy and resources that mothers invest in their offspring, and the time that mothers and infants spend together lead to the formation and maintenance of the mother-infant bond (Broad et al., 2006). For the infant, this will be its first social bond. The mother-infant bond is a powerful, unique social bond, typically considered the strongest bond that can exist among two individuals in mammals (Nicolson, 1987). On top of that, in primates, mothers and infants continue to associate after weaning, i.e., beyond infancy (Maestripieri, 2018). This association allows extended maternal influence and a reinforcement of the mother-infant bond, which may last a lifetime in female philopatric societies. The bond between a mother and an infant is considered an attachment bond. John Bowlby, the author of the *Attachment Theory* (1969), viewed the mother-infant bond of humans and rhesus monkeys to share a common evolutionary history, with phylogenetic origins tracing back to the Old-World monkeys, and saw the attachment between an infant and its mother as a developmental adaptation for the survival of infants. Further research has since contributed to the homology concept of the mother-infant bond in human and non-human primates (see Maestripieri & Roney, 2006; Suomi, 2016).

The mother-infant relationship is a dynamic one. Mother-infant relationships have been typically characterized by contact and proximity-seeking behaviours (Altmann, 1980; Harlow, 1958; R. A. Hinde et al., 1964; R. A. Hinde & Spencer-Booth, 1967, 1971). An infant's first year of life is a critical period. After birth, mothers and infants are found mostly in physical contact. Soon after, infants start venturing away to explore their immediate environment, and they use their mothers as a safe base to whom to return in case of insecurity or distress (Ainsworth & Bell, 1970; Bowlby, 1969). As infants grow older, these explorations, as well as interactions with other social partners, become more frequent (Altmann, 1980). While infants first drive the decline in contact and proximity with the mother, the onset of the weaning process changes these dynamics, and infants are more likely to seek contact than the mothers (R. A. Hinde et al., 1964; R. A. Hinde & Spencer-Booth, 1967).

While infant-mother dependency generally decreases during weaning, not all mothers are the same. How mothers treat their infants can affect the offspring's survival, development and weaning age (e.g., Altmann, 1980; Fairbanks, 1996). Individual differences in how mothers behave towards their infants are known as mothering styles (Altmann, 1980; Nicolson, 1987). Studies of mothering style usually describe mothering behaviours falling along two independent dimensions, named protectiveness and rejection (e.g., vervet monkeys, *Cercopithecus aethiops* [Fairbanks & McGuire, 1987]; yellow baboons, *Papio cynocephalus* [Altmann, 1980]; rhesus macaques, *Macaca mulatta* [Berman, 1990a, 1990b]; Japanese macaques, *Macaca fuscata* [Bardi & Huffman, 2002; Tanaka, 1989]; Yunnan snub-nosed monkeys, *Rhinopithecus bieti* [Li et al., 2013]).

Protective mothers (also referred to as “restrictive”) are generally more attentive, restrict the explorations of their infants, and prevent the infant from moving away. These mothers display a higher rate of behaviours aimed at decreasing distance and increasing contact rates between them and their offspring, such as retrieving, restraining, cradling, approaching, and making contact with the infant. Rejecting mothers (also referred to as “laissez-faire”) are usually more tolerant to separation, are less attentive (e.g., lower glance rates compared to protective mothers: Altmann, 1980) and allow more interactions with other group members in comparison with protective mothers (e.g., higher rates of grooming by other individuals in yellow baboons: Altmann, 1980). These mothers display behaviours to increase the distance between mother and infant, such as breaking contact and moving away. Higher rates of punitive or mild aggressive behaviours occur in rejecting mothers (e.g., biting, hitting, pushing away), and they allow less time for transport and nipple contact or actively prevent these behaviours (i.e., rejecting nipple contact and transport: Altmann, 1980; Fairbanks & McGuire, 1988a]).

Several studies show evidence that infants of rejecting mothers reach independence earlier, show more exploratory behaviour and are less afraid of novelty (Altmann, 1980; Fairbanks & McGuire, 1988b; Simpson & Datta, 1991), yet a rejecting mothering style might equally be associated with higher infant mortality. In yellow baboons, infants of “laissez-faire” mothers experienced higher rates of illness and death (Altmann, 1980), and infant mortality was more pronounced in vervet monkeys for those infants with lower rates of suckling success and early weaning (Lee, 1984). A more protective mothering style is associated with higher survival (Fairbanks, 1996), as these infants should be able to obtain more benefits from spending more time near their mothers (e.g., social support, knowledge transmission, and protection).

Variation in mothering style has been associated with social and demographic risk variables and maternal characteristics. For example, when social factors threaten the infant’s survival, such as those derived from maternal low dominance rank (Altmann, 1980), newly introduced males in the group (Fairbanks & McGuire, 1987), or the presence of "aunts" (i.e., other females that show interest in the infant, potentially "stealing" it from the mother) (Rowell et al., 1964), mothers show increased protectiveness. Conversely, mothers are more rejecting when social risks are relaxed, e.g., when females are surrounded by close kin or matrilines that offer social support (Altmann, 1980; Berman, 1980). Ecological risk variables might also trigger an increase in protectiveness, e.g., mothers became more protective after rhesus macaques were exposed to trapping activities in Cayo Santiago (Berman, 1989).

Variability in social systems might also promote differences in mothering style. For example, in despotic and nepotistic societies, characterized by strict dominance hierarchies, protective behaviours are more pronounced, as infants are more exposed to social risks and mothers might have to restrict the social contacts of their offspring (Altmann, 1980; Maestripieri, 1994). In contrast, in tolerant, egalitarian species, in which dominance hierarchies are relaxed, and kinship has a weaker effect, mothers do not need to be as protective, as these social systems provide a much safer social environment, and conspecifics do not pose such a risk for their infants' survival (Thierry, 2013). The latter is a social context that might allow other individuals to participate in infant care (McKenna, 1979) and in which social relationships might buffer the effect of the mother on the infant's fate.

Factors related to the characteristics of the mother, such as maternal age, parity, experience, and reproductive value, which are, to some degree, correlated, are also associated with variations in mothering style (Fairbanks, 1996). There are two different bodies of theory regarding the effects of maternal characteristics on mothering style, generating opposite predictions: the parental investment theory and the maternal experience hypothesis. The parental investment theory (Trivers, 1972, 1974) predicts that younger mothers should terminate investment in their offspring earlier and be more rejecting because they have more to gain in future reproductive potential than older mothers, who should invest more and be more protective of their current reproduction. In a study on Barbary macaques (*Macaca sylvanus*), old mothers weaned their infants later and spent more time in contact with their offspring than young mothers, thus supporting the parental investment theory (Paul et al., 1993).

The maternal experience hypothesis, in contrast, states that young mothers should be more protective than older mothers because they are more inexperienced and less proficient in rearing an infant and need more effort to get positive outcomes. Evidence in favour of the maternal experience hypothesis comes from research with captive individuals: in a study of rhesus macaques (Holley &

Simpson, 1981), primiparous mothers were less confident than multiparous mothers, and in a study with Japanese macaques (Schino et al., 1995), multiparous mothers were less protective than primiparous ones. The temperament and personality of the mother might also have an effect on mothering style (Fairbanks, 1996; Maestripieri, 1993), as well as and quality and availability of food and maternal condition: when food is restricted, lactating mothers should wean their infants earlier and therefore be more rejecting (Clutton-Brock, 1991).

Here, we investigate how differences in mothering style and parity influence the growth and survival of wild infant Guinea baboons (*Papio papio*) ranging near the DPZ field station Simenti in Senegal. Guinea baboons live in nested multi-level societies, formed by "units" at its basis, which are composed of one "primary" male, one to six females and their immatures (Goffe et al., 2016). Females almost exclusively mate with the "primary" male of their unit. "Bachelor" males are occasionally present in the unit, although females rarely establish sexual relationships with them (Goffe et al., 2016). Several units associate to form a "party", and two or more "parties" group together temporarily into "gangs" (Patzelt et al., 2014). Genetic and behavioural evidence indicates that Guinea baboons have female-biased dispersal (Kopp et al., 2015), with females transferring relatively freely between units, parties and gangs (Goffe et al., 2016). When mothers transfer, they might leave their weaned offspring behind. Guinea baboon males are spatially tolerant, maintain affiliative relationships, engage in coalitions, and form strong social bonds (Patzelt et al., 2014) even outside the unit level (Dal Pesco et al., 2021). Strongly bonded males are more closely related, suggesting that male-male relatedness plays a role in forming and maintaining relationships between males (Dal Pesco et al., 2021). Aggressions between individuals are rare, and outcomes are not always clear, rendering it impossible to accurately assess the male dominance hierarchy (Dal Pesco et al., 2021; Kalbitzer et al., 2015).

To address our research questions, we first characterized the mothering style for our population of Guinea baboons. We paid particular attention to those behaviours directed from the mother to the infant because, even though both mother and infant contribute to the mother-infant relationship, the mothering behaviours are the ones that ultimately define mothering style. Once we had characterized mothering style, we tested its effect on infant growth and survival. We predicted that infants of rejecting mothers would have slower growth trajectories than those from protective mothers. These infants must become independent foragers earlier, an activity in which they are still inexperienced. Infants of protective mothers, in contrast, have prolonged access to milk and spend more time in proximity with their mothers, which also gives them more time to continue learning foraging skills. We also predicted that infants from rejecting mothers would experience higher mortality. For a subset of the data for which we had information on maternal parity (i.e., primiparous, multiparous), we ran two additional models in which we included maternal parity to control for the fact that inexperience of the mother can harm infants' growth and survival.

We focussed on the first 1.5 years of life of immature Guinea baboons, which is the infancy period according to our age category classification (i.e., "black infants": 0-6 months, and "brown infants": 6-18 months: Dal Pesco & Fischer, 2022). Due to the data structure (detailed in the methods section), we developed a novel analytical framework to account for infant age and gaps in the data when analysing ontogenetic processes. Our study aimed to provide essential comparative data on mothering style variation during infancy and its effects in a baboon species living in a tolerant multilevel society with female-biased dispersal. We predicted that the high inter-individual familiarity across sub-groups and the potentially lower prominence of social risks for infants in such societies would result in a more permissive mothering style compared to mothers in more despotic and nepotistic societies, such as the one of yellow baboons in Amboseli.

2.3 Methods

2.3.1 Data collection

2.3.1.1 Study subjects and field site

Behavioural data were collected near the facilities of the Centre de Recherche de Primatologie (CRP) Simenti, a field station of the German Primate Centre (DPZ), in the Niokolo-Koba National Park, Senegal (described in Fischer et al., 2017; Maciej et al., 2013) from April 2017 to December 2021. In addition, growth data were collected using Parallel Laser Photogrammetry from April 2019 to August 2021. The study subjects were all black infants (0-6 months) and brown infants (6-18 months) belonging to the study parties for a total of 80 study subjects (see Table A2.1 of the Appendix for a description of both black and brown infants). All individuals were habituated and identified by physical characteristics. Data were first collected on two parties, party 5 and party 6, since April 2017. In December 2018, party 9 was included in the data collection.

For safety reasons, researchers left the field site due to the COVID-19 pandemic from April 2020 to November 2020. Upon return, all the individuals could be re-identified. Four infants were born during the researchers' absence. For these individuals, we determined age based on patterns of change of natal coat and skin from black infant to brown infant (see Table A2.1 for more information on fur and skin coloration for black and brown infants).

When we returned to the field site, party 6 had split into party 6W and party 6I (data since December 2020 for both newly formed parties), and just a subset of party 9 was present, which was then called party 9B. Further, parties 13 and 15, for which we only had demographic but no behavioural data, were included in the behavioural data collection starting in February 2021. Demographic information and party composition changes were recorded daily.

2.3.1.2 Behavioural data

Behavioural observations were conducted daily, from 06:30 to 13:00 hours. Data were collected electronically on handhelds (Samsung Galaxy Note II GT-7100 or Gigaset GX290), using the software Pendragon version 7.2.21 (Pendragon Software Corporation, Chicago, IL, USA). We collected a total of 571 observation hours (5.13 median observation hours per individual; IQR: 2.005-11.693). We conducted 2371 focal behavioural observations (median: 15 minutes; IQR: 13.22-15.25 minutes) (focal-animal sampling: Altmann, 1974), in which we recorded all movements within a 1 m radius (i.e. approaches/leaves and, for mothers and their infants, overall time spent within 1m proximity), nipple contact bouts including attempts by the infant and rejections by the mother, carry bouts and including rejections by the mother, contact-sit and grooming bouts, protective behaviours (e.g. retrieve and restrain), rejection behaviours (e.g., mock bite and push away), and all aggressive interactions. The ethogram containing a detailed description of the collected behaviours can be found in Tables A2.2 and A2.3 of the Appendix.

2.3.1.3 Parallel Laser Photogrammetry and collection of arm-length measures

We used Parallel Laser Photogrammetry (PLP) to determine infant growth over time. PLP is a method that combines digital photography with the use of parallel lasers, by which body size measurements of wild animals can be determined. Morphometric measures have been obtained with PLP from marine mammals (e.g., killer whales, *Orcinus orca* [Durban & Parsons, 2006]), ungulates (e.g., Alpine ibex, *Capra ibex* [Bergeron, 2007]), and primates (e.g., chimpanzees, *Pan troglodytes* [Sandel et al., 2022]; western gorillas, *Gorilla gorilla gorilla* [Galbany et al., 2016]; mountain gorillas, *Gorilla beringei beringei* [Galbany et al., 2017; Richardson et al., 2022]; yellow baboons, *Papio cynocephalus* [Richardson et al., 2022]; Assamese macaques, *Macaca assamensis* [Anzà et al., 2022]; red colobus monkeys, *Procolobus rufomitratus* [Rothman et al., 2008]; geladas, *Theropitecus gelada* [Lu et al., 2016]; mantled howler monkeys, *Alouatta palliata* [Barrickman et al., 2015]). PLP is gaining popularity for measuring body size in wild animals since it is non-expensive, allows to obtain large amounts of data, and, importantly, is a non-invasive method that does not require anaesthesia or animal manipulation.

The strength of the PLP method, compared to other photogrammetry techniques, lies in the fact that the distance between the camera and the photographed object (i.e., object distance) does not need to be known. With PLP, laser pointers are set in a parallel orientation and are separated by a known distance (i.e., inter-beam distance), which remains equidistant regardless of the object's distance. Then, laser dots of paired lasers are projected on the body to be photographed, and a picture is taken. This method allows to take a larger number of pictures in a shorter time, compared to other photogrammetry methods in which the object distance needs to be measured with a laser distance measurement tool (e.g., laser range finder) every time a picture is taken (e.g., Breuer et al., 2007). The laser dots are then visible in the photography and provide a scale of known dimension that can be used to measure specific parts of the body of the study animal (Bergeron, 2007; Galbany et al., 2016, 2017; Richardson et al., 2022; Rothman et al., 2008).

In our study, PLP was used to measure the infants' length of the lower arm. We used a three-laser-based system in which the horizontal and vertical lasers were separated by 20 millimetres (inter-beam distance). Pictures were taken every month from April 2019 to August 2021 for 52 infants. See the Appendix for details about the PLP apparatus, body landmarks, and lower arm measurement in infant Guinea baboons (*Supplement PLP*, Fig. A2.1 and Fig. A2.2).

A total of 1878 infant pictures (31 median number of pictures per individual; IQR: 12-57.75) were analysed with ImageJ version 1.53k, an open software for scientific image processing and analysis (Schneider et al., 2012). ImageJ allowed us to calculate a length of interest, which in our case was the arm size in millimetres. The number of pixels between the paired lasers projected on the surface of the body (inter-laser distance) that appear in the photo is used as a scale (Richardson et al., 2022) since a relationship can be made between inter-laser distance and the already-known inter-beam distance (see formula below). The scale is then used to convert the arm size in pixels (determined by the distance between body landmarks) into arm size in millimetres (see formula below). Unfortunately, due to calibration issues in the field, only the horizontal paired lasers could be used as a scale (see *Supplement PLP* of the Appendix for details about calibration issues).

$$\boxed{\text{Arm length (mm)} = \frac{\text{inter-beam distance (mm)}}{\text{inter-laser distance (pixels)}} \times \text{Arm length (pixels)}}$$

Pictures were measured by four separate researchers that were trained in body landmark identification and picture measuring (for a detailed explanation of landmark identification and picture measuring, see *Supplement PLP* of the Appendix). Pearson correlations revealed an excellent inter-observer reliability for all measurers ($r = 0.98$, $N = 30$ pictures, $P < 0.001$). Frequently there were measures of arm lengths for several pictures taken from the same infant on the same day ($N = 273$ infant-day combinations; maximum of 14 measures per day). For these, we evaluated the range of the arm length measures taken for the same infant and date. The average maximum difference between two such measures was 7.3 mm (median), and the maximum difference was 24.2 mm.

2.3.2 Data preparation

We ultimately wanted to estimate the impact of mothering style on infant growth and survival. However, when the predictor, the response variable, or both change over time, a lack of homogeneity in the data is problematic (Box 1). This problem also occurred in the present study, where our predictor (mothering style) and one of our response variables (growth) changed with age. Here, we could not use mothering style and growth directly from the data because these would be confounded with infant age. We, therefore, first developed a method that allowed us to determine the mothering style and infant growth while controlling for infant age. After applying this method, we conducted our main statistical analysis.

2.3.2.1 Issues that arise when dealing with ontogenetic data and working with wild animals

When studying a period in which it is vital to consider the time scale, as in processes related to ontogeny, researchers often face a problem of lack of homogeneity in the data. Data homogeneity is even more challenging when working with wild animal populations since, for instance, it is impossible to monitor the animals constantly. When studying infancy, ideally, researchers should aim to have data for individuals that span from birth until the end of infancy (Fig. 2.1, Infant 1) at regular spaced and equal intervals for all infants. However, most of the time, researchers face a much less perfect but more realistic situation in which data are not equally available for all individuals for the entirety of the

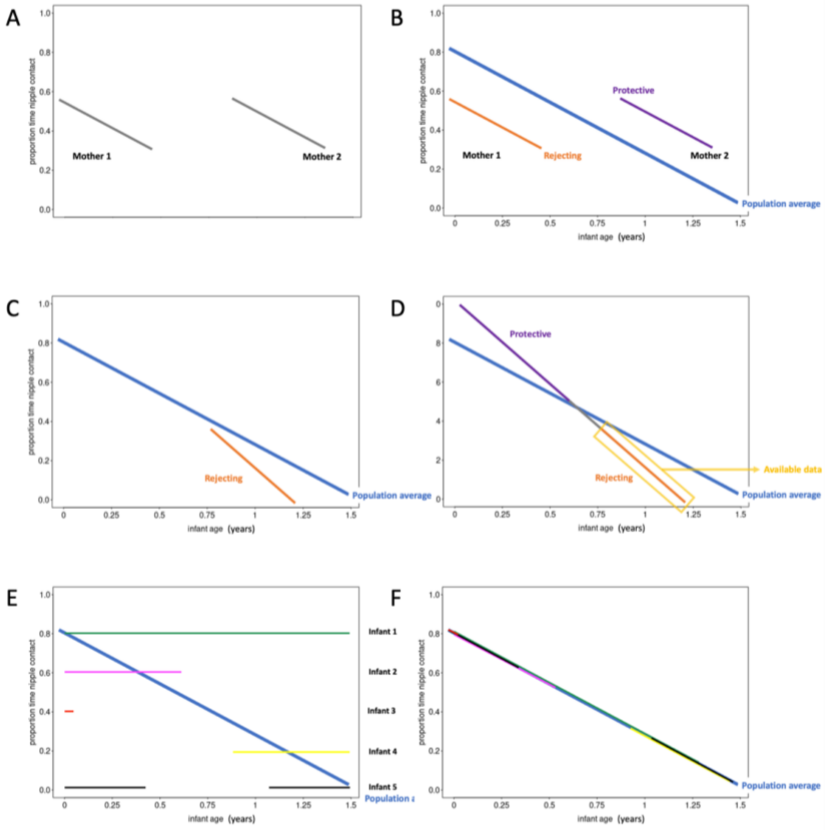
Box 1 | **Issues that might arise when not considering infant age and when data are not available data for the whole study period**

We further illustrate the issues that could arise as a result of not considering infant age when studying ontogeny and/or when data might not be available for the whole study period, as occurs when studying wild animals. We use nipple contact as an example, but any other maternal behaviours could be used to visually represent these situations:

If we do not consider infant age, mother differences might not be perceivable (A, B)
Two mothers (mother 1 and mother 2) might apparently behave in a similar way if we do not consider infant age (A). However, when taking into account infant age, the proportion of time that mother 1 is allowing her infant to be in nipple contact is actually below the population average (blue line, all plots), indicating this mother being rejecting (B, orange line). On the contrary, mother 2 is allowing more time in nipple contact than the average, being therefore a protective mother when infant age is considered (B, purple line).

We can only make claims about the data that we have (C, D)
We may only have data for a mother-infant dyad for a certain period of the ontogeny, in which the mother might be represented as rejecting because she is behaving below the average population (C). However, caution must be taken when assuming that this mother has been rejecting for the whole infancy period, because she might have behaved very differently in another moment of the infancy (D). Mothering style changes with ontogeny, therefore we can only interpret the data that we have available and assign a mothering style accordingly just for that period.

Individuals might be considered different as a result of having different observation periods (E, F)
Data for various infants might be available for different periods of the infancy (Fig. 2.1). Infant differences might be inferred, but they might just be the result of having different observation periods (E). However, if we would have had data for the whole infancy period, the different individuals might have actually behaved in very similar ways (F).



infancy period. This lack of homogeneity can, for instance, result from infants dying before reaching the end of infancy (Fig. 2.1, Infant 2) or shortly after birth (Fig. 2.1, Infant 3), in which case data would only represent the first stages of infancy.

Further, data may be available only for later infancy stages; this might happen in species with female-biased dispersal when mothers transfer with an infant into the study group (Fig. 2.1, Infant 4). Finally, gaps in the data might also cause a lack of homogeneity, which may be the result of study groups disappearing for weeks or months (Fig. 2.1, Infant 5). All these scenarios occurred on occasions in our study population, and although in most cases some groups were just not seen for a few days or weeks, one of the most extreme cases occurred when a sub-party of party 9 was not seen for ca. 10.5 months (324 days) between July 2018 until May 2019. Further, the COVID-19 pandemic also caused a gap in our data (see “Study subjects and field site” in the section “data collection”). Of the five infants represented in Figure 2.1, only *Infant 1* shows a complete representation of the infancy period.

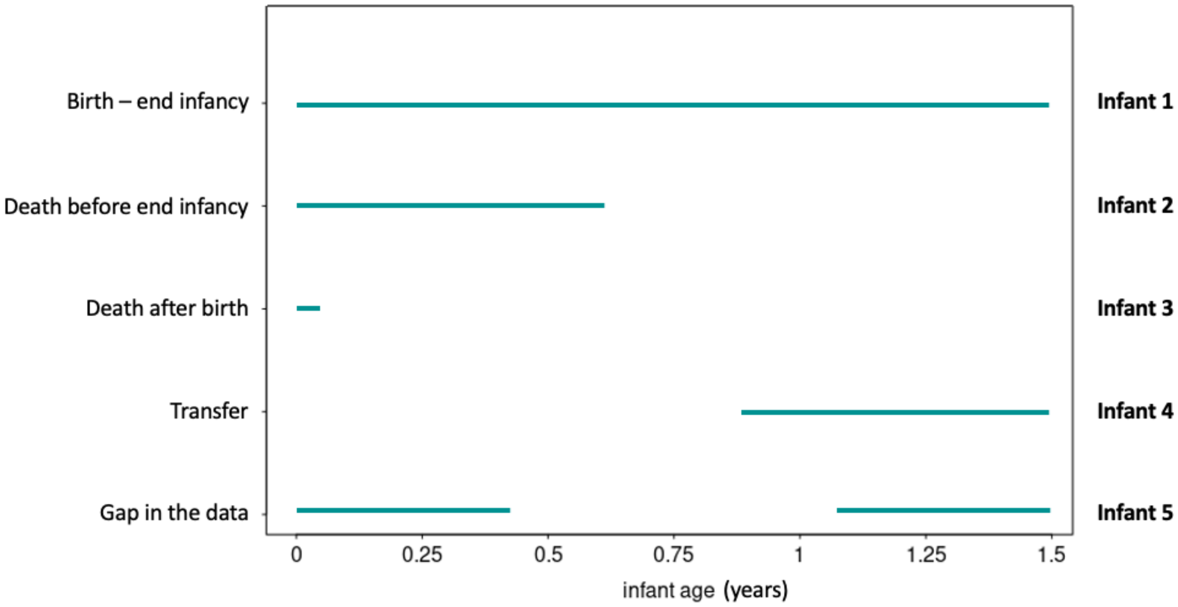


Figure 2.1. Schematic representation of the distribution of infant data obtained under field conditions. Infant 1 illustrates a complete representation of the infancy period, which goes from birth until the end of infancy (1.5 years in our example based on our study population). Data for Infant 2 and Infant 3 only comprise from birth until death, which occurs before reaching the end of infancy; Infant 3 dies shortly after being born, so its representation of the infant period is even smaller. Infant 4 represents the later stages of infancy and might be the consequence of a mother-infant dyad transferring to a study group. Finally, for Infant 5 there is a gap in the data, which might result from study groups not being seen for some time or interrupted data collection.

2.3.2.2 Age-corrected determination of mothering style

We first aimed to define the mothering style of the mothers in our study. Studies with non-human primates typically use Factor Analysis (FA) to identify factors that explain relationships between correlated maternal behaviours in order to obtain composite measures of mothering style (e.g., Altmann, 1980; Bardi & Huffman, 2002; Maestripieri, 1998; Tanaka, 1989). As we aimed to define the mothering style, which has a clear maternal perspective, we selected 15 behaviours according to the following criteria: 1) behaviours directed from the mother to the infant in case the behaviour could be bidirectional (e.g., grooming from the mother to infant, but not from infant to mother); 2) the mother had an active role in the behaviour (e.g., rejection of carrying, protection, rejection, cradling); 3) the mother influenced the occurrence of an infant's behaviour (e.g., nipple contact, carry); 4) mother and infant contributed equally (e.g., contact sit).

The seven state behaviours (i.e., behavioural durations) that we initially considered for the FA were the following: grooming, contact (derived from contact sit), mother and infant already/still at <1 m of proximity at the beginning/end of a focal behavioural observation (also referred here as "proximity-1"), mother and an infant in <1 m of proximity initiated by the mother (i.e., after the mother approached; also referred here as "proximity-2"), nipple contact, carry, and cradle (see Table A2.2 of the Appendix for the ethogram of the state behaviours). The eight event behaviours (i.e., behavioural counts) initially considered for the FA were the following: protection, rejection, nipple contact rejection, nipple contact attempt, carry rejection, aggression, leaves received (by the mother), and mother approaches followed by immediate infant leaves (see Table A2.3 of the Appendix for the ethogram of the event behaviours). Occasionally, both states and events were available for a given behaviour (e.g., nipple contact); in these cases, only durations were selected, as they are more informative than frequencies.

Data were available for 80 infants (45 females and 35 males) and 49 mothers. For 16 infants, their mother was primiparous, and for 54 infants, their mother was multiparous; parity was unknown for the mothers of ten infants (age categories for these mothers were one young, eight mature, and one old adult female). Four of the 49 mothers transferred to another unit during the study period, and the infant did not follow her; one mother died. The mothers of 17 infants were young, those of 50 were mature, and those of 13 were old (see Table A2.1 of the Appendix for a description of young, mature, and old adult females). Our dataset consisted of 580 data points, and each data point represented the monthly aggregate behaviours of a mother-infant dyad.

To control for infant age and deal with the issues previously mentioned (Fig. 2.1; Box 1), we fitted one Generalized Linear Mixed Effects Model (GLMM) for each of the behaviours initially considered for the FA, in which the fixed effect was infant age. Five event behaviours were infrequent and excluded from the modelling, namely: carry rejection (25 cases of 580; 4.3% of observations), nipple contact rejection (51 cases of 580; 8.9% of observations), nipple contact attempts (31 cases of 580; 5.3% of observations), aggression (9 cases of 580; 1.5% of observations) and mother approaches followed by immediate infant leaves (15 cases of 580; 2.3% of observations).

For the remaining ten behaviours for which we fitted a GLMM, the response was the maternal behaviour, and random intercept effects were mother ID and infant ID. The random intercept of mother ID accounted for the different mothers in the study. The random intercept of infant ID was important for mothers with more than one infant in the sample. It accounted for 1) the contribution of the infants to the variation of mothering style and 2) the contribution of the mothers to the variation in mothering style. The latter could be due to potential differences of the mother towards their different infants. The model also included random slopes of age within mother ID and age within infant ID to account for variation in the effect of age on mothering style between mothers and infants (Barr et al., 2013; Schielzeth & Forstmeier, 2009). The model, therefore, determined the effect of infant age on the mothers' behaviours and the contribution of differences between mothers and infants concerning the mothering style. At the same time, these GLMMs allowed us to explore infant development with regard to the mother-infant behaviours and their monthly changes, which are explained in more detail in the results section 2.4.1. Information about model specification and model outputs can be found in the Appendix (Fig. A2.3, Fig. A2.4, Fig. A2.5, Fig. A2.6, Fig. A2.7, Fig. A2.8, Fig. A2.9, Fig. A2.10, Fig. A2.11, Fig. A2.12; Table A2.5)

For the state behaviours, proportions of time were determined from durations in relation to observation time, and the models were fitted with a Beta error distribution and logit link function (Bolker et al., 2009; McCullagh & Nelder, 1989). For the event behaviours, the response was considered a count, and we fitted the models with Poisson error distribution and log link function. To account for varying observation durations per month, we included the logarithm of the monthly observation duration as an offset term (McCullagh & Nelder, 1989). In some of these models, the response was overdispersed given the fitted model (average of dispersion parameters: 1.55; range: 0.68-5.29; maximum dispersion parameter for variables used as mothering style: 0.91. A complete overview of the dispersion parameters for all the models is given in Table A2.4 of the Appendix). Parameters for correlations between random intercepts and slopes were excluded from the models whenever they revealed a high correlation. These correlations were considered separately for the random effect of mother ID and infant ID.

From these models, we obtained Best Linear Unbiased Predictors (BLUPs; Baayen, 2008), which were eventually entered into the FA. The BLUPs are the estimated deviations of intercepts and slopes from the common average per level of grouping factor. Therefore, in our study, the BLUPS are the estimated deviations of intercepts and slopes for every mother ID and for every infant ID from the common average intercept and slope for mothers and immatures, respectively. We included only BLUPs estimated for random intercepts but not those estimated for random slopes in the subsequent analyses. The reason was that the BLUPs for the random intercepts inform about deviations of the individual mothers' mothering styles from that of the average mother.

For each model, we first inspected the estimated standard deviation of the random intercept effects of mother ID and infant ID (see *Supplement mother-infant behaviours* for detailed information on the models, estimated standard deviations for random effects, and figures for each behaviour). When both standard deviations were below 0.1, we omitted the respective BLUPs in further analysis. Such a low standard deviation indicates little variation between mothers or infants regarding mothering style. Low standard deviations were observed for grooming, cradling, and proximity (<1 m, after the mother approached; proximity-2). Two behaviours were excluded from further consideration because data were not available for all the infants of the study: protection and rejection (64 infants, 45 mothers). The behaviours that showed standard deviations larger than 0.1 for the mother ID or the infant ID random intercept effects and, therefore, indicated enough mother variation were: 1) contact, 2) carry, 3) proximity (<1 m at the beginning/end of a focal behavioural observation; proximity-1), 4) leaves received, and 5) nipple contact. The BLUPS of these five behaviours were then considered in an additional step before the FA, in which we inspected their correlations (Fig. 2.2).

Factor Analysis

Before conducting the FA, we plotted the behaviours contact, carry, proximity (<1 m at the beginning/end of a focal behavioural observation; proximity-1) leaves received, and nipple contact against one another and inspected the correlations between them (Fig. 2.2, Table A2.6). After doing so, we could establish that the behaviours contact, proximity-1 and nipple contact were correlated to one another (min. correlation = 0.66; see Table A2.6). Therefore, we conducted the FA with these three behaviours, with a one-factor solution and varimax rotation. The resulting factor had an Eigenvalue of 2.1 and explained 70% of the total variance. The loadings of the three variables on the single factor were 0.88 for contact, 0.79 for proximity-1 and 0.84 for nipple contact. From the results of the FA, we extracted the specific mother-infant dyad factor scores, which we used later in our main models as one of the measures of mothering style. The other two variables, carry and leaves received, were uncorrelated to the other variables and with each other and were taken as a second and third quantitative measure of mothering style (Fig. 2.2, Table A2.6).

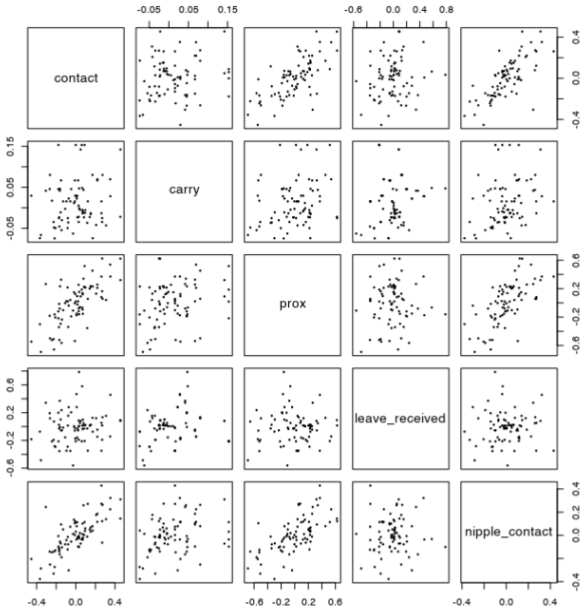


Figure 2.2. Scatter plot depicting the correlations between the behaviours that showed enough variation between mothers (i.e., >0.1 Standard Deviation). Each point represents the BLUPs for the random intercept effects of the 580 aggregated measures.

2.3.2.3 Age-corrected determination of infant growth

Infant growth, which was the response variable for one of our two main models, also needed to be corrected for age because growth changes with ontogeny and because we faced again a problem of lack of homogeneity in our dataset (detailed in the section 2.3.2.1).

Our dataset consisted of N = 1878 PLP pictures obtained from 52 infants, with measures of the length of the lower arm of infant Guinea baboons. We wanted to use infant growth rather than infant size because growth represents the size change over time. Differences in sizes between individuals of the same age can be based on genetic differences rather than conditions affecting infant development. However, growth changes within individuals compared to the average population growth for infants of the same age are a better indicator of infant development.

We first plotted all the arm length sizes obtained from the pictures and identified the infant growth curve in Guinea baboons aged up to 1.5 years, which followed an exponential function with decreasing pace (Fig. 2.3). Of the 52 infants used to determine the infant growth curve, one was excluded from all other analyses (including behaviours for determining mothering style, explained above) since we did not have behavioural data for this individual.

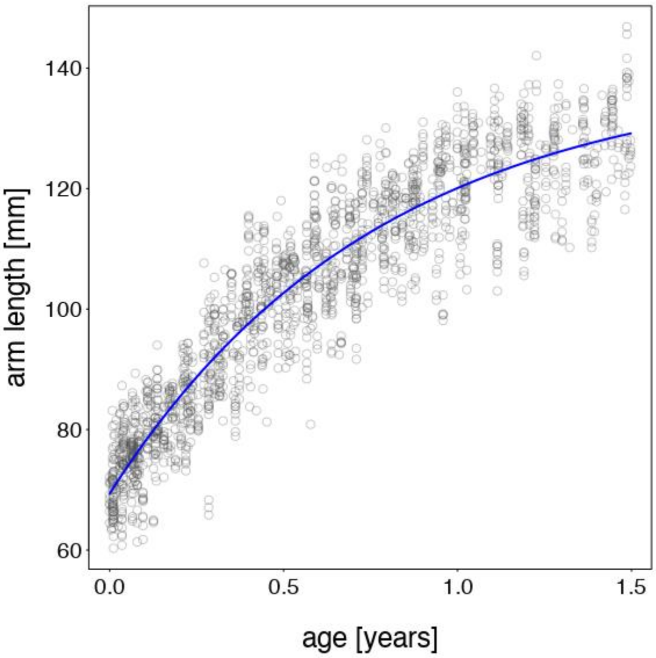


Figure 2.3. Growth curve obtained from plotting the lower arm length of our sample of infant Guinea baboons. Grey dots represent the 1878 PLP pictures obtained from 52 infants, and the blue line represents the average population growth curve, which follows an exponential function with decreasing pace.

Next, we expressed infant growth as its deviation from the average growth of infants of the same age. To this end, we fitted a non-linear mixed effects model, in which the response was the arm length measure, and the principal predictor was infant age. We parameterized the dependency of size from infant age as follows:

$$\boxed{\text{Arm length} = c + a \times b^{age}}$$

where *c* is larger than 0, *a* is smaller than 0, and *b* ranges between 0 and 1. In the model, we let the coefficients *c*, *b* and *a* vary between infants. We modelled them as random effects, which implies that they are assumed to originate from a normal distribution with a standard deviation to be estimated. The model eventually provides estimates for the values of *c*, *a*, and *b* in the population of infants and also how each infant deviated from the population level values of *c*, *a*, and *b*. Next, we extracted the individual-specific infant growth parameters from the fitted model. As the last step, we determined the instantaneous fitted growth (i.e., the derivative of the fitted model) of each infant for each day between its first and last arm length measure, then subtracted from each of the values the population level growth at the same day, and finally averaged the deviations (Fig. 2.4). Hence, these values, which are the slope differences, express how fast an infant grew compared to an average infant of the same age (i.e., the relative infant growth). The slope differences were then used as a response in our growth models.

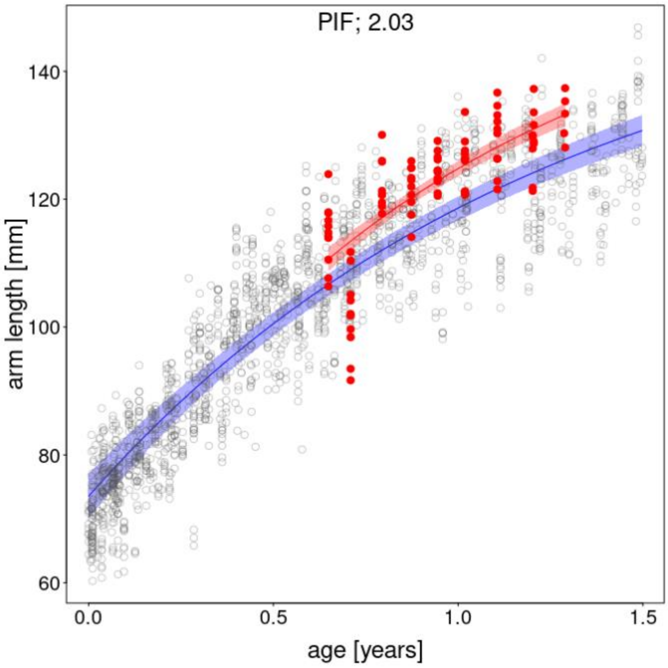


Figure 2.4. Growth from birth until 1.5 years of age, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average of infants (*N* = 51 infants, 1878 PLP pictures), and the red line depicts the fitted model for a single infant for the period that data were available for that specific individual. In the plot, the red line and red dots represent the infant named PIF (indicated at the top of the plot, together with the value of the slope difference next to it). Shaded areas in blue and red represent the bootstrapped 95% confidence intervals of the fitted model. Grey circles represent arm-length measurements (indicated in millimetres) for all the infants of the population (i.e., each grey circle is a measurement obtained from a PLP picture for a specific day), and red dots depict measurements for the specific infant considered in the plot. In the plot, the red line is steeper (i.e., positive values of slope difference) than the blue line, indicating that the infant grew faster than the population average growth compared to infants of the same age. In contrast, a red line that would be less steep (i.e., negative values of slope difference) than the blue curve would indicate that an infant grew more slowly than the population average. A red line above the blue line represents an infant whose arm length is longer than the average for individuals of the same age, and a red line below the blue depicts an infant whose arm length is shorter than the average for individuals of the same age.

2.3.2.4 Control predictors

1. Infant sex

We included infant sex as a control predictor because we wanted to examine potential differences in growth and survival depending on the sex on the infants, for instance, those due to early emergence of sexual dimorphism. Infant sex was a categorical variable with two levels: female and male.

2. Unit size

The unit size was included as a control predictor on the premise that females compete over access to the primary male, and infant protection is one of the resources males can provide. The unit size was calculated by computing the weighted average number of adult and subadult females associated with the primary male of the unit where the infant belonged throughout the study period; if changes in unit ID occurred, these were considered.

3. NDVI

We controlled for environmental conditions due to the potential effect of food availability on the infant survival and growth. Senegal has a pronounced seasonality: a rainy season from June to October and a dry season from November until April. Rains are primarily concentrated in the rainy season (Fischer et al., 2017), with an average annual precipitation of 956 mm (Zinner et al., 2021). The Guinea baboons' home ranges and daily travel distances increase in the rainy season (Zinner et al., 2021). Seasonality is reflected in plant productivity, notably constrained during the dry season, and highly pronounced during the months of rain. Seasonality strongly impacts food availability in other baboon species (Alberts et al., 2005).

The Normalized Difference Vegetation Index (NDVI) was used as a proxy for food availability. The NDVI is a widely used bio-geophysical indicator of the land's green plant coverage - or vegetation density - and, therefore, it is considered an indirect measure of rainfall. The NDVI products were obtained from the Copernicus Global Land Service (CGLS) (https://land.copernicus.eu/global/), which is part of the Earth Observation programme of the European Commission. We downloaded the NDVI products at 300 m spatial resolution from 2016-2022 (accessed in July 2022); although the behavioural data for the infants of the study were first collected in 2017, we included NDVI data since 2016 because some of the infants in the survival model had been born during that year. Values of NDVI were based on a 10-day maximum composite value derived from daily acquisitions of Earth land surface reflectance observations from the sensor PROVA-B (product version 1, from 2016-2020:

Swinnen & Carolien, 2016) and sensor Sentinel-3 OLCI (version 2, from 2021: Swinnen & Carolien, 2022).

We limited values of NDVI to our study region (Lat 13°0’14.252'' to 13°5'39.647''; Long -13°13'24.813'' to -13°18'54.438'') and used the function ncvar_get of the package ncdf4 (version 1.19: Pierce, 2021) in R (R Core Team 2022) to extract the NDVI values from the downloaded files. We excluded non-optimal observations (digital value >250), which created interferences due to their origin in cloud coverage and ocean. In case of missing NDVI values, we computed a linear interpolation between the last and next days for which we had available data (Fig. 2.5). The daily NDVI values were later used as a control fixed effect for our main growth and survival models.

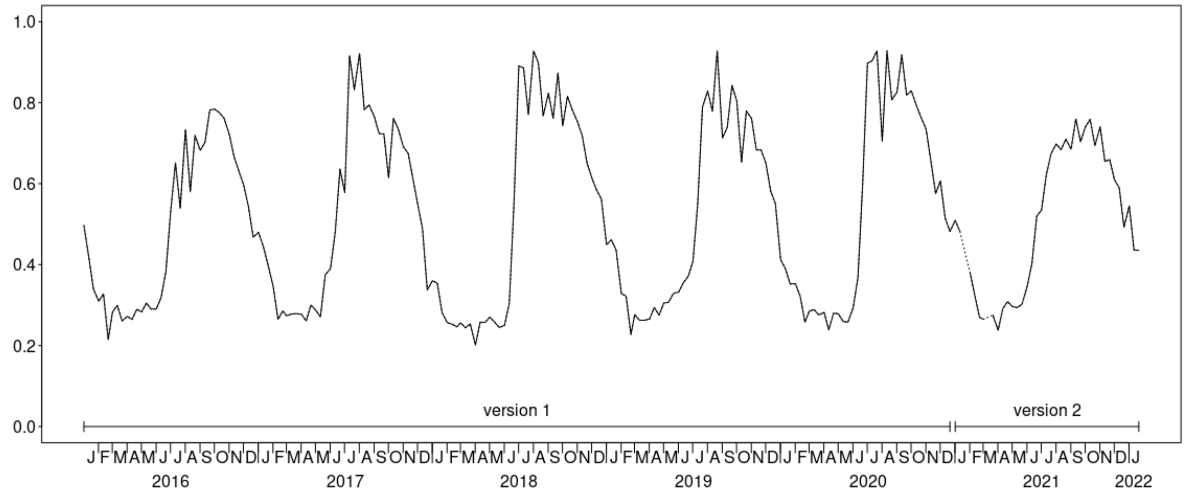


Figure 2.5. NDVI values in the study region during the study period extracted from versions 1 and 2 of the Copernicus Global Land Service (CGLS). Note the pronounced seasonal variation in plant productivity, being lowest in the driest months (March-May) and most pronounced in the rainy season (June-October). The dashed line represents interpolated values.

To control for the fact that we used both versions of the NDVI, we created an additional indicator variable which denoted whether the actual NDVI value for a given day was determined using version 1 or version 2. Since some of the daily NDVI values were interpolated between NDVI version 1 and 2, the indicator variable denoted the relative contribution of NDVI version 2 to a daily NDVI value. This step seemed important because the two versions of NDVI were not 100% comparable.

4. Parity

We included mother parity because differences in maternal experience can potentially influence infant growth and survival. Parity was defined as a categorical variable with two levels: primiparous (i.e., mothers that gave birth to one infant) and multiparous (i.e., mothers that gave birth to more than one infant). Because multiparous mothers are more experienced, maternal care should be optimized and infant growth and survival enhanced, compared to primiparous mothers. We decided to use parity instead of mother age because we do not have precise age data for many mothers in our study population. First, the habituation of the animals started in 2007, and we began to identify females in 2011 individually. Therefore, we only have exact birth dates since then. Second, due to female-biased dispersal, many females transfer to our study population from other groups, making it impossible to know their age with certainty. For the same reason, we did not know parity for all the mothers. Therefore, we only included those females for which parity information was certain and fitted the models with a subset of the data. However, for informative purposes, we provide some information about maternal age in the results section (see Table A2.1 of the Appendix for a complete description of maternal age, defined according to our age category classification: young, mature, and old adult female: Dal Pesco & Fischer, 2022).

2.3.3 Statistical analysis

All statistical analyses were conducted in the R environment (version 4.2.0: R Core Team, 2022) in the RStudio interface (version 2022.2.3.492: RStudio Team, 2022). For Linear Mixed Effects Models (LMM) and GLMMs (Baayen, 2008) we used the “lmer” and “glmer” functions of the R package “lme4” (Bates et al., 2015). Beta models were fitted with the “glmmTMB” function of the package “glmmTMB” (Brooks et al., 2017). For the survival analysis, we used the “coxme” function of the package “coxme” (Therneau, 2022). Model stability was assessed using a function that Roger Mundry provided. Bootstrapped confidence intervals of model estimates and fitted values were obtained with the function “bootMer” of the package “lme4” or the function “simulate” of the package glmmTMB. We determined degrees of freedom and *P*-values for the LMMs using the function “lmerTest” from the package “lmerTest” (Kuznetsova et al., 2017).

2.3.3.1 Growth and survival

We wanted to test if mothering style affected infant growth and survival. To analyse the influence of mothering style on 1) infant growth, we fitted a LMM (Model 1a), and on 2) infant survival, we fitted a survival analysis (Cox proportional hazards model) (Model 2a). For both of these models, the test predictors were the three variables that represented mothering style: factor scores, carry, and leaves received. The control fixed effects were infant sex, unit size, and NDVI and its interaction with the indicator variable denoting the version of the NDVI.

From our initial sample of 80 infants, one infant was excluded from all the growth and survival models because of unit ID uncertainty: the mother had transferred to a different party, and the infant had not followed her; however, it was not possible for us to assess to which unit the infant belonged after the mother had transferred since the infant was seen associating with several units. The resulting sample for the survival model comprised 79 infants (44 females and 35 males) and 48 mothers. The unit membership was the same throughout the study period for 69 infants; for ten infants, there was a unit change (average transfers: 2; maximum transfers: 4). For the additional model including mother parity, the sample size was 69 infants (40 females and 29 males). Mothers of 16 infants were primiparous, and mothers of 53 infants were multiparous. For the growth model with a subset of the data, the sample size consisted of 50 infants (25 females and 25 males) and 35 mothers. Throughout the study period, the unit was the same for 43 infants, and there was a change of unit for 7 of the infants (average transfers: 2; maximum transfers: 4). For the additional model including mother parity, the sample size was 43 infants (24 females, 19 males), and mothers for nine infants were primiparous and 34 multiparous. If an infant changed the unit during the period considered for all survival and growth models, we assigned it to the unit to which it belonged longer.

In all models, mother ID and unit ID were included as random intercept effects to account for repeated measures, as they might appear several times in the dataset. To reduce Type I error rates, we checked for theoretically identifiable random slopes (Barr et al., 2013; Schielzeth & Forstmeier, 2009). However, no random slope components were identifiable for any of the models.

We included mother parity as an additional fixed effects control factor in two further models for growth (Model 1b) and survival (Model 2b). We fitted these models with a subset of the original data set because we did not have information regarding parity for all the mothers in our study; parity was known for 43 of the 49 mothers in our study, which were the mothers of 70 of the 80 infants of the initial dataset (45 females, 35 males). Asides from the addition of parity, the model structure was the same as in Model 1a and 1b.

Before fitting a model, we inspected whether the distribution of the response variable (in LMMs) and the quantitative predictors was roughly symmetrical. No log-transformations were required. To ease model convergence and the comparison of the estimates, we *z*-transformed all the covariates to a mean of zero and a standard deviation of one before fitting each model (Schielzeth, 2010). After fitting the models and before conducting inference, several diagnostic validations were performed that revealed no deviations from the assumptions of normality and homoscedasticity of residuals of the LMM, which we assessed by visually inspecting a QQ-plot of residuals (Field, 2005) and scatterplots of residuals fitted against fitted values (Quinn & Keough, 2002). Model stability was evaluated by comparing the estimates obtained when running the models with the levels of the random effects excluded one at a time with the ones obtained for the complete data set (Nieuwenhuis et al., 2012). These analyses showed that the models were of acceptable stability.

As a general test of the significance of mothering style and in order to avoid “cryptic multiple testing” (Forstmeier & Schielzeth, 2011), we conducted a full-null model comparison, whereby the null model lacked the three fixed effect predictors of mothering style (Factor scores, carry and leaves received), but aside from that, was identical to the full model. We used a likelihood ratio test for the full-null model comparison (Dobson, 2002). We employed the Satterthwaite approximation to test for the effects of the individual fixed effects in LMMs (Luke, 2017). To this end, we refitted the models with restricted maximum likelihood. For the survival analysis, we determined the significance of the individual fixed effects by dropping them from the model one at a time (R-function “drop1”).

2.4 Results

2.4.1 Development of behaviours between mothers and infants throughout infancy

In our population of wild Guinea baboons, some behaviours between mother and infant rarely occurred and barely changed during the 18 months of infancy, while others slightly decreased, steadily increased, or considerably decreased over time. Grooming rarely occurred and remained at low levels throughout infancy. Around the time of birth (month 0), mothers groomed their infants 2.2% of the time. Grooming amounted to 2.3% at month six, 2.4% when infants were one year old, and 2.5% at month 18 (Table A2.5). These patterns closely resemble the average amount of grooming males exchange with other males (2.41%) and females (2.94%), suggesting that the amount of grooming exchanged in our population seems stable throughout the lifespan. Other behaviours between infants and mothers that were infrequent and stayed practically unchanged were rejection behaviours (e.g., mock bite, push away), proximity (<1 m, after the mother approached; proximity-2), and cradle. For more information on the development of these behaviours over the 18 months of infancy, see Table A2.5 of the Appendix. Furthermore, carry rejection, nipple contact rejection, nipple contact attempts, aggression, and mother approaches followed by immediate infant leaves were very infrequent, which were the behaviours that were excluded from the modelling for this reason.

Protective behaviours (i.e., retrieve, restrain), which are most frequent when infants are more vulnerable and dependent, experienced a slight decrease throughout infancy. During the first month of life, protective behaviours occurred at 2.92 times per hour, and the behaviour experienced a noticeable decrease until month 3, in which the occurrence was 0.88 events per hour. When infants were six months old, protective behaviours occurred 0.26 times per hour and remained low until the end of infancy, reaching values of <0.01 times per hour when infants were 18 months old. See Table A2.5 of the Appendix for detailed information on the monthly development of protective behaviours.

Leave behaviour by the mother (i.e., events in which mothers moved to >1 m away from their infants), which is to be expected when infants are moving towards the independence of their mothers, steadily increased during infancy. Mothers left their infants 1.29 times per hour by the time of birth (month 0). Leaves by the mother increased to 2.06 events per hour at the six months of age, to 3.29 times per hour by the time infants were one year old, and to 5.25 by the end of infancy (month 18) (Fig.2.6; see Table A2.5 of the Appendix for detailed information on the monthly development of the behaviour).

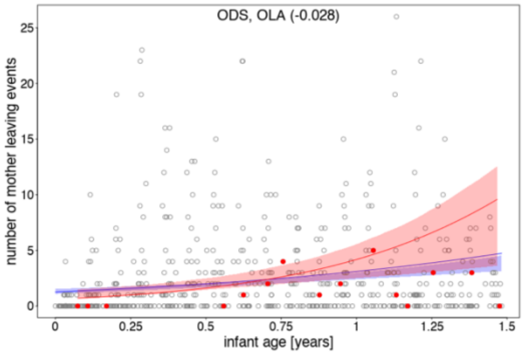


Figure 2.6. Leave behaviour by the mother (i.e., events in which mothers moved >1 m away from their infants; indicated as the number of events per hour) increased throughout infancy. The blue line represents the fitted model for the population's average. The red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 data points). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad. The ID of the mother and infant (i.e., mother-infant dyad) is indicated at the top of the plot, with a three-letter code for each individual (e.g., ODS: mother; OLA: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals.

Finally, carry, nipple contact, contact, and proximity (<1 m at the beginning/end of a focal behavioural observation; proximity-1), which are behaviours that are typically frequent when infants are most dependent on their mothers and whose decline is considered an indicator of weaning, considerably decreased throughout infancy (Fig. 2.7). For instance, infants were carried by their mothers 41.4% of their time just after they were born (month 0). At six months of age, carry decreased to 23.5% and continued to decrease to 11.9% of the time when infants were one year old and to 5.5% by the end of infancy (month 18) (Fig. 2.7, A). Also, infants spent 49.6% of their time in nipple contact with their mothers just after they were born (month 0), and by six months, nipple contact decreased to 28.4%. When infants were 12 months old, time in nipple contact was 13.7%, and by the end of infancy (18 months), it was only 6% (Fig. 2.7, B; Table A2.5). For more information on the development of carrying, nipple contact, contact, and proximity (<1 m at the beginning/end of a focal behavioural observation; proximity-1), see Table A2.5 of the Appendix.

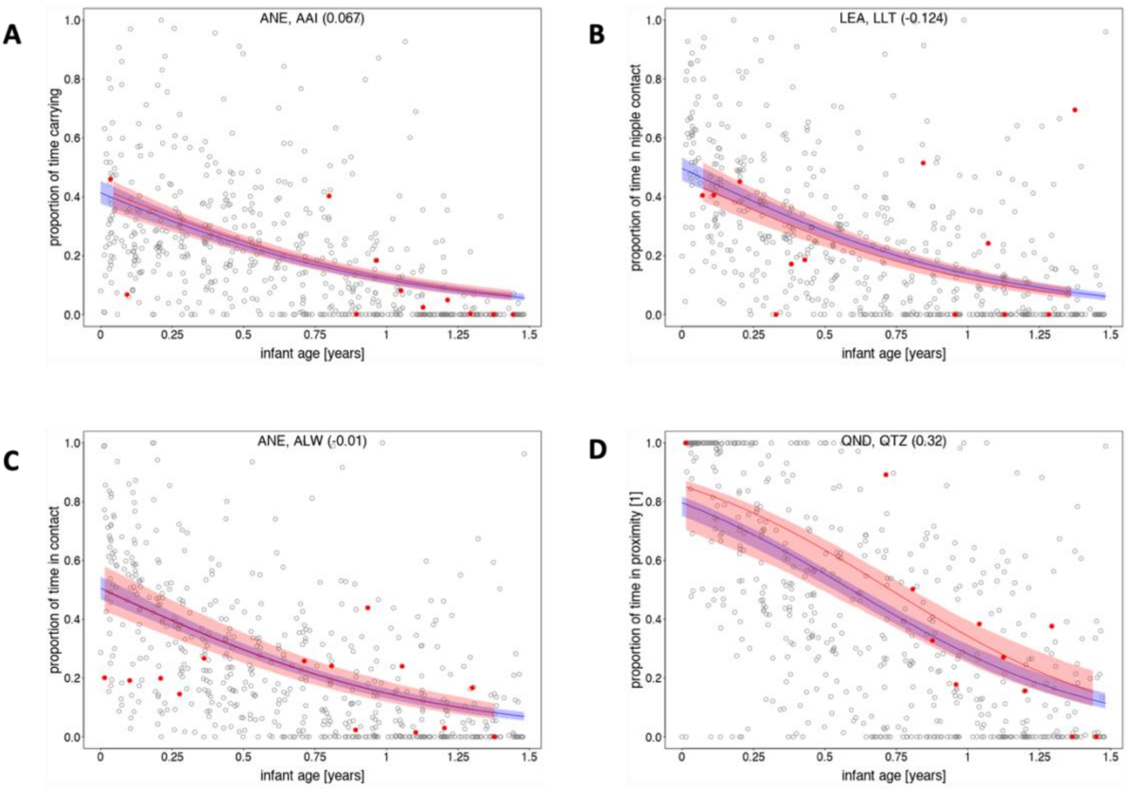


Figure 2.7. Behaviours that considerably decreased during the infancy period. (A) Carry, (B) nipple contact, (C) contact, (D) proximity (<1 m at the beginning/end of a focal behavioural observation; proximity-1). All behaviours are indicated as proportions of time. For all plots, the blue line represents the fitted model for the population average. The red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints, for all behaviours). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for a specific mother-infant dyad. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., ANE: mother; AAI: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals.

Of the behaviours mentioned above, leaves by the mother (i.e., events in which mothers moved >1 m away from their infants), carry, nipple contact, contact, and proximity (<1 m at the beginning/end of a focal behavioural observation; proximity-1) were the ones that were ultimately implemented to define the mothering style, which was the main predictor in our models. These behaviours were selected because they showed considerable maternal variation (SD > 0.1 for the random intercept effects of mother ID and infant ID) after we fitted GLMMs controlling for infant age. The mothering style was characterized by the factor scores obtained from the factor analysis (contact, nipple contact and proximity-1 correlations), along with carry behaviour and leaves by the mother (see section 2.3.2.2 for a detailed explanation of the GLMMs and mothering style determination).

2.4.2 Infant growth

Of the 50 infants for which we had growth data, 29 grew faster than the population average, and 21 grew more slowly. Sex did not seem to have an effect on growth, since we did not find evidence for differences between sexes among faster and slower growth groups. Mother parity and age did not appear to have a detrimental effect on growth since primiparous females also were able to produce offspring that grew faster than the population average. Table 2.1 contains a summary of the distribution of infant sex, infant status (i.e., alive, dead), mother parity, and mother age of those infants that grew faster and slower than the population average.

Infant death occurred similarly in the group of infants that grew faster than the average population (four infants) and in the group that grew more slowly (three infants), which suggests that infant death is not necessarily linked to growth speed. Information about the infants that died can be found in Table 2.2 and Table 2.3.

The lower arm of the infants measured, on average, 73.74 mm (min: 60.30; max: 89.32) just after they were born (month 0). By the end of infancy, it measured 130.6 mm on average (min: 116.53; max: 146.85). Therefore, from birth to the end of infancy, the lower arm of infants increased by 56.9 mm on average. In our population, the individual that grew slower had a slope difference in the growth curve of -5.62 (Fig. 2.8, A), and the individual that grew faster had a slope difference of 8.8 (Fig. 2.8, B).

Table 2.1. Growth summary and related demographic information

	Faster growth than population average[1]	Slower growth than population average[2]
Total individuals	29	21
Infant sex		
Females	16	9
Males	13	12
Infant status		
Alive	25	18
Dead	4	3
Mother parity		
Primiparous	5	4
Multiparous	22	12
Unknown	2	15
Mother age		
Young	5	14
Mature	21	13
Old	3	4

[1] Mean: 2.929, median: 2.073, range: 0.127 – 8.80, IQR: 0.8367 – 4.421; expressed in slope differences, which is our growth measure

[2] Mean: -1.674, median: -1.269, range: -5.621 – -0.001, IQR: -2.191 – -0.740; expressed in slope differences, which is our growth measure

Table 2.2. Infants that grew faster than the population average and died

Infant case	Sex	Mother parity	Mother age	Infant age at death (days)	Growth (slope difference)
1	Male	Multiparous	Mature	156	0.127
2	Female	Multiparous	Mature	230	3.465
3	Male	Multiparous	Mature	212	4.421
4	Female	Multiparous	Mature	13	6.848

Table 2.3. Infants that grew more slowly than the population average and died

Infant case	Sex	Mother parity	Mother age	Infant age at death (days)	Growth (slope difference)
1	Male	Multiparous	Old	38	-0.368
2	Male	Multiparous	Mature	388	-1.269
3	Male	Multiparous	Old	36	-0.740

The main growth model (Model 1a) revealed no obvious effect of mothering style on infant growth: the full model with the three test predictors (i.e., factor scores, carry and leaves received) did not explain the data better than the null model (full-null model comparison: χ^2 = 2.800, *df* = 3, *P* = 0.423; Table 2.4). When examined individually, none of the three test predictors representing mothering style had an obvious effect on the growth of the infants: although there was high variation in the response, the fitted values did not strongly change with increasing Factor scores (*P* = 0.656; Fig. 2.9, A; Table 2.4) or when being carried by their mothers for longer (*P* = 0.729; Fig. 2.9, B; Table 2.4) and increased only slightly when receiving more mother leaves (*P* = 0.236; Fig. 2.9, C; Table 2.4). Detailed information on the model specification for the main growth model (Model 1a) can be found in the section *Supplement models* of the Appendix.

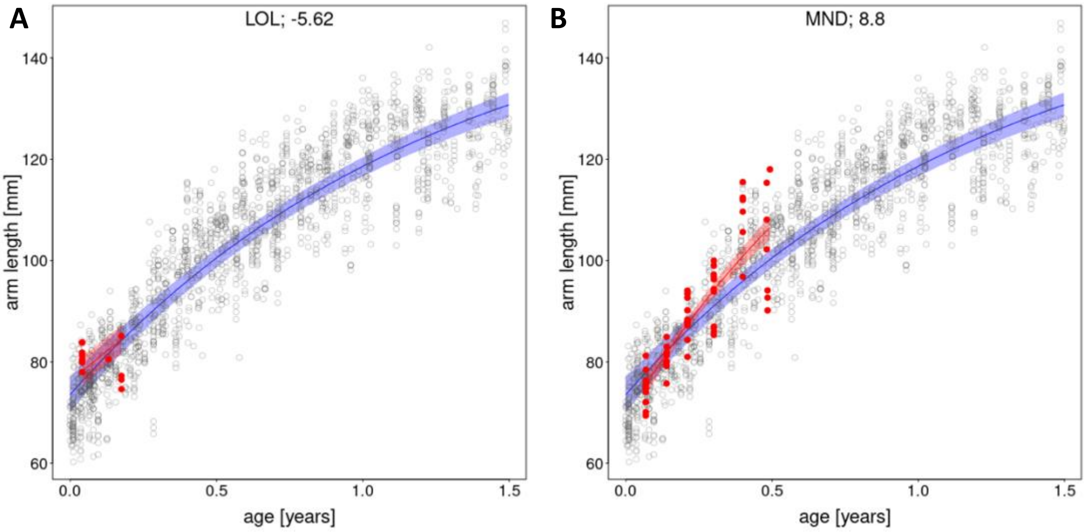


Figure 2.8. Slowest and fastest growth curves in our population of infant Guinea baboons. (A) The individual LOL had the slowest growth in our population, with a slope difference in the growth curve of -5.62. A red line being less steep (i.e., negative values of slope difference) than the blue curve indicates an infant that grew slower than the population average. (B) The individual MND had the fastest growth, with a slope difference in the growth curve of 8.8. A red line that is steeper (i.e., positive values of slope difference) than the blue line indicates that the infant grew faster than the population average growth compared to infants of the same age. The ID of each specific individual and the value of the slope difference is indicated at the top of each plot. In each plot, the blue line represents the fitted model for the population average of infants (*N* = 51 infants, 1878 PLP pictures), and the red line depicts the fitted model for an infant for the period that data were available for that specific individual. Shaded areas in blue and red represent the bootstrapped 95% confidence intervals of the fitted model. Grey circles represent arm-length measurements (indicated in millimetres) for all the infants of the population (i.e., each grey circle is a measurement obtained from a PLP picture for a specific day), and red dots depict measurements for the specific infant considered in the plot. A red line above the blue line represents an infant whose arm length is longer than for individuals of the same age, and a red line below the blue depicts an infant whose arm length is shorter.

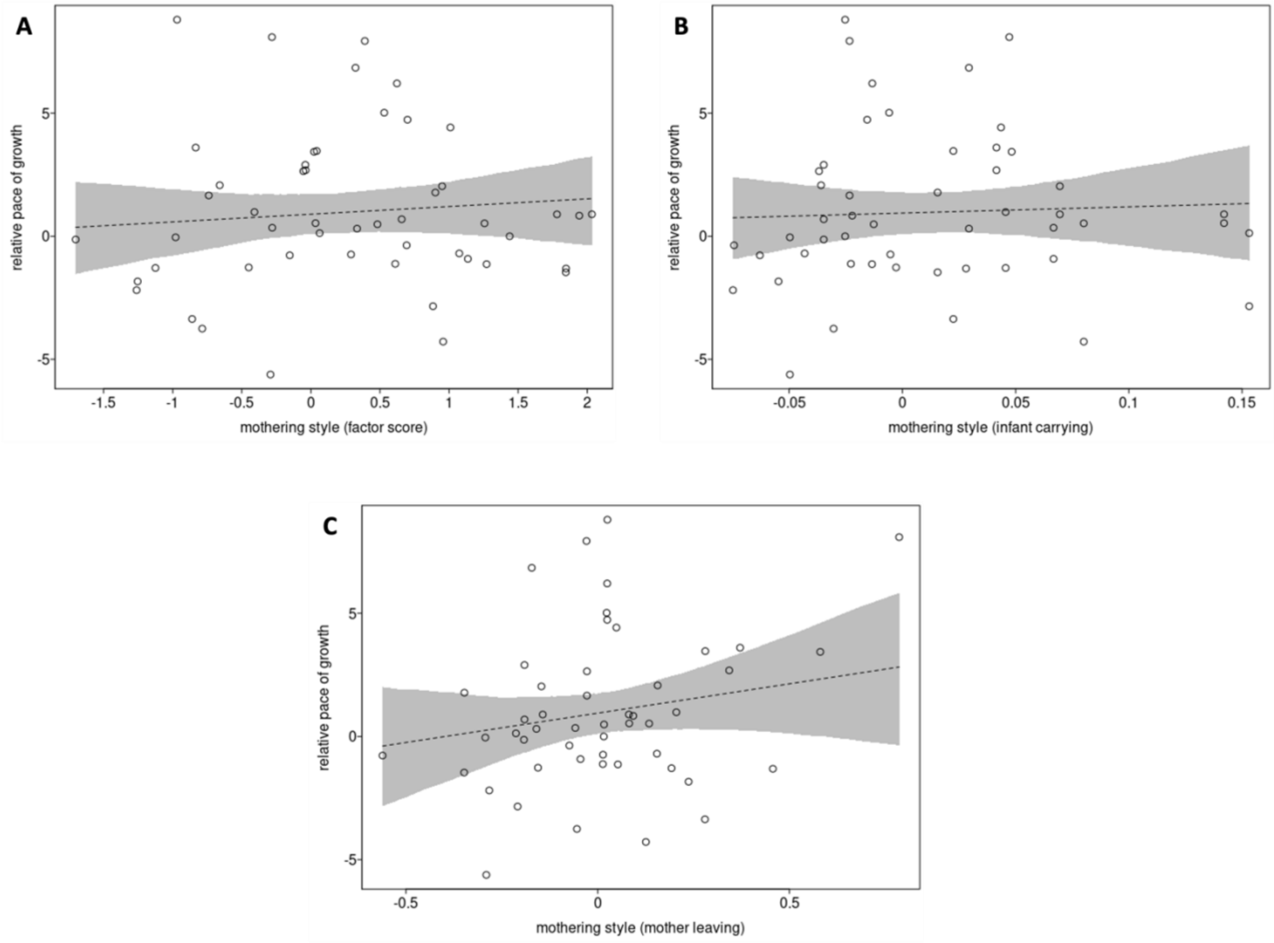


Figure 2.9. Relationship between the relative pace of growth of infants up to 1.5 years of Guinea baboons and (A) FA score of mothering style, (B) proportion of time being carried by their mother, and (C) and the number of leaves received by the mother. There was no obvious effect of FA score on growth (LMM: *N* = 50 infants, 35 mothers; *P* = 0.656), infant carrying (LMM: *N* = 50 infants, 35 mothers; *P* = 0.729) or leaves received by mother (LMM: *N* = 50 infants, 35 mothers; *P* =0.236). Each point represents an infant. The dashed line depicts the fitted model and the shaded areas, the bootstrapped 95% confidence intervals for all other terms in the model being at their average. Mothering style Factor scores, carry, and leaves received were *z*-transformed to a mean of 0 and a standard deviation of 1.

Table 2.4. Results of the Linear Mixed Model (LMM) analysing the influence of the test predictors of mothering style (i.e., Factor scores, carry, and leave received) on infant growth (Model 1a). Control predictors are infant sex, unit size, and NDVI values. Estimates are shown, along with standard errors (SE), confidence limits, significance tests, and minimum and maximum estimates from model stability analysis.

Term	**Estimate**	**SE**	**CL_{lower}**	**CL_{upper}**	***t***	***df***	***P***	**min**	**max**
Intercept	1.453	0.562	0.291	2.468	(1)	(1)	(1)	0.681	1.931
Factor scores (2)	0.292	0.423	-0.483	1.197	0.450	25.472	0.656	-0.204	0.462
Carry (3)	0.147	0.467	-0.845	1.070	0.351	22.023	0.729	-0.042	0.536
Leave received (4)	0.585	0.469	-0.330	1.439	1.205	34.255	0.236	0.014	1.002
Infant sex (5)	-0.954	0.809	-2.754	0.753	-1.256	40.057	0.216	-1.547	-0.059
Unit size (6)	-0.603	0.489	-1.626	0.313	-0.564	9.385	0.586	-0.948	-0.035
NDVI (7)	-0.686	0.457	-1.639	0.235	(1)	(1)	(1)	-1.166	-0.185
NDVI version (8)	0.882	0.445	0.043	1.823	(1)	(1)	(1)	0.509	1.435
NDVI*NDVIversion	0.334	0.483	-0.598	1.316	0.660	36.865	0.513	0.152	0.775

(1) Not shown due to very limited interpretability

(2) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.259 and 0.934, respectively

(3) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.013 and 0.058, respectively

(4) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.012 and 0.246, respectively

(5) Dummy coded with female being the reference level

(6) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 3.9 and 1.1, respectively.

(7) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.461 and 0.135, respectively

(8) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.376 and 0.469, respectively

None of the control predictors in the main growth model, which were infant sex, unit size, and NDVI, showed any obvious effect on infant growth (Table 2.4).

When we fitted the additional model including mother parity as a control predictor with a subset of the original dataset (Model 1b), mother parity also did not have any obvious effect on infant growth (t = -0.404, df = 20.157, P = 0.69; Table A2.8), and did not have substantial effects on the conclusions about the other predictors present in the model: infant sex, unit size, and NDVI also did not show any obvious effect on infant growth when considering parity (Table A2.8). Detailed information on model specification for the growth model including parity (Model 1b) can be found in the section *Supplement models* of the Appendix.

2.4.3 Infant survival

Of the 79 infants in our sample, 62 survived (37 females, 25 males). None of the sexes seemed to be differentially affected by mortality, since death was similarly spread among the 17 infants that died: seven were females and ten were males. Table 2.5 contains a summary of distribution of infant sex, mother parity and mother age of those infants that died and survived.

Of these 17 infants, mortality occurred throughout all the infancy period, with infants dying from 13 days to 1.3 years (135 median survival days; IQR:47-230). The highest infant mortality occurred in the first three months of age, during which time seven infants died. Tree infants died before reaching six months, four between six and nine months, and just one between nine months and one year. Only two infants died after the first year: one was approximately 13 months old and the other was 16 months old (Table 2.5).

Infant mortality did not seem to occur mainly in young and old mothers, since only two of the dead infants were offspring of young mothers, and three of old mothers, while eleven infants were offspring of mature mothers (Table 2.5). Infant mortality also did not seem linked to mother inexperience: for the infants for which mother parity was known, two were infants of primiparous mothers, and 12 were infants of multiparous (Table 2.5). Interestingly, all four infants whose mothers had either transferred or died survived. Infants of Guinea baboons are thus able to survive their mother's absence after the first year of life since these four infants whose mothers died or transferred were older than a year by the time of the mother's disappearance (11.6 months, 14.9 months, and 16.4 months for the infants whose mothers transferred, and 12.9 months for the infant whose mother died).

The main survival model (Model 2a) showed no obvious effect of mothering style on infant survival; the full model containing the three test predictors (i.e., factor scores, carry, and leaves received) was non-significant (full-null model comparison: $\chi^2 = 0.133$, $df = 3$, $P = 0.988$; Table A2.8). Further, when examined individually, none of the mothering style variables had an effect on infant survival: factor scores positively affected infant survival ($P = 0.741$, Table 2.6), and both carry and leaves received had a slight negative effect (carry, $P = 0.844$; leave received, $P = 0.936$; Table 2.6) but all the effects were non-significant and negligible. Detailed information on the model specification for the main survival model (Model 2a) can be found in the section *Supplement models* of the Appendix.

Table 2.5. Summary and related demographic information of infant survival and mortality.

	Infants that died	**Infants that survived**
Total individuals	17	62
Infant sex		
Females	7	37
Males	10	25
Mother parity		
Primiparous	2	14
Multiparous	12	41
Unknown	3	7
Mother age		
Young	2	15
Mature	11	38
Old	2	9

Table 2.6. Results of Cox proportional hazard model analysing the influence of the test predictors of mothering style (i.e., Factor scores, carry, and leave received) on infant survival (Model 2a). Control predictors are infant sex, unit size, and NDVI values. Estimates are shown, along with standard errors (SE), confidence limits, significance tests, and minimum and maximum estimates from model stability analysis.

Term	**Estimate**	**SE**	**χ^2**	***df***	***P***	**min**	**max**
Factor scores (2)	0.081	0.245	0.109	1	0.741	-0.074	0.327
Carry (3)	-0.045	0.228	0.039	1	0.844	-3.995	2.028
Leave received (4)	-0.024	0.294	0.006	1	0.936	-1.041	0.487
Infant sex (5)	0.703	0.526	1.795	1	0.180	0.460	1.102
Unit size (6)	-0.191	0.297	0.396	1	0.529	-0.738	0.127
NDVI (7)	0.645	0.433	(1)	(1)	(1)	-5.983	9.225
NDVI version (8)	-0.327	0.401	(1)	(1)	(1)	-14.577	-1.886
NDVI*NDVI version	0.605	0.414	2.031	1	0.154	2.659	22.951

(1) Not shown due to very limited interpretability

(2) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.026 and 0.915, respectively

(3) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.014 and 0.056, respectively

(4) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were -0.003 and 0.222, respectively

(5) Dummy coded with female being the reference level

(6) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 4 and 1, respectively.

(7) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.534 and 0.109, respectively

(8) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.343 and 0.441, respectively

Similar to the growth models, none of the control predictors in the main survival model (infant sex, unit size, and NDVI) showed obvious effect on infant survival (Table 2.6). When we included mother parity as a control predictor in a subset of the original dataset, mother parity also did not reveal any obvious effect on infant survival ($\chi^2 = 0.261$, $df = 1$, $P = 0.609$; Table A2.10). The inclusion of parity also did not have substantial effects on the conclusions about the other predictors present in the model: the control predictors, i.e., infant sex, unit size, and NDVI, showed no obvious effect on infant survival when considering parity. Detailed information on model specification for the survival model including parity (Model 2b) can be found in the section *Supplement models* of the Appendix.

2.5 Discussion

The primary aim of this study was to characterise mothering styles in wild Guinea baboons and examine their effects on infant growth and survival for individuals up to 1.5 years. With this first study on mother-infant relationships in this species, we also aimed to contribute to the current knowledge on the variation in these relationships between species. In our model of infant survival, we studied 79 infants, born to 48 mothers. Of these 79 infants, 62 survived. The highest mortality (41% of the infants that died) occurred during the first three months of life. In our model of infant growth, we used a subset of 50 infants born to 35 mothers. Contrary to our initial predictions, infants of rejecting mothers did not have slower growth trajectories and reduced survival compared to protective mothers. The finding that mothering style had no apparent effects on infant growth or survival may be due to methodological issues and issues with the sample, or they could reflect a genuine absence of an obvious effect.

Generally, there is a trade-off between dense sampling of a few infants (e.g., Assamese macaques, 17 infants [Berghänel et al., 2015]; yellow baboons, 18 infants [Altmann, 1980]) or more sparse behavioural sampling of a relatively large number of infants as in our study. A very dense sampling of a few infants has the advantage that solid inferences can be drawn for these individuals. Still, it remains unclear whether these few cases represent the population. For instance, Paul (1984) observed seven infant Barbary macaques every other day, obtaining 544 observation hours per infant over a two-year period (except for one infant that died). On the other hand, a sparse sampling of many infants can better approximate the population average at the cost of limited information for any given individual. Nevertheless, our approach allowed us to compensate for the seven-month hiatus of behavioural observations in 2020 due to the COVID-19 pandemic. Due to the relatively sparse sampling, however, we may have lacked precision in how we characterised mother-infant relationships.

In addition, we found that the PLP is associated with a significant measurement error. While the interobserver reliability in extracting inter-laser distance, recognising body landmarks in the picture, and extracting arm length in pixels was excellent, there was considerable variation for different photographs taken on the same day. The average error was equivalent to two months of growth (7.3 mm), with a maximum of eight months of growth (24.2 mm). The combination of high uncertainty for both the predictor and the response variable might thus have contributed to our failure to detect an effect. In the analysis of survival, however, the response variable was unambiguous. Note that neither the predictors nor the control variables impacted survival.

Infant sex, a control fixed effect in our models, had no noticeable effect on infant growth and survival. In some species, male and female infants differ already in their birth weights. In a study considering neonatal body mass in 109 primate species, neonatal sexual dimorphism positively correlated with adult dimorphism (Smith & Leigh, 1998). In that study, body mass in Guinea baboon females at birth was 603.6 g, and 681 g in males. However, the sample comprised only seven males and three females, respectively, and the authors noted that some individuals might have been born prematurely. Thus, there is no reliable information on potential dimorphism in body mass at birth in this species.

Patterns of development for somatic variables such as skeletal dimensions, body mass, and dental eruption are strongly intercorrelated in members of the genus *Papio* (Leigh, 2009; Leigh & Bernstein, 2006). Adult male and female Guinea baboons show a pronounced sexual dimorphism; the male and female ratio average body size (i.e., sexual dimorphism in body size for adults) reported is of 1.7 (average of 20.2 kg for males and 11.8 kg for females) (Fischer et al., 2017). A study of growth comprising several species of baboons (Leigh, 2009) showed that arm length grew until five years in females and until six and a half years in males. Body mass increased until the age of five to six years in females and until eight years in males, with an apparent increase at three years of age for males (Leigh, 2009). Although the study of Leigh (2009) mainly comprised olive baboons (161 females and 181 males) and only one male and one female Guinea baboon, his results suggest that sex differences might not be present during infancy but arise later. In a recent study by Anzà and colleagues (2022) in which they also used PLP to measure forearm length and derive growth trajectories in Assamese macaques, they found no differences in forearm length in infants up to 0-1 years, and sexual dimorphism in forearm length did not arise until males were 5-7 years, which was the age in which they were larger than females. The lack of effect of infant sex in growth in our study indicates that sexual dimorphism in forearm length arises later in Guinea baboons.

Mother parity was not a prominent determinant of infant growth and survival, which suggests that mother inexperience does not entail negative consequences for the infant in Guinea baboons: in our sample, only 12% of the infants that died were offspring of primiparous mothers. In contrast, in other baboon species, such as chacma baboons (*Papio ursinus*), the highest infant mortality was observed for the offspring of primiparous mothers (44%) (Cheney et al., 2004). Further research should investigate if other characteristics of the mother affect infant growth and survival in Guinea baboons, such as maternal condition, using age as a predictor, for instance. In addition to comparing the impact of certain factors on infant mortality, it is also interesting to compare overall infant mortality rates between species. In our study, the infant mortality within the first year was 19% (64/79), while in chacma baboons, it was 38% (46/120) (Cheney et al., 2004).

We also controlled for the potential effects of unit size, following the conjecture that females may compete over access to the primary male for infant protection. We found no effect of unit size on growth and survival. There might indeed be no effect, or male quality (as indicated by the preference of many females for that male) in some way offsets the costs of increased female-female competition. Detailed analyses of male behaviour in relation to unit size will be needed to address this question.

To reflect potential ecological conditions influencing growth and survival in our sample of infants, we also considered NDVI as a control fixed effect. Again, we found no apparent effect on infant growth and survival. This finding is perhaps not surprising: NDVI is an index that indicates plant productivity in terms of plant coverage (i.e., greenness) more adequate for species that feed on leaves or plants. However, NDVI might not reflect the feeding ecology of Guinea baboons since our study population barely feeds on plants and leaves. Aside from fleshy fruits, which are restricted mainly to the rainy season, Guinea baboons around Simenti feed on a variety of woody vegetation, dry fruits, and seeds in the dry season (Zinner et al., 2021). Thus, a low NDVI value of vegetation cover does not necessarily translate to low food availability. In addition, our study population has other food sources that do not depend on rainfall, as it often feeds at the evergreen gallery forest of the Gambia river, where, for instance, the fruit of the palm *Borassus akeassii* can be found almost all year round.

Several factors might explain why mothering style did not seem to affect infant growth and survival in Guinea baboons. First, differences in mothering style and mother-infant relationships might be less pronounced in Guinea baboons than in yellow baboons. Much of what we know about wild primate mother-infant relationships comes from Jeanne Altmann's book "Baboon mothers and infants" (1980). This classic text paved the way for understanding mother-infant relationships in wild primates and established a framework for inter-specific comparisons. However, Altmann's analyses were based on a total of 18 infants, with twelve infants at the beginning of the study and only one infant representing twelve months of age. Altmann classified mothers as "restrictive" (protective) or "laissez-faire" (rejecting) respectively, based only on the occurrence of restraining behaviours by the mothers during the first two months of infancy.

The observed differences between yellow and Guinea baboons might result from differences in the social system between the two species. For example, yellow baboons live in multi-male-multi-female groups with female philopatry. Females form linear dominance hierarchies in which daughters acquire a rank position adjacent to their mothers, resulting in societies organised around matrilines (Altmann, 1980; Samuels et al., 1987; Semple et al., 2002). Guinea baboons, in contrast, live in tolerant multi-level male-philopatric societies with female-biased dispersal. Although females in a unit exhibit a linear and relatively steep hierarchy (Faraut et al., 2019; Fischer et al., 2017), there are no matriclans and rank does not depend on female relatedness patterns.

Guinea baboon mothers showed less variation regarding the range of being protective or rejecting than yellow baboon mothers. In yellow and Guinea baboons, all mothers were most protective and in contact or close proximity just after birth (month 0), as expected due to the new-born's high dependency and vulnerability. However, in yellow baboons, the most protective mothers did not break any body contact with their infants for the first two months, nor did the most rejecting mothers for the first month after birth. Guinea baboon mothers, in contrast, left their infants behind occasionally from their first month of life.

Rejection behaviours (e.g., biting, pushing) were infrequent in Guinea baboons compared to yellow baboons. Yellow baboon mothers rejected infants already at month four, and by the time infants were six months, they all had experienced some rejection behaviour by their mothers. In contrast, in Guinea baboons, only 21 of 80 infants experienced these rejection behaviours at least once during the entire infancy period. Furthermore, Altmann (1980) reported that mothers rejected transport and nipple contact when infants were already 4 to 5 months old, with the most frequent rejections occurring around 8 to 12 months (when weaning occurs in yellow baboons). Although rates for carrying and nipple contact rejection were not provided for yellow baboons, carrying and nipple contact rejections were surprisingly infrequent for Guinea baboons throughout infancy; higher rates would have been expected towards the end of the infancy period since weaning is marked by the end of nutritional and transport dependency. At the end of infancy (18 months), we observed a maximum rate of 0.026/h for transport rejection and 0.254/h for nipple contact rejection. In conclusion, Guinea baboon mothers show fewer rejections toward infants than yellow baboons.

Differences between yellow and Guinea baboons also became apparent when comparing the time mothers and infants spent together, pointing to a more rapid decrease in association in yellow than in Guinea baboons. By the time infants were six months old, both yellow and Guinea baboons spent a similar amount of time within 1 m: around 48% and 55%, respectively (Altmann, 1980). However, by the time yellow baboon infants were eleven months old, the time within 1 m had decreased to around 15%, whereas in Guinea baboons, it had only decreased to 32%. Altmann (1980) did not provide time in nipple contact for yellow baboons, but she mentioned that nipple contact declined rapidly within the first four months. In Guinea baboons, in contrast, the nipple contact time was 49.6% at month 0 and only decreased to 38.4% by the fourth month. In another study, Altmann and Samuels (1992) also provided information about the time mothers carried their infants. Differences in the amounts of carrying were not so visible between the two species just after the infants were born (month 0), which was 30% of the time in yellow baboons, and 41.4% in Guinea baboons. However, in yellow baboons, the proportion of time carrying decreased remarkably to 5% by month six, whereas in Guinea baboons, it was still 23% at that age. Furthermore, in yellow baboons carrying time was close to zero by nine months, whereas it reached that value only at the age of 18 months in Guinea baboons. In conclusion, Guinea baboon infants and mothers associate for longer than yellow baboons.

We propose that the overall rare rejection and protection observed in Guinea baboons, which points towards a more relaxed and permissive mothering style, is a consequence of their tolerant social system. First, in tolerant species, social risks are low, and the social environment is relatively safe, as conspecifics pose a low risk for infant survival. In this context, mothers do not need to be especially protective since they have more freedom to allow their infants to roam freely and interact with others (Berman, 1980; Thierry, 2013). For instance, in tolerant Indian langurs (*Presbytis entellus*), mother permissiveness allows for the occurrence of allomothering behaviour (McKenna, 1979).

Since neither mothering style nor any control predictors seemed to have a noticeable effect on infant survival, the next step would be to elucidate which factors may have driven the death in 17 of the 79 infants in our sample. Mothers play a significant role in the development and fitness of their offspring (Clutton-Brock, 2016). A high maternal rank usually confers advantages from early life (Altmann, 1980; Kleindorfer & Wasser, 2004) regarding both growth and survival. Maternal rank, for instance, predicted faster growth in yellow baboons (Altmann & Alberts, 2005), although a study by Archie and colleagues (2014) did not find a clear effect of dominance rank on infant survival. In yellow baboons, negative infant handling of unrelated infants (i.e., rough handling, rough carrying and grab-pulling the infant off the mother) predicted infant mortality. Negative infant handling has thus been proposed as a mechanism by which mothers would be able to modify the long-term social position of their infants (Kleindorfer & Wasser, 2004). Although infant handling is frequent in Guinea baboons, we rarely observed rough negative infant handling by unrelated females (pers. observation). We, therefore, consider it an unlikely cause of infant death. Instead, infant handling in Guinea baboons is usually preceded by grunts, i.e., vocalisations expressing benign intent (Faraut et al., 2019).

Further, in yellow baboons, infants of low-ranking mothers are often kidnapped by others (Altmann, 1980). In contrast, in Guinea baboons, kidnapping is very rare. We witnessed that an adult primiparous female whose infant had disappeared months before kidnapped an infant for a few days. This infant eventually died, being the only instance of kidnapping ending in death ever witnessed by researchers since the start of the project. In most of the other observed kidnapping occurrences, however, mothers retrieved their infants in a short time, ranging from minutes to a few hours (pers. observation). Therefore, kidnapping and negative infant handling seem to be unlikely causes of infant death in our population.

Another common cause of infant death in some primate species, for instance, chacma baboons, is infanticide (Palombit et al., 2000). However, infanticide has never been witnessed in our population of Guinea baboons. Therefore, it seems an unlikely reason. Further, lactating and pregnant females can transfer to a new primary male without subsequent occurrences of feticide or infanticide (Goffe et al., 2016). Moreover, males frequently protect infants of their units (pers. observation) even when there is high certainty that they are not their fathers, which might occur when a mother transfers with her infant from a different unit, party, or gang. Thus, illness, injury, and predation (for infants that become more independent) are the most likely explanations for our population's relatively high infant mortality. First, Guinea baboons are subject to predation from lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), and African wild dogs (*Lycaon* *pictus*), and are common prey for lions in the Niokolo-Koba National Park (Dagorne et al., 2020). A current survey in the park places baboons as the second most common prey for leopards and lions, and a common prey for wild dogs (Robin Horion, pers. comm.). Second, accidental falls and injuries could also be common causes of death. Even though Guinea baboons are mainly terrestrial, they also forage and sleep in trees, and the terrain is frequently rough and the vegetation dense and thorny.

We have presented the first study analysing mother-infant relationships in Guinea baboons during the first 18 months of life. In light of the lack of effect that mothering style had on infant growth and survival, we discussed alternative explanations for the observed variation in infant mortality. In our analysis, we have placed particular emphasis on the role of the mother. Future research should address the dynamics of the mother-infant relationship from the infant's perspective. Infants are not only passive recipients of maternal behaviour but also contribute to the relationship (Fairbanks & Hinde, 2013). For instance, beyond the first months of life of highest dependency and vulnerability in which mothers are more responsible for maintaining contact and proximity, infants maintain an active role in keeping spatial proximity with their mothers, which increases as they approach weaning (Altmann, 1980; Fairbanks & Hinde, 2013).

Further, when mothers are more rejecting, infants counteract by exerting effort to maintain proximity (Fairbanks & Mcguire, 1995). Infants also seem to learn during which maternal activities they are less likely to be rejected by their mothers. For instance, yellow baboon infants are more likely to be in contact with their mothers and get access to the nipple when mothers are resting (Altmann, 1980). In addition, it would be interesting to study how the social network of the infants gradually expands and what the role of other unit members and peers are in predicting infant health and survival.

Since there is a frequent lack of homogeneity in the data when studying wild infant primates, we encourage further studies to follow a method similar to the one presented here, as this will allow to control for infant age when studying ontogenetic processes and avoid possible confounds with the age of the infant. We also advocate for avoiding a rigid categorization of mothering style into “protective” and “rejecting” since mothers can be more rejecting or protective compared to other mothers. Furthermore, their degree of protection and rejection can vary as their infants move along infancy or even with their own successive infants.

2.6 Acknowledgements

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2.7 Compliance with ethical standard

Approval and research permission was granted by the DPN and the MEPN de la République du Sénégal. Research was conducted within the regulations set by the Senegalese agencies as well as by the Animal Care Committee at the German Primate Centre.

2.8 Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals followed the ethical standards of the institution or practice at which the studies were conducted.

2.9 Appendix

Table A2.1. Age category definitions

“Black infant”	From 0-6 months. After birth and for the first ~3 months, the hair is completely black (natal coat), and the skin is light pinkish (more reddish just after birth). Fur starts to change into brown at ~3 months in some body areas (eyebrows, arms, body sides), and skin begins to darken. The transition into full brown hair and dark skin lasts until ~6 months. Young infants are carried ventrally, and at around 3-4 months they begin to ride dorsally. The end of the black infant age category is recorded at 6 months of age. The changes in fur colour can be used in case the birth is unknown.
“Brown infant”	~6-18 months (1.5 years) Hair is brown, and skin is dark (both might still be in transition during the 7th month). Still frequently being carried by their mothers and suckling until about 1 year of age, when weaning period starts. Suckling and carrying progressively decline until ~1.5 years.
“Young adult female”	Once females become pregnant and give birth, they are considered young adults. These females are primiparous (i.e., they gave birth once). They are sexually mature and undergo sexual swellings regularly. Females in this stage are in general still physically smaller and thinner than mature adult females. The coat is shiny, and they typically have few scars. The teeth appear white and unchipped.
“Mature adult female”	Females that have reached full body size. These females are multiparous (i.e., they gave birth more than once). The teeth appear mostly white and unchipped, but some may appear slightly yellowing or present some chipping or wear.
“Old adult female”	The coat begins to thin out. Teeth present some discoloration on several teeth and evident breaks chipping or tooth wear.

Supplement PLP

The apparatus, or Parallel Laser Photogrammetry (PLP) system, consisted of a digital single-lens reflex (DSLR) Camera Canon EOS 200D and an objective Canon EFS 55-250mm, along with a laser box that contained three parallel lasers (laser class 2 520 nm 1mW DI520-1-3) (Fig. A2.1). We chose a three-laser system because a third laser creates a right isosceles triangle with the other two lasers, which allows to become aware and correct whenever the photographed object deviates from the perpendicular plane of the camera-object axis, or to detect if the photographed object has tilts on the surface. In both cases, the right angle of the triangle would be lost, as one of the laser dots would appear displaced (Anzà et al., 2022). We used green lasers, as in daylight they are more visible than red lasers (Bergeron, 2007; Durban & Parsons, 2006). Three PLP systems were used during the duration of the study: PLP1, PLP2 and PLP3.

Figure A2.1. Apparatus for Parallel Laser Photogrammetry (PLP) used in the study, seen from different angles. The apparatus, also referred as PLP system, consisted of a camera and a laser box with three lasers and a switch. Batteries were allocated inside the laser box. Horizontal and vertical lasers were separated by 20 millimetres.

The individuals were photographed in their natural habitat, in lateral view. Observer distance was about 2 to 5m. To determine the length of the lower arm, which was our size of interest, we defined two landmark endpoints for our measurements (Fig. A2.2, A-B): the olecranon and the ulnar styloid process. The olecranon is a large, thick, curved bony eminence at one of the ends of the ulna, a bone in the lower arm that projects behind the elbow. The olecranon forms the most pointed portion of the elbow. Also in the lower arm, the ulnar styloid process is a bony prominence with a round ending located at the distal end of the ulna (or head of the ulna), aligned with the pinkie. The olecranon and the ulnar styloid process are opposite ends of the ulna.

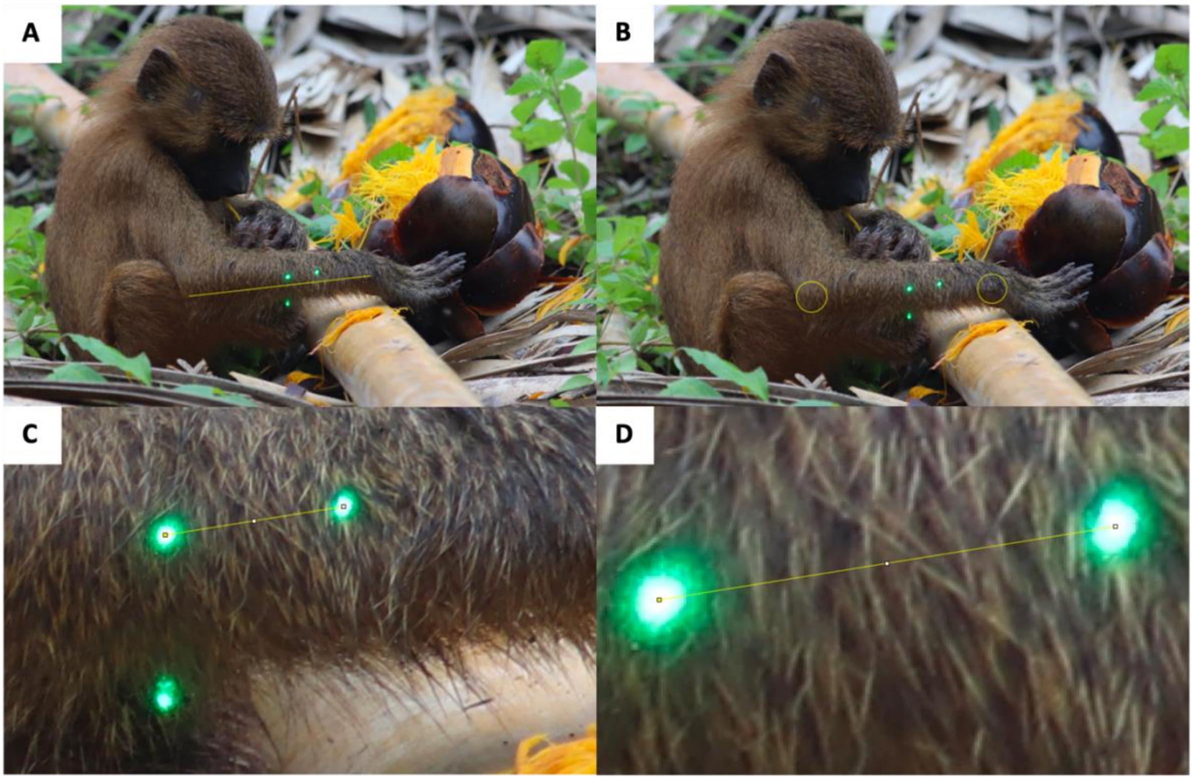

Figure A2.2. Lower arm measurement (A) in infant Guinea baboons is determined by body landmarks: olecranon (B, left yellow circle) and ulnar styloid process (B, right yellow circle). The horizontal lasers were used as a scale (inter-beam distance: 20 mm). Inter-laser distance was measured in ImageJ from centre to centre of the green laser dot (C, D). In our study, only horizontal lasers were used, due to a calibration issue with the vertical lasers.

To minimize error, when we selected pictures to be measured, we met the following criteria (adapted from Galbany et al., 2017): landmarks were identifiable in the picture, and in focus; individuals had to be either sitting or standing, but always flexing their arm (Fig. A2.2, A-B); an ideal position was one in which the individual had the upper and lower arm forming a right angle. Laser points were on the same plane as the body landmarks of the infant. This plane was visually perpendicular to the optical axis of the camera objective lens and to the projection of the laser beams, so that the body of the infant was not rotated. Further, preferably the infant was situated in the centre of the picture.

To control for possible irregularities in the laser alignment and because it was not possible for us to adjust and calibrate the lasers (i.e., inter-beam distance) during the field season, we projected them onto a millimetre paper and took a picture at 2 and 5 m before and after a given photo session (i.e., a day in which we took pictures), that would later be measured with ImageJ. This way, we could know the exact daily inter-laser distance and, therefore, the exact scale, in case of potential calibration problems. Some issues with inter-beam distance did in fact arise throughout the study period. With time, the vertical lasers considerably lost equidistance, as did slightly the horizontal ones. The vertical lasers were ultimately not used for measuring growth, as the differences were too large when increasing object distance from the photographed object. The calibration issues might have occurred as a result of carrying the apparatus when doing field work and occasionally walking through some dense terrain. Temperature changes might have also affected, as for two years, the inter-laser distance was shorter in the peak of the dry and hottest season.

Table A2.2. Ethogram of state behaviours between a mother and her infant that were considered for the FA. Adapted from the CRP Simenti ethogram (version August 2022: Dal Pesco & Fischer, 2022).

Behaviour	Description
Grooming	The mother moves her fingers and/or lips through the fur of her infant. A grooming bout ends when active manipulation is interrupted for more than 5 s. Grooming and contact sit are mutually exclusive. A grooming bout is considered finished only once the mother has stopped grooming her infant for more than 5 s.
Contact (sit)	Mother and infant are sitting, sitting, lying, or standing within < 10 cm of one another, meaning that the individuals either touch skin-to-skin or are so near that their fur touch, with at least one individual sitting or lying down. This applies to the body, the hairs, and the different body parts (e.g., feet or hands) of the two individuals. However, if one individual is in contact with another one only with its tail, body contact is recorded only if it is the base of the tail that is in contact. Grooming and contact sit are mutually exclusive. A contact-sit bout is considered finished only once the individuals stopped contact sitting for more than 5 s.
Proximity-1: <1 m at the beginning/end of a focal behavioural observation	Time in proximity that a mother and infant are found in 1 m or less of each other when the focal observation started, or that remained in a distance of 1 m or less of each other once the focal observation finished. In the first case, it is the time in proximity from start of focal until either mother or infant leave one another further away than 1 m. In the second case, it is the time in proximity since either mother or infant approached from further away than 1 m and stayed together until the end of the focal observation.
Proximity-2: <1 m, after the mother approached	Time between a mother’s approach from further away than 1 m and a leave further away than 1 m (either by mother or infant), thus, being the time in which the distance between mother-infant dyad is 1 m or less, but without being in contact sit, and initiated by the mother.
Nipple contact	The infant has its mother’s nipple in its mouth, either holding onto it or suckling. This behaviour is not mutually exclusive to contact sit, since the infant can be in nipple contact without being in contact sit.
Carry	The infant is carried by its mother, either ventrally or dorsally. If the mother stops walking but the infant is still holding on to the mother’s fur with all four extremities, it is still carrying behaviour. On the contrary, when the mother is not walking and the immature is grabbing the mother’s fur only with the forelimbs, this is not coded as carried, but as contact sit. Carried and contact sit are mutually exclusive.
Cradle	Within a contact sit bout, ventro-ventral contact of mother and infant with the mother holding one or both arms around the infant (i.e., embracing it).

Table A2.3. Ethogram of event behaviours between a mother and her infant that were considered for the FA. Adapted from the CRP Simenti ethogram (version August 2022: Dal Pesco & Fischer, 2022).

Behaviour	Description
Protection	Aggregate of two protective behaviours: retrieve and restrain. *Retrieve*: the mother approaches (or approaches within 1 m) the infant and recovers it by grabbing or holding it with one or both arms. The mother then pulls the infant closer to its body, and carries it or starts a contact sit, either way impeding that the infant moves away from her. It might be the case that before the retrieval either mother or infant, or both, are in a situation of distress, with possible presence of vocalisations such as keck or scream (plus moaning/tantrum in the case of the infant). This behaviour also includes the instances in which the mother retrieves the infant from another individual. *Restrain*: the infant tries leave the mother, who is in contact or in close proximity (within 1 m), but the mother stops the infant from moving away by grabbing one of its extremities or the tail and holding or pushing the infant back towards herself. The infant might produce vocalisations such as keck, scream, moaning or tantrum.
Rejection	Aggregate of two protective behaviours: mock-bite and push away. *Mock-bite*: the mother bites her infant with moderate strength. *Push away*: the mother presses or shoves her infant away from her, avoiding either contact or proximity between them.
Rejection of nipple contact	The mother avoids her infant from starting nipple contact. Kecking, screaming, moaning and/or tantrum vocalizations might occur at the same time.
Attempt of nipple contact	The infant grabs and releases its mother's nipple repeatedly with one or both hands, sometimes approaching its mouth to the nipple or making brief contact (<2 s) between mouth and nipple. Kecking, screaming, moaning and/or tantrum vocalizations might occur at the same time.
Rejection of carrying	The mother prevents her infant from being carried. Kecking, screaming, moaning and/or tantrum vocalizations might occur at the same time.
Aggression	Aggregate of five aggressive behaviours: threat, lunge/charge, chase, physical fight, submissive behaviour between a mother and her infant. *Threat*: the mother individual stares at the other individual (intense look with eyebrows lifted) or the individual stands on all four limbs with hands placed slightly in front of the body. Head bob may occur. The individual conducts a small but fast movement forward while all legs and arms remain on the ground, or one arm loses ground (ground slap). *Lunge/charge*: individual A leaps or runs towards individual B but B does not flee. *Chase*: Individual A runs towards and pursues individual B. Individual B runs away often screaming, often being followed by individual A for a certain distance. *Physical fight*: individual A hits or bites or throws individual B on the ground. *Submissive behaviour*: individual B displays submissive behaviour such as fear grin, crouch, or tail-raise towards the other individual, who was already involved in an aggressive episode or not. Vocalisations such as keck or scream (plus moaning/tantrum in the case of the infant) might occur at the same time.
Leaves – initiated by mother	The mother moves further away than 1 m, increasing therefore the distance to the infant to > 1 m.
Mother approached; infant left	The mother moves from further away than 1 m to the infant, decreasing the distance to the infant to < 1 m, followed by an immediate leaving by the infant, who moves further away than 1 m from the mother, increasing the distance between them to > 1 m.

Supplement mother-infant behaviours. Model description, standard deviations of the random effects for immature ID and mother ID, and resulting model depictions for the behaviours initially considered for the FA.

1.Proportion of time grooming

Model	full.prop.time.mo.gr = glmmTMB (tr.prop.time.mo.gr ~ z.age + (1|immature_ID) + (0+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = xdata, family = beta_family)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.00001
immature_ID.1	z.age	0.00001
mother_ID	(Intercept)	0.00003
mother_ID.1	z.age	0.00002

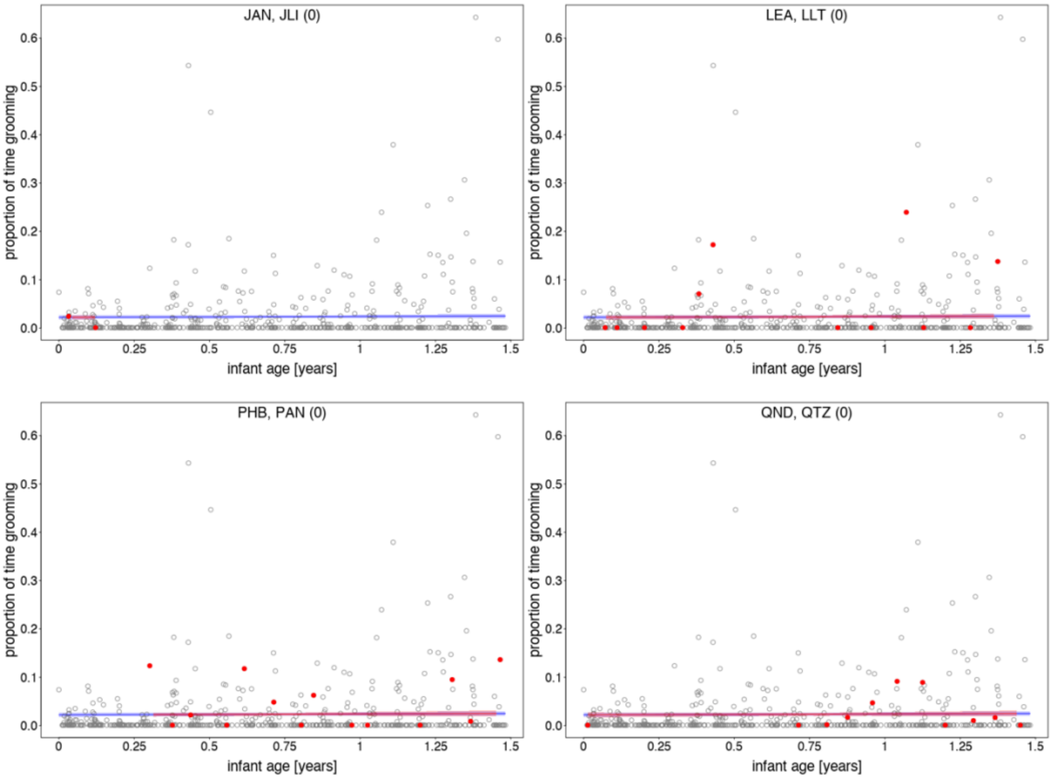

Figure A2.3. Development of grooming behaviour (expressed in proportion of time) directed from mothers to infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., JAN: mother; JLI: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Note that the individual mothers displayed did not recognizably differ from the population average.

2.Proportion of time in contact sit

Model	full.prop.contact_sit_duration_sec = glmmTMB (tr.prop.contact_sit_duration_sec ~ z.age + (1|immature_ID) + (0+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = xdata, family = beta_family)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.31073
immature_ID.1	z.age	0.00005
mother_ID	(Intercept)	0.00004
mother_ID.1	z.age	0.00000

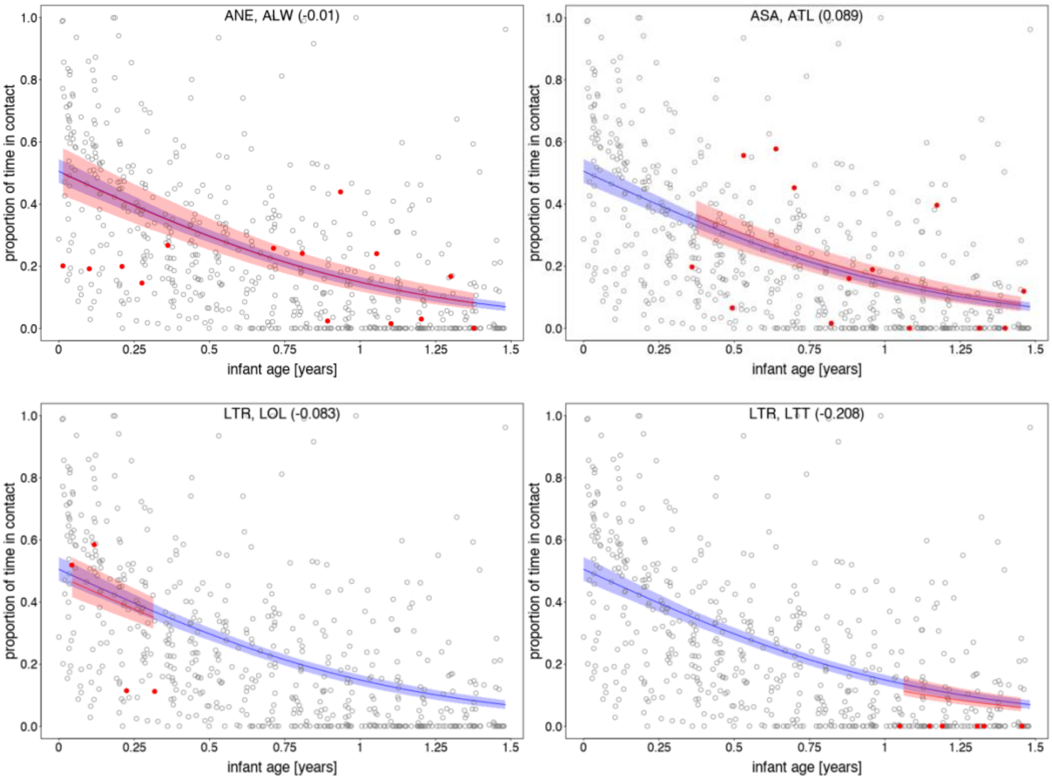

Figure A2.4. Development of contact behaviour (expressed in proportion of time; derived from contact sit behaviour) between mothers and infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., ANE: mother; ALW: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more protective than the average for the specific period depicted, and lines below the blue line show mothers that were more rejecting.

3.Proportion of time in proximity (<1 m at the beginning/end of a focal behavioural observation); proximity-1

Model	full.mother_alreadystillin_proxy_duration_sec = glmmTMB (tr.prop.mother_alreadystillin_proxy_duration_sec ~ z.age + (1+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = xdata, family = beta_family)

Groups	Name	Standard Deviation	Correlation
immature_ID	(Intercept)	0.43734	
immature_ID.1	z.age	0.24958	-0.229
mother_ID	(Intercept)	0.00001	
mother_ID.1	z.age	0.00008	

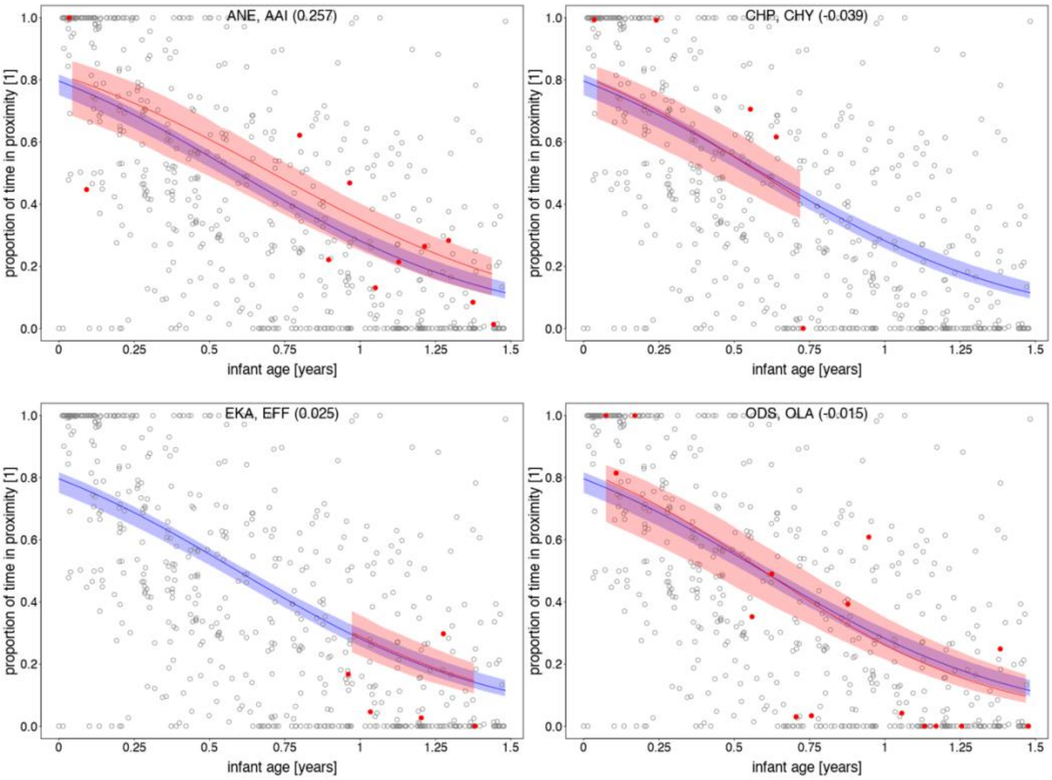

Figure A2.5. Development of time in proximity (<1 m) (expressed in proportion of time) that mothers and infants spent together, when were found already in proximity or were still in proximity at the beginning or at the end of the focal observation, respectively, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., ANE: mother; AAI: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more protective than the average for the specific period depicted, and lines below the blue line show mothers that were more rejecting. The lower-right plot depicts an instance in which a mother is more protective than the population average at the beginning of ontogeny and becomes more rejecting afterwards.

4.Proportion of time in proximity (<1 m, after the mother approached); proximity-2

Model	full.prop.all_approach_received_duration_sec = glmmTMB (tr.prop.all_approach_received_duration_sec ~ z.age + (1|immature_ID) + (0+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = xdata, family = beta_family)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.00001
immature_ID.1	z.age	0.00001
mother_ID	(Intercept)	0.00003
mother_ID.1	z.age	0.00001

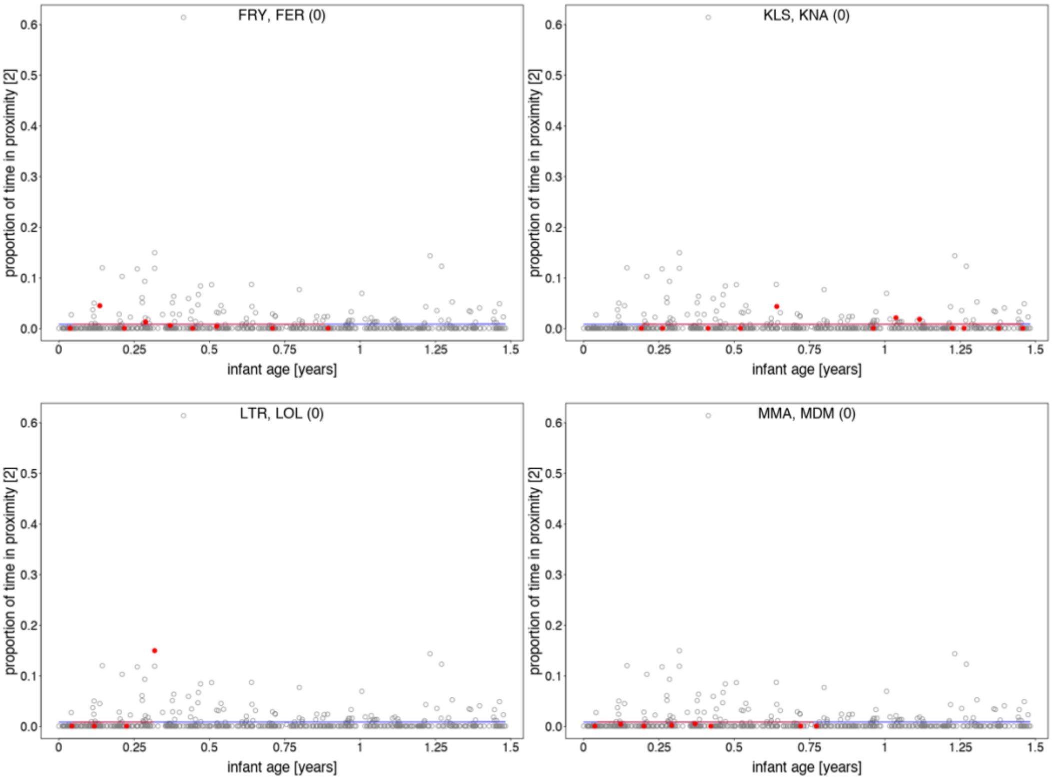

Figure A2.6. Development of time in proximity (<1 m) (expressed in proportion of time) that mothers and infants spent together after an approach of the mother to the infant, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., FRY: mother; FER: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Note that the individual mothers displayed did not recognizably differ from the population average.

5.Proportion of time in nipple contact

Model full.prop.nipple_duration_sec = glmmTMB (tr.prop.nipple_duration_sec ~ z.age + (1|immature_ID) + (0+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = xdata, family = beta_family)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.27759
immature_ID.1	z.age	0.00000
mother_ID	(Intercept)	0.00012
mother_ID.1	z.age	0.00000

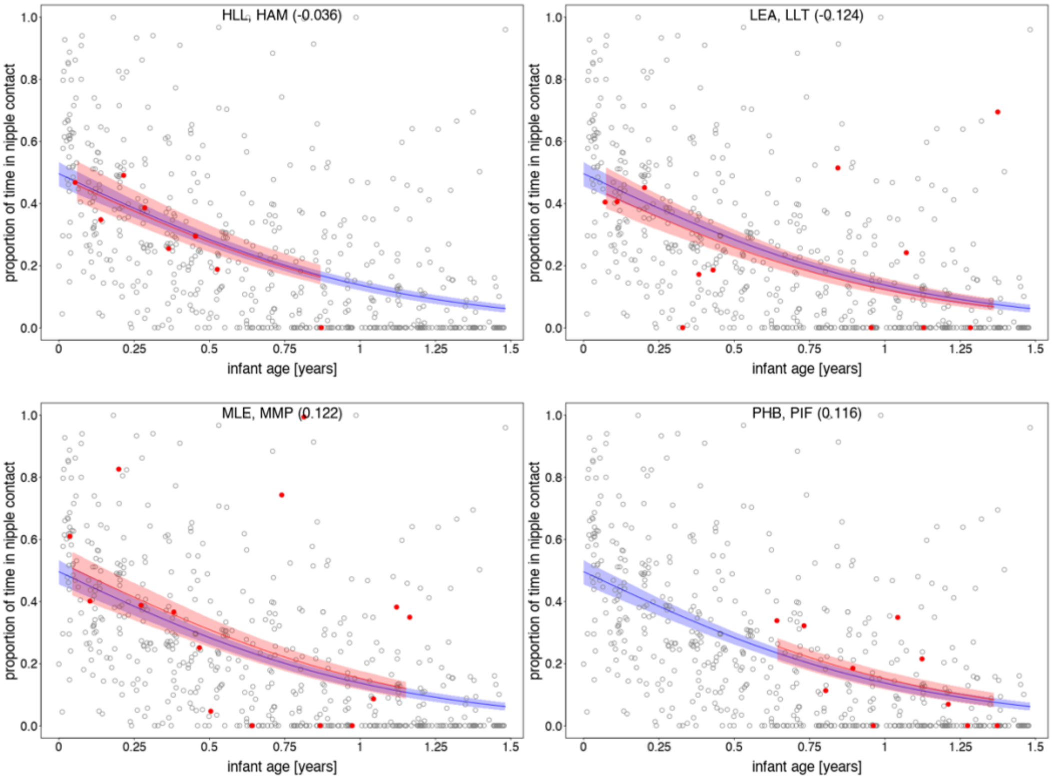

Figure A2.7. Development of nipple contact behaviour (expressed in proportion of time) between infants and their mothers, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., HLL: mother; HAM: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more protective than the average for the specific period depicted, and lines below the blue line show mothers that were more rejecting.

6.Proportion of time carrying

Model full.prop.carry_duration_sec = glmmTMB (tr.prop.carry_duration_sec ~ z.age + (1|immature_ID) + (0+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = xdata, family = beta_family)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.00008
immature_ID.1	z.age	0.00001
mother_ID	(Intercept)	0.12830
mother_ID.1	z.age	0.00001

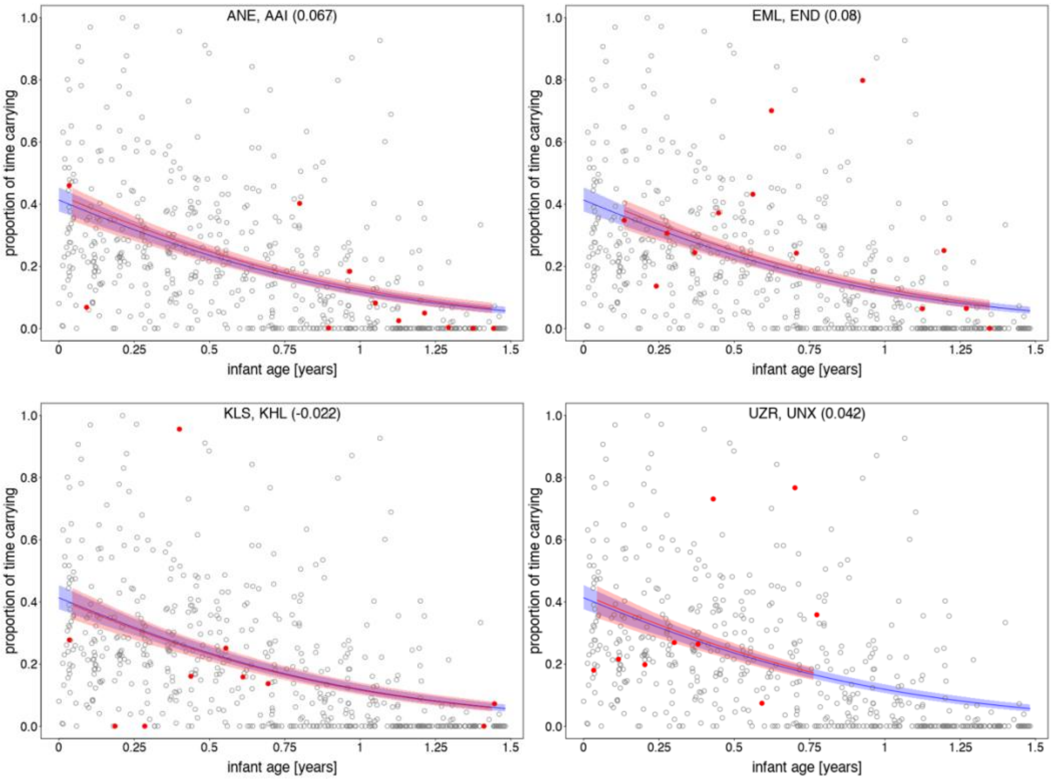

Figure A2.8. Development of carry behaviour (expressed in proportion of time) between mothers and their infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., ANE: mother; AAI: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more protective than the average for the specific period depicted, and lines below the blue line show mothers that were more rejecting.

7.Proportion of time cradling

Model	full.prop.cradle_duration_sec = glmmTMB (tr.prop.cradle_duration_sec ~ z.age + (1|immature_ID) + (0+z.age|immature_ID) + (1|mother_ID) + (0+z.age|mother_ID), data = sel.data, family = beta_family)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.00002
immature_ID.1	z.age	0.00001
mother_ID	(Intercept)	0.00002
mother_ID.1	z.age	0.00001

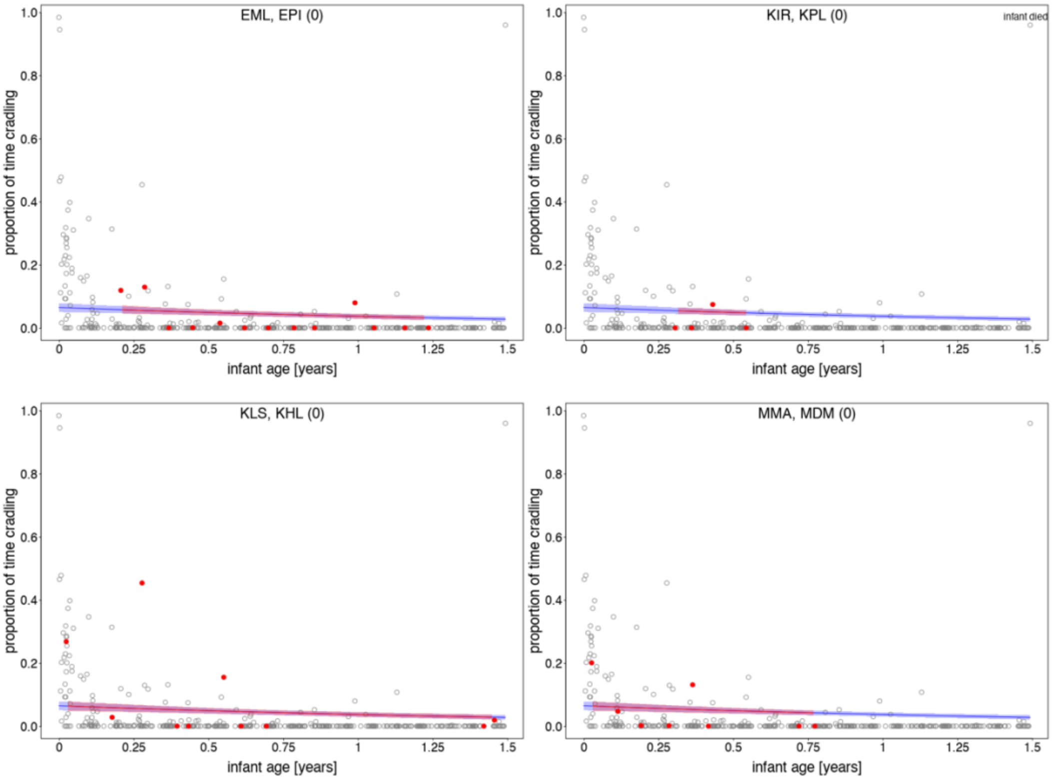

Figure A2.9. Development of cradle behaviour (expressed in proportion of time) directed from mothers to their infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 64 infants, 45 mothers; 425 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., EML: mother; EPI: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Note that the individual mothers displayed did not recognizably differ from the population average. The upper-right plot shows one case in which data is interrupted is due to infant death.

8.Count protective behaviour

Model full.Protect_all_freq = glmer (Protect_all_freq ~ z.age + offset (log.focal_duration_min) + (1+z.age||immature_ID) + (1+z.age||mother_ID), data = sel.data, family = poisson)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.00004
immature_ID.1	z.age	0.43008
mother_ID	(Intercept)	0.25320
mother_ID.1	z.age	0.00000

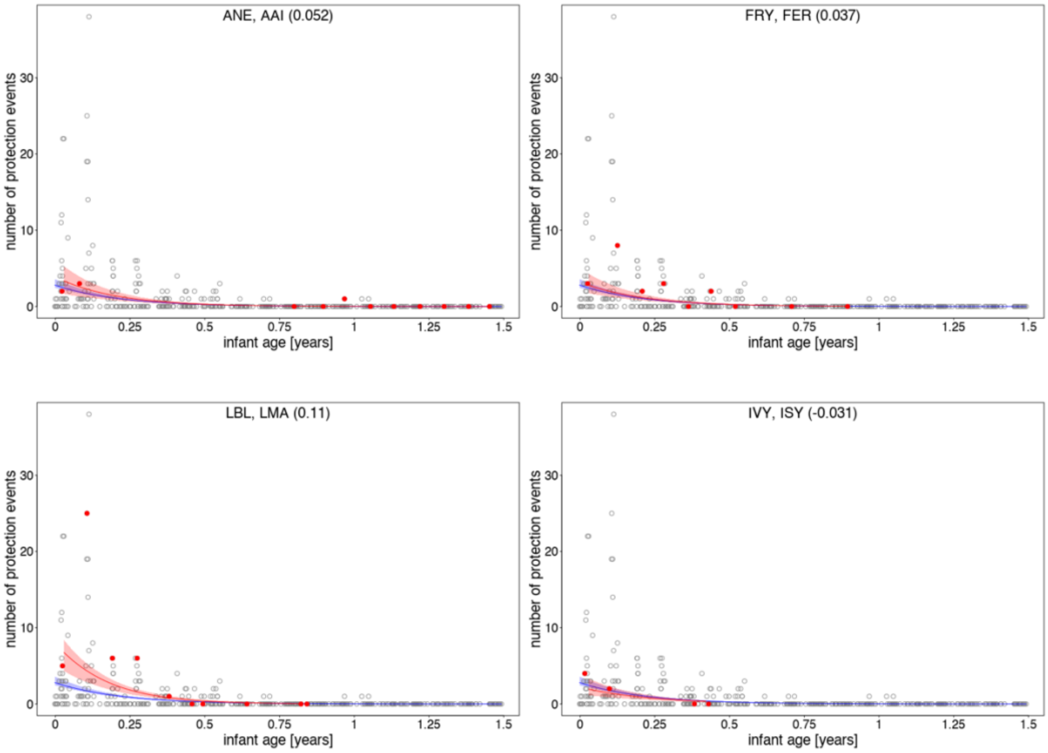

Figure A2.10. Development of protective behaviour (expressed in counts per hour) directed from mothers to their infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 64 infants, 45 mothers; 425 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., ANE: mother; AAI: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more protective than the average for the specific period depicted, and lines below the blue line show mothers that were more rejecting.

9.Count rejection behaviour

Model full.Reject_all_freq = glmer (Reject_all_freq ~ z.age + offset (log.focal_duration_min) + (1+z.age||immature_ID) + (1+z.age||mother_ID), data = sel.data, family = poisson)

Groups	Name	Standard Deviation
immature_ID	(Intercept)	0.55361
immature_ID.1	z.age	0.00001
mother_ID	(Intercept)	0.35064
mother_ID.1	z.age	0.00000

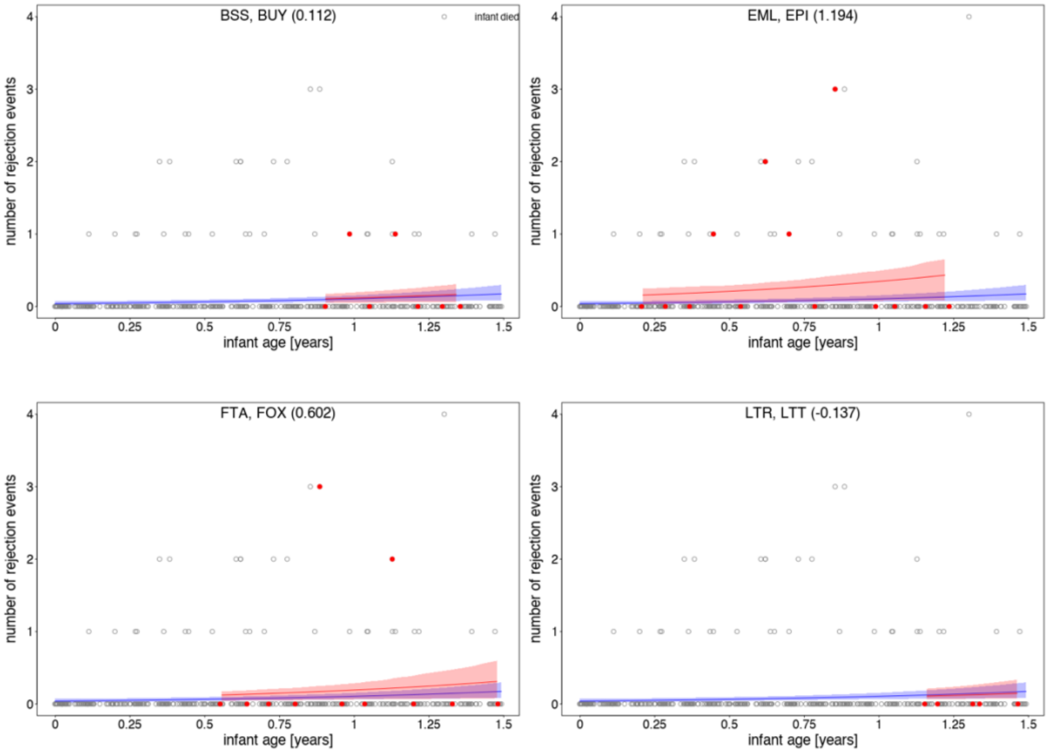

Figure A2.11. Development of rejection behaviour (expressed in counts per hour) directed from mothers to their infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 64 infants, 45 mothers; 425 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., BSS: mother; BUY: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more rejecting than the average for the specific period depicted, and lines below the blue line show mothers that were more protective.

10.Count leave received

Model	full.all_leave_received_freq.wsc.nb = glmer.nb (all_leave_received_freq ~ z.age + offset (log.focal_duration_min) + (1+z.age||immature_ID) + (1+z.age|mother_ID), data = xdata)

Groups	Name	Standard Deviation	Correlation
immature_ID	(Intercept)	0.05050	
immature_ID.1	z.age	0.00000	
mother_ID	(Intercept)	0.36659	
mother_ID.1	z.age	0.50870	0.606

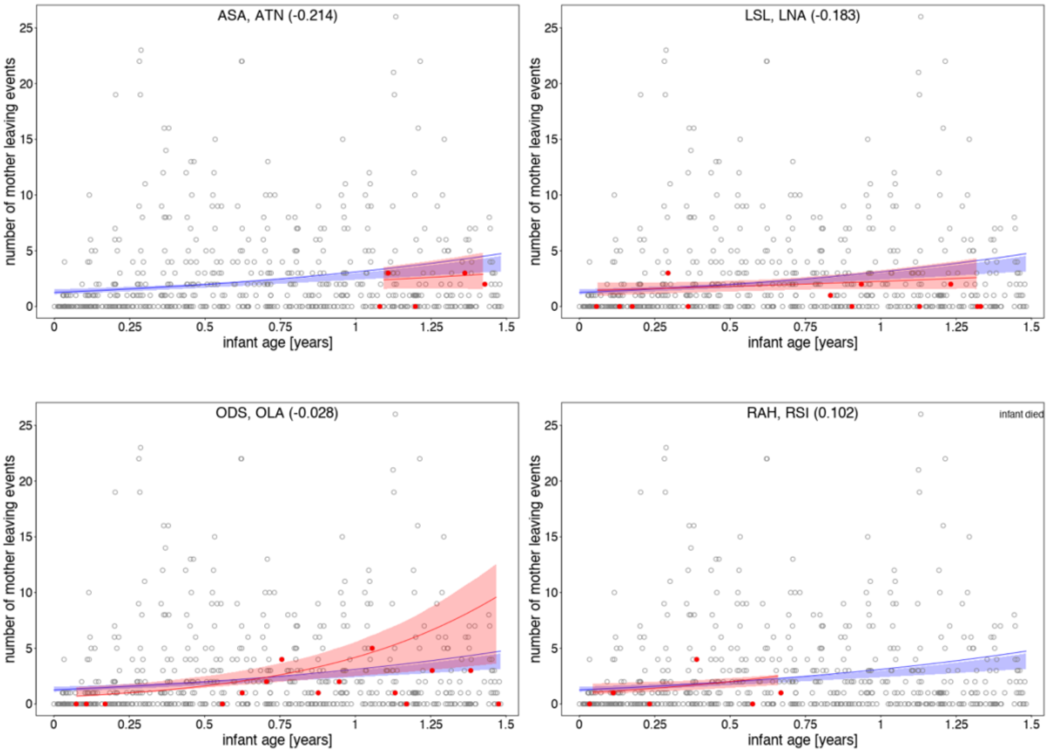

Figure A2.12. Development of leave behaviour (expressed in counts per hour) directed from mothers to their infants, from birth until 1.5 years, which marks the end of infancy in Guinea baboons. The blue line represents the fitted model for the population average behaviour, and the red line depicts the fitted model for the behaviour of a particular mother-infant dyad for the period of time that data were available for that dyad (GLMM: *N* = 80 infants, 49 mothers; 580 datapoints). Grey circles represent the observations for the mother-infant dyads of the dataset aggregated by month and dyad, (i.e., each grey circle represents the behaviour of a given mother-infant dyad per month), and red dots depict the monthly aggregated behaviour for the specific mother-infant dyad highlighted in the plot. The ID of mother and infant (i.e., mother-infant dyad) is indicated at the top of each plot, with a three-letter code for each individual (e.g., ASA: mother; ATN: infant), and next to it, the BLUP for the specific dyad is indicated between brackets. The shaded areas represent the bootstrapped 95% confidence intervals. Red lines above the blue line can be considered as mothers that were more rejecting than the average for the specific period depicted, and lines below the blue line show mothers that were more protective. The lower-right plot shows one case in which data is interrupted is due to infant death.

Table A2.4. Dispersion parameters for the GLMMs for the behaviours initially considered for the FA.

Behaviour	Dispersion parameter
Time proportions	
Grooming	2.431
Contact	0.816
Carry	0.849
Cradle	1.548
Proximity-1	0.682
Proximity-2	5.289
Nipple contact	0.876
Counts	
Protect	1.244
Reject	0.846
Leave by mother	0.911

Table A2.5. Fitted values of the GLMMs for the behaviours initially considered for the FA, representing the population average behaviours throughout the infancy period. Counts are indicated as number of events per hour.

	Months																		
Behaviour	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Time proportions																			
Grooming	0.022	0.022	0.022	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.024	0.024	0.024	0.024	0.024	0.024	0.025	0.025	0.025
Contact	0.505	0.469	0.432	0.397	0.362	0.329	0.297	0.267	0.240	0.214	0.190	0.169	0.149	0.131	0.115	0.101	0.089	0.077	0.068
Proximity-1	0.796	0.763	0.727	0.687	0.644	0.599	0.553	0.505	0.457	0.410	0.365	0.321	0.281	0.244	0.211	0.180	0.154	0.131	0.110
Proximity-2	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009	0.009
Nipple contact	0.496	0.458	0.421	0.384	0.349	0.316	0.284	0.254	0.226	0.201	0.177	0.156	0.137	0.120	0.105	0.092	0.080	0.069	0.060
Carry	0.414	0.380	0.349	0.318	0.289	0.261	0.235	0.211	0.189	0.169	0.151	0.134	0.119	0.105	0.093	0.082	0.072	0.063	0.055
Cradle	0.066	0.063	0.060	0.057	0.055	0.052	0.050	0.048	0.046	0.044	0.042	0.040	0.038	0.036	0.035	0.033	0.031	0.030	0.029
Counts																			
Protect	2.919	1.955	1.31	0.877	0.588	0.394	0.264	0.177	0.118	0.079	0.053	0.036	0.024	0.016	0.011	0.007	0.005	0.003	0.002
Reject	0.039	0.042	0.046	0.05	0.054	0.059	0.064	0.069	0.076	0.082	0.089	0.097	0.106	0.115	0.125	0.136	0.148	0.161	0.176
Leave by mother	1.289	1.393	1.507	1.629	1.761	1.904	2.059	2.226	2.407	2.602	2.813	3.042	3.289	3.556	3.844	4.156	4.494	4.859	5.253

Table A2.6. Correlations between behaviours that showed considerable variation to possibly enter the FA for defining mothering style.

	Contact	Carry	Proximity-1	Leave (received)	Nipple contact
Contact	1.00	0.15	0.70	0.15	0.74
Carry	0.15	1.00	0.27	0.15	0.28
Proximity-1	0.70	0.27	1.00	0.04	0.66
Protect	NA	NA	NA	NA	NA
Leave (received)	0.15	0.15	0.04	1.00	0.06
Nipple contact	0.74	0.28	0.66	0.06	1.00

Supplement models

Growth

Model 1a

```
Growth.1a = lmer (slope.diff ~ z.fa.scores + z.carry + z.leave_received + inf_sex +
            z.unit.size.growth +z.ndvi.growth*z.ndvi.growth.propV2 +
            (1|mother) + (1|unit.growth),
            data = growth.data, REML = F, control = lmerControl (optimizer = "bobyqa",
            optCtrl = list (maxfun = 100000)))
```

Model 1b

```
growth.1b= lmer (slope.diff ~ z.fa.scores + z.carry + z.leave_received + inf_sex +
           z.unit.size.growth + z.ndvi.growth*z.ndvi.growth.propV2 + mother.parity +
           (1|mother) + (1|unit.growth),
           data = growth.par.data, REML = F, control = lmerControl (optimizer = "bobyqa",
           optCtrl = list (maxfun = 100000)))
```

Survival

Model 2a

```
surv.2a = coxme (surv.rv ~ z.fa.scores + z.carry + z.leave_received + inf_sex +
          z.unit.size.survival + z.ndvi.survival*z.ndvi.survival.propV2 +
          (1|mother) + (1|unit.surv),
          data=surv.data)
```

Model 2b

```
surv.2b = coxme (surv.rv ~ z.fa.scores + z.carry + z.leave_received + inf_sex +
          z.unit.size.survival + z.ndvi.survival*z.ndvi.survival.propV2 + mother.parity +
          (1|mother) + (1|unit.surv),
          data=surv.par.data)
```

Growth

Table A2.7. Results of the random effects part in the growth model (Model 1a). Indicated are the original estimate and the range of estimates when dropping mothers and units from the data, one at a time.

Group	**Effect**	**SD**	**min**	**max**
mother	Intercept	0.271	0.000	1.984
unit	Intercept	0.000	0.000	2.208
	Residual	2.711	1.793	2.809

Table A2.8. Results of the Linear Mixed Model (LMM) analysing the influence of the test predictors of mothering style (i.e., factor scores, carry, and leave received) on infant growth, with a subset of the data (Model 1b) adding an additional control predictor: mother parity (i.e., primiparous or multiparous). The rest of control predictors are the same as in Model 1a: infant sex, unit size, and NDVI values. Estimates are shown, along with standard errors (SE), confidence limits, and significance tests.

Term	**Estimate**	**SE**	**CL_{lower}**	**CL_{upper}**	***t***	***df***	***P***
Intercept	1.584	0.644	0.363	2.863	(1)	(1)	(1)
Factor scores (2)	0.210	0.462	-0.719	1.153	-0.094	18.414	0.926
Carry (3)	-0.195	0.527	-1.228	0.835	-0.437	26.083	0.665
Leave received (4)	0.963	0.553	-0.082	2.097	1.503	27.101	0.145
Infant sex (5)	-0.455	0.902	-2.431	1.398	-0.496	24.249	0.624
Unit size (6)	-0.735	0.543	-1.819	0.353	-0.597	12.573	0.561
NDVI (7)	-0.455	0.538	-1.500	0.689	(1)	(1)	(1)
NDVI version (8)	1.031	0.498	0.089	2.049	(1)	(1)	(1)
Mother parity (9)	-0.812	1.150	-3.226	1.546	-0.404	20.157	0.690
NDVI*NDVI version	0.477	0.527	-0.597	1.516	0.595	26.538	0.557

(1) Not shown due to very limited interpretability.

(2) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.347 and 0.884, respectively

(3) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.017 and 0.055, respectively

(4) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.005 and 0.244, respectively

(5) Dummy coded with female being the reference level

(6) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 4.0 and 1.2, respectively

(7) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.466 and 0.142, respectively

(8) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.391 and 0.471, respectively

(9) Dummy coded with primiparous being the reference level

Survival

Table A2.9. Results of the random effects in the survival model (Model 2a). Indicated are the original estimate and the range of estimates when dropping mothers and units from the data, one at a time.

Group	**Effect**	**SD**	**min**	**max**
mother	Intercept	0.000	0.000	0.150
unit	Intercept	0.010	0.000	0.346

Table A2.10. Results of Cox proportional hazard model analysing the influence of the test predictors of mothering style (i.e., factor scores, carry, and leave received) on infant growth, with a subset of the data (Model 2b) adding an additional control predictor: mother parity (i.e., primiparous or multiparous). The rest of control predictors are the same as in Model 1a: infant sex, unit size and NDVI values. Estimates are shown, along with standard errors (SE), confidence limits, and significance tests.

Term	**Estimate**	**SE**	**χ^2**	***df***	***P***
Factor scores (2)	0.031	0.264	0.015	1	0.903
Carry (3)	-0.004	0.273	0.000	1	1.000
Leave received (4)	-0.015	0.379	0.002	1	0.969
Infant sex (5)	1.158	0.647	3.347	1	0.067
Unit size (6)	-0.389	0.331	1.139	1	0.286
NDVI (7)	1.096	0.497	(1)	(1)	(1)
NDVI version (8)	-0.207	0.440	(1)	(1)	(1)
Mother parity (9)	-0.396	0.819	0.261	1	0.609
NDVI*NDVI version	0.150	0.462	0.095	1	0.757

(1) Not shown due to very limited interpretability.

(2) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.050 and 0.908, respectively

(3) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.016 and 0.054, respectively

(4) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were -0.010 and 0.222, respectively

(5) Dummy coded with female being the reference level

(6) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 4.0 and 1.1, respectively

(7) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.535 and 0.111, respectively

(8) *z*-transformed to a mean of zero and a standard deviation of 1; the original mean and standard deviation were 0.339 and 0.442, respectively

(9) Dummy coded with primiparous being the reference level

Chapter 3

Infant post-mortem care-taking behaviours and cannibalism in wild Guinea baboons (*Papio papio*)

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In preparation

Author Contributions

Anaïs Avilés de Diego, **Federica Dal Pesco** and **Julia Fischer** designed the study. **Anaïs Avilés de Diego** and **Federica Dal Pesco** collected the data. **Anaïs Avilés de Diego** and **Federica Dal Pesco** curated the data. **Anaïs Avilés de Diego** drafted the manuscript and prepared the figures. **Anaïs Avilés de Diego**, **Federica Dal Pesco** and **Julia Fischer** discussed the results and edited the manuscript.

3.1 Abstract

The growing field of comparative thanatology is investigating if non-human primates are able to understand death in similar ways as humans. Observations across different non-human primate species have reported care-taking behaviour of dead infants, but also cannibalism. Based on nine years of field observations (2014-2022), we report 13 cases of infant-death related responses in a wild population of Guinea baboons (*Papio papio*) in the Niokolo-Koba National Park in Senegal. Behaviours of carry, protection, grooming, and cannibalism were directed towards dead infants, mostly by their mothers, but occasionally also by other adult females. We discuss our observations in the context of different hypotheses that have been put forward to explain the occurrence of behaviours towards dead infants, while critically evaluating these explanations. We propose that selection has favoured post-mortem caretaking behaviours to avoid a type-II error in abandoning an infant that might be not responsive instead of dead, whereas social bond disruption and fading lead to the eventual abandonment of the corpse. The cannibalism observed suggests that the corpse is eventually seen as food. We advocate for scientific rigour and for elaboration of predictions that qualify for hypothesis testing, to move forward our knowledge in the field.

Keywords: thanatology, dead infant, post-mortem behaviours, care-taking, cannibalism, *Papio papio*

3.2 Introduction

Comparative thanatology has been defined as the scientific study of death and dying across animal taxa, including the underlying behavioural, psychological, physiological, and social processes that occur with the death of conspecifics (Anderson, 2016, 2017). Studying the effects associated with the passing of a relative or a social partner can elucidate the evolutionary trajectories behind death-related responses, from ancestral mechanisms to more derived traits. Within the field of primatology, comparative thanatology can shed light on the evolution of emotion and cognition, unravel how the complex post-mortem responses typical of humans emerged, and clarify if these are as unique as they seem. Questions like “what do animals know about death?” or “do animals grieve?” are central to the discipline of comparative thanatology (Anderson, 2011, 2016; Anderson et al., 2018; Bearzi et al., 2018; Carter et al., 2020; Fashing et al., 2011; Fernández-Fueyo et al., 2021; Gonçalves & Biro, 2018; Gonçalves & Carvalho, 2019; Soldati et al., 2022; Watson & Matsuzawa, 2018; Yang et al., 2022).

Historically, having a concept of death has been considered an exclusively human trait, and the most intricated responses to death are undoubtedly found in the extensive repertoire of rituals and religious ceremonies of humans (Anderson, 2016). Research in humans holds that complete awareness of death implies understanding four principal components: irreversibility, non-functionality, inevitability, and causality. *Irreversibility* is the understanding that an organism cannot go back to life; in other words, that death is a permanent state. *Non-functionality*, also called *cessation*, implies that the living functions stop working after death. *Inevitability*, also named *universality*, means knowing that all living organisms eventually die (Anderson, 2016; Speece & Brent, 1984, 1992). Finally, *causality* refers to knowing that death resulted from the disruption of one or several vital functions (Anderson, 2016; Kenyon, 2001). Literature on children's development suggests that children achieve the understanding of at least some of these components between five and seven years of age (Speece & Brent, 1984), but it is not until the age of ten years that children reach a mature understanding that comprises all four components (Speece & Brent, 1992).

Boosted by a growing interest in animal cognition and sentience, field and captive observations have triggered the question of whether animals share at least some of the components of death awareness with humans (Anderson, 2016). Responses to dead conspecifics in animals are highly variable and range from functional, innate patterns, absent of emotional components, such as *necrophobia* (i.e., corpse avoidance), to more elaborated behaviours, such as care-taking of dead conspecifics.

In eusocial insects like Hymenoptera (bees, ants, wasps) and Isoptera (termites), several corpse management strategies (i.e., undertaking behaviours) have evolved to dispose of dead colony members, namely: corpse removal or *necrophoresis*, burial and cannibalism (i.e., *necrophagia*) (Sun & Zhou, 2013; Visscher, 1983; E. O. Wilson & Durlach, 1958). Recognising and reacting to a corpse in these colony-living species is evolutionary advantageous (Gonçalves & Carvalho, 2019) since it prevents pathogen transmission and disease (Cremer et al., 2007).

Behaviours towards dead conspecifics (hereafter "post-mortem" behaviours) have also been described in corvid species. Black-billed magpies were observed to gather around a dead conspecific for a short time (ca. 5 min) before flying off simultaneously. No signs of aggression or scavenging were observed. The authors suggest that the gathering might have been motivated to obtain cues about an abnormal death of a flock member (Miller & Brigham, 1988). In western scrub jays, the sighting of a dead individual elicited the production of loud vocalisations that attracted other scrub jays and resulted in cacophonous aggregations, which have been referred to as “bird funerals” (Iglesias et al., 2012).

Across mammalian taxa, post-mortem behaviours range from immediate abandonment and necrophobia to nurturant behaviours and carrying of dead individuals. In cetaceans, carrying or supporting dead calves at the water surface has been observed by adult females, potentially the mothers (Bearzi et al., 2018; Reggente et al., 2016). In Kenya, elephants touched, sniffed, tried to lift, and stayed close to a visibly injured matriarch when she was not able to carry on. Once she died, the matriarch’s family visited and showed interest in the corpse (Douglas-Hamilton et al., 2006). In Amboseli, elephants have been seen carrying sick or dead infants on their tusks (Safina, 2015). In wild dingoes, a mother transported a dead pup for two days (Appleby et al., 2013), and in giraffes, a mother inspected and sniffed her dead new-born (Bercovitch, 2013).

The most extensive array of post-mortem behaviours has been described in the primate order; these include observations from captivity and the wild. In Old World monkeys, such observations include yellow baboons (*Papio cynocephalus* [Altmann, 1980]), chacma baboons (*Papio ursinus* [Carter et al., 2020]), Japanese macaques (*Macaca fuscata* [Sugiyama et al., 2009; Takeshita et al., 2020]), Sichuan snub-nosed monkeys (*Rhinopithecus roxellana* [Yang et al., 2022]), Indian langurs (*Presbytis entellus* [Jay, 1962]), Hanuman langurs (*Semnopithecus entellu*s [Sharma et al., 2011]), Geladas (*Theropithecus gelada* [Fashing et al., 2011]), Zanzibar red colobus (*Piliocolobus kirkii* [Georgiev et al., 2019]), bonnet macaques (*Macaca radiata* [Das et al., 2019]), and lion-tailed macaques (*Macaca silenus* [Das et al., 2019]); in New World monkeys, these species include blonde capuchins (*Sapajus flavius* [Andrade et al., 2020]), brown capuchins (*Sapajus apella* [Trapanese et al., 2020]), and northern muriquis (*Brachyteles hypoxanthus* [Freire Filho et al., 2022]). Post-mortem behaviours have also been observed in several ape species: chimpanzees (*Pan troglodytes* [Biro et al., 2010; Cronin et al., 2011; Matsuzawa, 1997; Soldati et al., 2022; Van Lawick-Goodall, 1968]), Sumatran orang-utans (*Pongo abelii* [Dellatore et al., 2009]) and gorillas (*Gorilla beringei* [Warren & Williamson, 2004]). In these studies, mothers’ most frequently observed responses have been care-taking behaviours directed towards their dead infants, such as inspection, protection, and grooming.

The most prominent post-mortem behaviour in nonhuman primates is dead infant carrying (e.g., chimpanzees [Biro et al., 2010; Soldati et al., 2022], gorillas [Masi, 2020; Warren & Williamson, 2004], Japanese macaques [Sugiyama et al., 2009], bonnet and lion-tailed macaques [Das et al., 2019], chacma baboons [Carter et al., 2020], and others (reviewed in Fernández-Fueyo et al., 2021; Gonçalves

& Carvalho, 2019; Watson & Matsuzawa, 2018). Whereas some mothers abandon their deceased infants soon after they die, others continue interacting with them for days, weeks, and even months. Interactions with the corpse ranged from less than a day to less than a week in northern muriquis (Freire Filho et al., 2022) and Japanese macaques (Sugiyama et al., 2009), from 1-3 days to more than three months in chimpanzees (Soldati et al., 2022), and from one hour to more than 48 days in geladas (Fashing et al., 2011). When the care-taking lasts, the corpse bloats, stenches, decomposes, ends up covered with flies, mummifies until just fragments of it are left, and the remains no longer resemble an infant (Sugiyama et al., 2009; Watson & Matsuzawa, 2018). In her book "Baboon mothers and infants", Jeanne Altmann (1980) describes an instance in which a baboon mother carried her deceased infant for several days; the corpse lost its head and, eventually, only some dry extremities remained.

However, not only post-mortem care-taking behaviours have been reported, but also cannibalism. Cannibalism, also referred to as *conspecific necrophagy*, is the act of consuming either parts or the totality of an individual of the same species after its death. Cannibalism has been observed in a large number of animal species, ranging from unicellular organisms (e.g., protozoa) to snails, insects, fish, centipedes, birds and mammals (reviewed in Fox, 1975). In nonhuman primates, cannibalism has been witnessed both in captivity and in the wild, and on most occasions, it involves a mother eating (parts of) her dead infant. Such behaviour has been termed *filial cannibalism* or *maternal cannibalism.* It has been observed in rhesus macaques (*Macaca mulatta* [Tian et al., 2016]), Tonkean macaques (*Macaca tonkeana* [De Marco et al., 2018]), orang-utans (Dellatore et al., 2009), bonobos (*Pan paniscus* [Fowler & Hohmann, 2010; Tokuyama et al., 2017]) and chimpanzees (Fedurek et al., 2020; Tokuyama et al., 2017), for instance. Sometimes, however, cannibalism involves conspecifics other than the mother (e.g., bonobos [Fowler & Hohmann, 2010], and white-faced capuchins, *Cebus imitator* [Kulick et al., 2021; Nishikawa et al., 2020]).

On the one hand, cannibalism can be deemed adaptive since it has nutritional and energetical benefits (Polis, 1981): it can provide relatively high-quality food, as animal source foods are rich in vitamins, elements (e.g., calcium, iodine), high-quality protein and essential fatty acids (Milton, 2003), which proves even more advantageous in periods of scarce food availability (Snyder et al., 2000). On the other hand, cannibalism might have detrimental consequences, such as those associated with pathogen transmission (Rudolf & Antonovics, 2007).

The increasing number of reports on post-mortem behaviours in nonhuman primates has led to several hypotheses. These hypotheses aim to account for the inter- and intra-specific variation in the responses towards dead individuals (reviewed in Gonçalves & Carvalho, 2019; Watson & Matsuzawa, 2018). More specifically, these hypotheses aim to explain why cannibalism may occur and why mothers may continue investing in a dead infant. Infant carrying is particularly interesting, as it is energetically costly and may also increase the risk of predation (Altmann & Samuels, 1992). Carrying a dead infant, in contrast, is maladaptive, as it hinders locomotion (mothers must now permanently hold an infant that is no longer able to hold to her mother's fur by itself), thus exacerbating predation risks for the carrier (Gonçalves & Carvalho, 2019).

Below, we summarise the most influential (not mutually exclusive) hypotheses that have been put forward to explain post-mortem behaviours in nonhuman primates directed to dead infants, mainly by the mothers, but occasionally also by other individuals:

3.2.1 Hypotheses that do not imply a concept of death

The *unawareness hypothesis* assumes that individuals do not possess an awareness of death and are not able to recognise that an individual has passed away. Regarding dependent offspring, this hypothesis holds that mothers cannot discern if their infants are dead or temporarily unresponsive and continue to treat them as alive because it is ultimately maladaptive to abandon a non-responsive infant (Sugiyama et al., 2009).

A subset of hypotheses refers to the mechanisms underlying post-mortem behaviours:

The *infantile cues hypothesis* proposes that, when alive, infants have physical characteristics that trigger maternal behaviour and, after death, they still retain these infantile features, eliciting care-taking behaviours in mothers and, occasionally, in other individuals (Alley, 1980). Examples of these infantile cues are small size and reduced proportion of infants, and colouration typical of the infant period, such as the natal coat or the skin colour.

The *post-parturition hypothesis* states that the concentration levels of pregnancy and post-partum hormones like prolactin, oxytocin and ß-endorphins, which are responsible for labour, milk production, maternal behaviours, and bonding and attachment (Broad et al., 2006; Rilling & Young, 2014), are still elevated when the infant dies. In addition, the neuroendocrine systems that regulate their secretion, such as the endogenous opioid system, are still activated (Broad et al., 2006); therefore, mothers continue to show post-mortem care-taking behaviours when they lose infants close to birth (Biro et al., 2010; Warren & Williamson, 2004). The resumption of cycling should end this process and promote corpse disposal (Biro et al., 2010).

The *mother-infant bond hypothesis* holds that the post-mortem behaviours depend on the formation of the mother-infant bond prior to the infant's death and predicts that these behaviours will last longer in older infants, as they are more strongly bonded with their mothers. This hypothesis is by far the most cited in the literature, repeatedly stating that because the mother-infant bond is the strongest social bond in primates, such attachment elicits maternal behaviours even after the death of the infant (e.g., Biro et al., 2010; De Marco et al., 2018; Matsuzawa, 1997; Yang et al., 2022).

Another subset of hypotheses refers to variation due to parity and mother age:

The *learning-to-mother hypothesis* suggests that nulliparous females are likely to interact with deceased infants of other females to gain mothering experience, such as skills related to infant carrying required for foraging and travelling, in benefit of raising their own future offspring and increase own future infant survival (Warren & Williamson, 2004; Watson & Matsuzawa, 2018). Primiparous mothers who had lost their infants at partum or in very initial states after giving birth are also susceptible to interacting with the deceased infants of other females

The *parity hypothesis* proposes that multiparous mothers will display behaviours towards dead infants for longer because they are more experienced in mothering, so the corpses are preserved better than in inexperienced mothers' hands (Biro et al., 2010). More extended interactions with dead infants by multiparous mothers could also be due to the maternal reproductive strategy under the life history theory principle of allocation of resources (Williams, 1966), which holds that older females will invest more in current offspring. After all, they have reduced future reproductive potential compared to younger females, who would discard the corpse earlier because they have more to gain in investing in future reproduction.

Another hypothesis focuses on the ecological factors that may favour the preservation of the corpses, but it is neither informative about awareness of death nor the underlying mechanisms that promote post-mortem behaviours: the *climate hypothesis* suggests that dry or cold climates favour the preservation of corpses; therefore, longer durations of interactions will presumably be observed under these conditions. On the contrary, interactions should be shorter in hotter and more humid climates, as these conditions favour decomposition, corpses ought to smell earlier, and mothers are expected to abandon the corpse sooner (Biro et al., 2010; Matsuzawa, 1997; Sugiyama et al., 2009).

3.2.2 Hypotheses that more or less explicitly assume a concept of death

The *learning-about-death hypothesis* (Cronin et al., 2011) suggests that individuals can achieve an understanding of death through exposure to sensory cues related to dead (e.g., olfactory: stench; visual: lack of movement; tactile: body temperature). For instance, older multiparous females should interact less with a dead infant because they have been exposed to death cues more frequently than young primiparous mothers.

The *grief-management hypothesis* holds that mothers continue interacting with their deceased infants to cope emotionally with loss and reduce the stress triggered by the infant's death (Takeshita et al., 2020).

Evidence in favour or against these hypotheses has been provided in several studies. For instance, research in favour of the *parity hypothesis* can be found in the study of Das and colleagues (2019), in which they analysed 43 cases from 18 primate species and revealed that older mothers displayed longer durations of dead infant carrying. However, others showed that dead-infant carrying was more likely when mothers were younger (Fernández-Fueyo et al., 2021). These authors compiled a database of 50 primate species and analysed 409 published cases of dead infant carrying. Finally, Sugiyama and colleagues (2009) found that young and older mothers' dead infant-carrying rates did not differ.

Here, we report our observations of care-taking behaviours and cannibalism towards dead infants (i.e., up to 18 months of age) in a wild population of Guinea baboons (*Papio papio*). Our reports, of anecdotal nature, aim to contribute to the general field of comparative thanatology by adding information to the general picture of animal responses to dead conspecifics, which can eventually allow for a better evaluation of the existent hypotheses and intra- and inter-specific comparisons. Based on our observations and the literature review, we propose the “fading bond” hypothesis, a modified version of the unawareness hypothesis, which considers the protection of group members in nonhuman primates and the feedback dynamics of social relationships.

3.3 Methods

3.3.1 Study species and site

We studied wild Guinea baboons living in the Niokolo-Koba National Park, in Senegal, near the facilities of the Centre de Recherche de Primatologie (CRP) Simenti, a field station of the Cognitive Ethology Laboratory of the German Primate Centre (DPZ) (Fischer et al., 2017). Guinea baboons live in nested multi-level societies. “Units” are at the base of the society, which are formed by one “primary” male and one to seven females and their immatures (Fischer et al., 2017). Most units have at least one associated bachelor male, and bachelor males usually associate with several primary males simultaneously (Dal Pesco et al., 2021). Females in a unit almost exclusively mate with the “primary” male and rarely with other males (Dal Pesco et al., 2022; Goffe et al., 2016). Several units group together into a “party”, and two or more “parties” associate to form “gangs” (Patzelt et al., 2014).

Among Guinea baboon males, it is not possible to evaluate the dominance hierarchy with certainty since aggressions between individuals are rare and decided outcomes are not always evident (Dal Pesco et al., 2021; Kalbitzer et al., 2015). Males are spatially tolerant and form strong social bonds with other males (Patzelt et al., 2014). Strongly bonded males are more highly related on average, but also males with low degrees of relatedness may form strong bonds (Dal Pesco et al., 2021). Genetic and behavioural evidence points to female-biased dispersal in this species (Kopp et al., 2015). The community of Guinea baboons in our study area comprises 350-400 individuals (Dal Pesco et al., 2021; Zinner et al., 2021). In 2014, the primary study population consisted of three parties of habituated baboons, and over the years, new parties have been identified and incorporated into the study population, while previous parties have disappeared, split, or merged with other parties. All individuals in our study population are identified by physical characteristics.

Senegal has a marked seasonality, with a dry season that lasts from November until May and a rainy season from June to October. The average annual precipitation is 956 mm, primarily in the rainy season (Fischer et al., 2017; Zinner et al., 2021). The Guinea baboons’ home range size varies with the season. In the rainy season, the median home range size is 27.4 km^2 (IQR 6.6 km^2) and 19.1 km^2 (IQR 7.6 km^2) in the dry season. The median daily travelled distance in the dry season is 3.5 km (IQR: 2.2 km), and in the rainy season is 4.4 km (IQR 2.4 km), with two peaks per year: one at the beginning and one towards the end of the rainy season (Zinner et al., 2021). The average temperature is around 30ºC, although, in the peak of the dry season, it can reach 48ºC (Fischer et al., 2017). The average humidity in the dry season is 44.2%, and 65% in the rainy season (Ohrndorf et al., 2022).

3.3.2 Data collection

For nine years (2014 to 2022), data were collected opportunistically each time behaviours towards dead individuals were observed in our population of Guinea baboons. Data were recorded with the handhelds Samsung Galaxy Note II GT-7100 or Gigaset GX290, using electronic forms designed with the software Pendragon version 7.2.21 (Pendragon Software Corporation, Chicago, IL, USA). The information recorded consisted of the date of the event, infant ID (i.e., corpse), the ID of the actor of the post-mortem behaviours, type of relationship between corpse and actor ID (i.e., mother versus non-mother), duration of interactions between actor ID and corpse, and type of post-mortem behaviours observed; all other potentially relevant information was recorded *ad-libitum*. Furthermore, the age of the infant at death and parity of the actor (in case the actor was a female) was determined from our long-term demographic database, which contains daily information on significant life history and social events such as births, deaths, health status, transfers, and female reproductive states (Goffe et al., 2016). In addition, data on meteorology was recorded daily, which consists of minimum and maximum temperatures, minimum and maximum relative humidity, and precipitation.

3.4 Results

In the study period, we observed 13 cases of behaviours directed at dead infants, which are summarised in Table 3.1. The median age of the deceased infants was 34 days (IQR: 1-38 days). In all cases except one (case 2), the actors of the post-mortem behaviours were the mother of the dead infants, who were generally protective of the corpse and prevented other individuals from accessing the corpse. In the remaining case (case 2), the mother of the infant had previously died, which we assumed to have caused the infant's death, and the behaviours were displayed by two females that were not the mother of the infant corpse (hereafter non-mother females), one after the other. Interactions with the corpse lasted from a few hours to 5 days (median: 2 days; IQR: 0-4 days; zero here means for just a few hours). The distribution of events was not restricted to one season, with 38.5% and 61.5% of events occurring in the rainy and dry season, respectively (see Table 3.1).

The behaviours observed were dead infant carrying (Fig. 3.1), protection, which consisted of closely holding and retrieving the corpse before other individuals approached it, grooming (Fig. 3.2) and cannibalism (Fig. 3.3). Carrying occurred in all 13 cases, one of them by a nulliparous non-mother (case 2). The corpse was always carried either in the actor's arm or mouth (Fig. 3.1) and never on the back, as observed, for instance, in chimpanzees (Biro et al., 2010). Protection occurred in six cases and grooming in three. Cannibalism was seen on three occasions; one of them was the case in which the mother had previously died. In this case, the primiparous non-mother displayed cannibalism after the nulliparous non-mother had discarded the body (case 2).

Figure 3.1. Dead infant carrying. (A) Mother-infant dyad APL-APL1 (case 1); the mother is carrying the deceased infant with both one arm and the mouth; (B) and (C) Mother-infant dyad SLY-SLY2 (case 5); both pictures show the mother carrying the corpse in her mouth (Photo (A) by Federica Dal Pesco, Photo (B) and (C) by Lauriane Faraut; Cognitive Ethology Laboratory, German Primate Centre).

Figure 3.2. Dead infant grooming. The pictures show the AXL-APX mother-infant dyad (case 10) (Photos by Anaïs Avilés de Diego, Cognitive Ethology Laboratory, German Primate Centre).

Figure 3.3. Filial cannibalism by ASA in the ASA-ALI mother-infant dyad (case 6). In the second picture, the mother is pulling the tongue of the deceased infant with her teeth (Photos by Anaïs Avilés de Diego, Cognitive Ethology Laboratory, German Primate Centre).

Cause of death was unknown for all infants except, to a certain extent, for TKI2 (case number 11); this infant was seen alive three days before the onset of post-mortem behaviours, and two possible causes of injury were witnessed on that day: first, the mother walked through a particularly dense thorny area and, second, that infant was dragged on the floor for several meters by the primary male of her unit; although male-infant dragging is not unusual in Guinea baboons, the male dragged the infant for several meters, while the infant seemed extremely distressed (pers. observation). Later that day, when researchers saw the mother-infant dyad again, the infant had wounds on her body and was bleeding (Fig. 3.4). Besides case number 11, none of the remaining reports informed about open wounds or missing body fragments.

Neither the moment of death nor the abandonment of the corpse was ever witnessed by the researchers. The two infants observed dead on the day they were born (cases 3 and 8) could have been stillborn. No signs of illness, malnourishment or mishandling were detected in any case. Infanticide seems unlikely since it has never been observed in our population of Guinea baboons, and pregnant and lactating females may transfer to a new primary male without any following feticide or infanticide occurrences. Accidental falls could be one cause of death, as even though Guinea baboons have terrestrial locomotion, they also forage and sleep in trees. Although Guinea baboons are subject to predation from lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), and African wild dogs (*Lycaon pictus*) (Zinner et al., 2021), it is unlikely that any of the dead infants reported here died due to predator attacks.

Figure 3.4. Mother-infant dyad TKI-TKI2 (case number 11) after the infant TKI2 had been injured. Blood is visible on the left side of the infant's body (Photos by Anaïs Avilés de Diego, Cognitive Ethology Laboratory, German Primate Centre).

Table 3.1. Events of post-mortem behaviours observed in a wild population of Guinea baboons from 2014 to 2022.

Case no.	Female-infant dyad	Date event (month and year)	Relationship to corpse	Parity	Infant sex	Age at death (days)	Duration of Interactions (days)	Season	Carry	Protect	Grooming	Cannibalism
1	ATA-ATA3	July 2015	Mother	Multiparous	Male	1	2	Rainy	✓			
2[1]	DPH-; YKO-BMB	August 2015	Non-mother	Nulliparous Primiparous	Male	36	5 (4+1)[2]	Rainy	✓			✓
3	APL-APL1	Sept. 2015	Mother	Primiparous	Unknown	0	2	Rainy	✓			
4	LCY-LCY3	May 2016	Mother	Multiparous	Female	2	5	Dry	✓			
5	SLY-SLY2	February 2017	Mother	Multiparous	Male	1	<1	Dry	✓	✓		
6	ASA-ALI	January 2018	Mother	Multiparous	Male	135	3	Dry	✓	✓		✓
7	EKA-ERE	October 2018	Mother	Multiparous	Female	226	<1	Rainy	✓		✓	
8	URS-URS1	February 2019	Mother	Unknown	Female	0	<1	Dry	✓	✓	✓	
9	RAH-RCK	February 2019	Mother	Multiparous	Male	89	<1	Dry	✓	✓		✓
10	AXL-APX	May 2019	Mother	Multiparous	Male	38	4	Dry	✓	✓	✓	
11	TKI-TKI2	March 2020	Mother	Multiparous	Female	34	3	Dry	✓	✓		
12	BTR-BRC	October 2021	Mother	Multiparous	Male	38	<1	Rainy	✓			
13	LSL-LSL4	February 2022	Mother	Multiparous	Unknown	1	4	Dry	✓			

[1] A female nulliparous non-mother first carried the dead infant, and a primiparous non-mother female cannibalised the same infant afterwards.

[2] The nulliparous mother, who was pregnant at the time, carried the infant for four days. Then, on the fifth day, the primiparous mother cannibalised the infant

3.5 Discussion

We observed post-mortem care-taking behaviours towards 13 dead infants in our study population of wild Guinea baboons during nine years (2014-2022). On three occasions, we also observed cannibalism. In all cases, the deceased individuals were infants, and only in one instance was the infant older than six months. Consistent with reports from other nonhuman primate species, dead infant carry was the most observed post-mortem behaviour (see Introduction), and protection and grooming were observed occasionally (Biro et al., 2010; Carter et al., 2020; Cronin et al., 2011; Fashing et al., 2011; Yang et al., 2022).

The duration of interactions towards the infants in this study (<1 to 5 days) was in line with the reports in other species (e.g., Northern muriquis: 1-3 days [Freire Filho et al., 2022], chacma baboons: 2-10 days [Carter et al., 2020], Japanese macaques: mean 3.3 days (range, 1-17; SD, 2.7) [Sugiyama et al., 2009], Sichuan snub-nosed monkeys: 5 days [Yang et al., 2022]), but relatively short compared to the maximum registered in other primate species (e.g., Tonquean macaques: 25 days [De Marco et al., 2018], Hanuman langurs: 27 days [Sharma et al., 2011], geladas: 48 days [Fashing et al., 2011], chimpanzees: 68 days [Biro et al., 2010] and 89 days [Soldati et al., 2022]). In a similar study with chacma baboons, Carter and colleagues (2020) proposed that the cost derived from carrying a dead infant in species that travel long daily distances leads to short durations. On some occasions, the corpse had lost body mass and hair (Fig. 3.2), likely due to infant dragging; however, mummification was never observed, which may be due to the relatively short interactions with the corpses in Guinea baboons.

We first discuss hypotheses that do not imply a concept of death:

Infantile cues hypothesis

The presence of infantile characteristics in the dead infants may act as a releaser (i.e., a stimulus that triggers an innate behaviour: Lorenz, 1937), eliciting the care-taking behaviours in both mothers and non-mothers.

Post-parturition hypothesis

Pregnancy and post-parturition hormones, such as prolactin, oxytocin and ß-endorphins, are responsible for maternal behaviours, bonding and attachment (Broad et al., 2006; Rilling & Young, 2014). It has been proposed that these pregnancy and post-parturition hormones should be present until ovulation resumption or lactation cessation (Biro et al., 2010; Kaplan, 1973), and while they are present in the organism, mothers might continue to show post-mortem care-taking behaviours. While hormones might play a role in post-mortem care-taking behaviours, they are not needed to trigger maternal care in Old World monkeys and apes (including humans) (Broad et al., 2006), nor do they explain by themselves the mechanisms underlying post-mortem behaviours. For instance, the observation that non-mothers also engage in post-mortem behaviour speaks against the post-parturition hypothesis. In other words, post-parturition hormones are not necessary for eliciting such behaviours, although they may be involved.

Mother-infant bond

The mother-infant bond is typically known as the most vital social bond that exists in mammals (Nicolson, 1987). While the mother-infant bond has a hormonal component that involves, for instance, the presence of oxytocin (Broad et al., 2006; Kendrick, 2000), behaviours such as contact, proximity, suckling, mother-infant mutual gaze, facial expressions and reciprocity of interactions between a mother and her infant are essential contributing factors to the maintenance of the bond (Cerrito & DeCasien, 2021; Ferrari et al., 2009; Maestripieri, 2001; Mogi et al., 2011). Further, in primates, bonding can occur in the absence of pregnancy, parturition, and lactation, even in individuals that are not the mothers of the infants (Broad et al., 2006), which might explain why post-mortem behaviours also occur in non-mothers.

Learning-to-mother hypothesis

One of the non-mother females that showed care-taking behaviours was nulliparous. This female, who was also pregnant then, could have benefited from learning care-taking skills in favour of her own infant’s future survival. From an evolutionary perspective, however, it seems questionable that dead infant carrying and care-taking evolved because it proved beneficial to acquire care-taking skills. Firstly, the key care-takers are the mothers themselves, so there is little opportunity for non-mothers to learn to mother; secondly, a dead infant does not provide much opportunity to establish a bond.

Parity hypothesis

Of our 13 cases, nine females showing post-mortem behaviours were multiparous. These females also displayed the lengthiest interactions. Although our observations could align with the parity hypothesis, this hypothesis fails to explain why post-mortem behaviours occur or why they might have evolved and just offers descriptions of observed variation between females. Caution should be made, therefore, when assigning causation of post-mortem behaviours to parity. Further, several studies show opposite results about parity and behaviours directed towards dead individuals (see Introduction).

Climate hypothesis

The climate hypothesis is only informative about the ecological conditions surrounding the death of an infant that could promote the opportunity for post-mortem behaviours. The observed distribution of post-mortem behaviours does not indicate a strong effect of season, but due to the small sample size, our data do not allow us to make strong claims regarding the effect of season. Other studies with more comprehensive datasets have failed to find evidence in support of the *climate hypothesis*, however (Fernández-Fueyo et al., 2021; Lonsdorf et al., 2020).

In the following, we turn to hypotheses that more or less explicitly assume a concept of death:

Learning-about-death hypothesis

The fact that more experienced mothers tended to care for the dead infants for longer speaks against the *learning-about-death hypothesis*; this hypothesis predicted that multiparous females should show shorter interactions with dead infants compared to primiparous females.

Grief-management hypothesis

Research in humans shows that the loss of a loved individual leads to grief and distress (Boelen & Lenferink, 2020; Webb & Guarino, 2011) and that bereavement is associated with an activation of the hypothalamic-pituitary-adrenal (HPA) axis, causing an increase in glucocorticoid (GC) secretion (McCleery et al., 2000). The increase of stress-related hormones has also been reported for several nonhuman primate species after experiencing loss. For example, in female chacma baboons, glucocorticoids were more elevated after the death of a close relative (Engh et al., 2006). In chimpanzees, maternal loss triggered a cortisol increase in orphaned immatures (Girard-Buttoz et al., 2021).

According to the grief-management hypothesis (Takeshita et al., 2020), caring for an infant after its death could be a grieving coping mechanism for the mothers, by which they can mitigate stress and, thus, adjust to the loss. In most human societies, caring for a dead body is a coping mechanism after a loved one has died (Beder, 2002). Further, in humans, seeing and holding a stillborn reduces anxiety and depression in mothers compared to those mothers that did not see nor hold their stillborn babies (Cacciatore et al., 2008).

The grief-management hypothesis equates grief with distress. We advocate distinguishing between the two concepts, as grief implies a concept of death while distress does not. Along those lines, an animal might experience distress in response to the loss of a social partner but not grief. Regarding the care-taking of dead infants, it might be possible that the mothers experience neither, assuming that the animals do not have a concept of death. One would expect that the animals show signs of distress and experience elevated GC-levels when a social partner or the infant suddenly disappears, while no such distress occurs when the infant's body is still present. Interestingly, Barbary macaque (*Macaca sylvanus*) females in a managed population at La Forêt des Singes in Rocamadour produced long series of specific contact screams after their dead infants had been removed from by the park management. In contrast, mothers who were allowed to hold on to their dead infants showed no such signs (Hammerschmidt & Fischer, 1998). In our study, we never witnessed such vocalisations. Secondly, the grief-management hypothesis is not testable: even if we recorded elevated GC levels after the infant’s death, these would not allow us to conclude that the animals experience grief. More importantly, if we would *not* observe elevated GC levels after an infant’s death (when the mother still carries the infant), we would not be able to decide whether this is due to the handling of the infant as a means of soothing grief, or because the mother does not experience grief.

Regarding the concept of “death awareness”, it has been proposed that a relative awareness of death could be possible in nonhuman primates, as they should be able to perceive and differentiate animate/inanimate conceptual categories (reviewed in Gonçalves & Carvalho, 2019) and gather some death-related information through olfactory, tactile or visual cues, for instance, by touching, sniffing or seeing a dead individual (Cronin et al., 2011). Other studies suggest that primates may share the *non-functionality* and *irreversibility* components of death awareness with humans (Lonsdorf et al., 2020), although the evidence provided seems inconclusive since, for instance, they state that the fact that mothers eventually abandon the corpse is proof for *irreversibility*. However, we contend that as long there is no strong evidence for an understanding of the concept of death (and clear criteria to identify the components of death awareness), no such concept should be attributed. Monsó and Osuna-Mascoró (2021) argued that the criteria established to attribute a concept of death are a form of intellectual anthropocentrism and should therefore be revised. In addition, they lament emotional anthropocentrism with “an excessive focus on grief as a reaction to death” (p. 2251). Instead, they advocate Monsó’s (2022) “minimal concept of death”. This minimal concept assumes that animals are able to classify other beings as “dead” if they used to show characteristics of living beings but now no longer do so and if this change appears irreversible. Convincing examples are unfortunately not provided. For the time being, we, therefore, propose sticking to the more parsimonious explanation, which holds that all the observed behaviours may be explained without invoking any concept of death. Note that we agree with the view that many animals can distinguish between a living and a dead animal, as several studies have shown that animals have a strong sense of animacy (reviewed in Monsó and Osuna-Mascoró, 2021). However, being able to distinguish between living and dead organisms is not the same as having a concept of death.

Our interpretation of the processes concerning post-mortem behaviours towards infants is as follows: evolution has placed a high premium on avoiding a type-II error and abandoning an infant that is only listless but not dead. Mothers are selected to “err” on the side of over-care-taking and continue to carry and groom the infant. At the same time, the mother experiences a change in the infant's appearance and a lack of infant responses. The change of appearance will decrease the power of the infant's appearance as a releaser for care-taking behaviour; the infant's lack of responses, such as gazing at the mother, lip-smacking, or suckling, will lead to a fading of the bond. In this sense, the post-mortem behaviour of females provides deep insights into the importance of mutual feedback for maintaining a social bond (see Fischer, 2017 for further examples).

Furthermore, the cannibalism observed indicates that at some point during this process, the infant corpse may be represented as both: something requiring care-taking and a food item (meat). Guinea baboons opportunistically hunt and feed on prey, such as young antelopes (*Tragelaphus scriptus*), hares (*Lepus microtis*) and birds (Goffe & Fischer, 2016); therefore, meat consumption is not unusual. In two of the three cases of cannibalism, the corpse was consumed when it already produced a pungent stench (pers. observation). Interestingly, in our population of Guinea baboons, we also observed grooming and protection during meat-eating events involving a prey.

In addition to the observed care-taking behaviour directed at the infant, we have personally experienced in Barbary macaques and chacma baboons that the animals may be highly protective of the corpse, even if it has begun to resemble a piece of dried leather rather than an infant monkey. For instance, in their book “Baboon metaphysics: the evolution of a social mind” Dorothy Cheney and Robert Seyfarth (2007) mention guards of infant corpses from other group members when the mothers move away from the dead infant. Thus, the animals appear to have a strong sense of protecting their group members, again erring on the safe side (from their perspective). Our observations when we dart Guinea baboons at the field site in Simenti corroborate this observation: once a darted baboon falls asleep amidst the other group members, there is little attention from others. Nevertheless, the darting team must take extreme precautions that all other baboons have left the scene before they can approach and handle the darted baboon (pers. observation).

Our observations are in line with previous reports of nonhuman primates in which care-taking behaviours are directed towards dead infants, with the occasional presence of cannibalism. We encourage studies in the field, as well as in captivity, to communicate their observations of behaviours directed towards dead individuals, despite being anecdotal; these events are rare, even when observation periods are long, highlighting the importance of reports from long-term studies. Additionally, we welcome data sharing (e.g., “ThanatoBase”; https://thanatobase-data-entry.mystrikingly.com) to produce more extensive and comprehensive datasets that allow for hypothesis testing and phylogenetic comparisons. At the same time, we feel that more rigour is needed in the advancement of hypotheses. Specifically, testable predictions should be developed, potentially allowing us to rule out specific hypotheses. Caution should be made when assuming or interpreting cognitive and emotional processes underlying post-mortem behaviours, such as the capacity to experience grief or the attribution of awareness of death due to the ability to distinguish between animate and inanimate categories. We advocate for physiological processes related to social bond disruption and subsequent fading of the social bond, along with releasers as mechanisms underpinning post-mortem behaviours. Of course, it might be possible that the animals have a concept of death, but from a scientific perspective, it is mandatory to retain a sceptical stance. Simply invoking the possibility of a more sophisticated understanding is not sufficient to claim its existence.

3.6 Acknowledgements

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3.7 Compliance with ethical standard

Approval and research permission was granted by the DPN and the MEPN de la République du Sénégal. Research was conducted within the regulations set by the Senegalese agencies as well as by the Animal Care Committee at the German Primate Centre.

3.8 Ethical approval

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals followed the ethical standards of the institution or practice at which the studies were conducted.

Chapter 4

General Discussion

The aim of this study was to investigate mother-infant relationships in wild Guinea baboons, and to shed a light into the mechanisms underlying the occurrence of behaviours directed from mothers to dead infants in this species. Guinea baboons are an interesting model to study mother-infant relationships, since they live in a tolerant, multi-level society, with female-biased dispersal, in which the social environment is considerably safe for the infants due to the high inter-individual familiarity across sub-groups and the low degree of social risks. In this final chapter, I will discuss some aspects that I regard necessary for taking a broader perspective on the understanding of mother-infant relationships in Guinea baboons and in human and non-human primates in general, and for the steps to follow when formulating future research.

4.1 Summary of results

In study 1 (**chapter 2**), I describe the developmental trajectory of behaviours between mothers and infants in wild Guinea baboons. I show that, while some of these behaviours follow a similar pattern compared to other primate species, other behaviours appear to be very rare. I characterize mothering style in Guinea baboons, which is based on three continuous variables: 1) factor scores obtained from a factor analysis including nipple contact, proximity, and contact, 2) carry behaviour, and 3) instances in which the mother left her infant. Contrary to other studies, I show that mothering style does not have a noticeable effect on infant growth and survival in Guinea baboons up to 1.5 years of life. I offer explanations about potential infant mortality causes in Guinea baboons, and I critically examine the results obtained. I further present a new approach that allows to control for infant age, which is of great significance in processes associated with ontogeny, and to correct for lack of homogeneity in the data, a common issue when working with wild animals.

In study 2 (**chapter 3**) I report and discuss the observations of post-mortem care-taking behaviours and cannibalism recorded during nine years in our study population of Guinea baboons. I show that the post-mortem behaviours observed in Guinea baboons do not significantly differ from the ones reported from other non-human primate species. I further critically examine hypotheses that have been proposed to explain post-mortem behaviours in non-human primates.

4.2 Mothering style in a tolerant species: the Guinea baboons

The individual differences in the way mothers behave towards their infants are typically defined as mothering style, and it has been shown that different mothering styles might affect infant's survival, growth, general development, and age of weaning (Altmann, 1980; Fairbanks, 1996; Nicolson, 1987). Studies on mothering style have typically classified mothers along two dimensions referred to as protectiveness and rejection (Fairbanks, 1996). Protective mothers tend to produce offspring that have higher survival rates (e.g., Altmann, 1980), and faster growth trajectories are expected in infants from protective mothers since they associate for longer times with the mother, who is a source of milk and social learning for acquiring foraging skills (R. A. Hinde & Spencer-Booth, 1967; Suomi, 2005). Rejecting mothers produce infants that are bolder but, since they spend more time away from their mothers, they benefit less from maternal protection and are more exposed to risks, thus experiencing higher mortality rates (e.g., Altmann, 1980). With study 1 (chapter 2) I contribute to the general knowledge of the variation in mother-infant relationship and mothering styles in primates from the perspective of Guinea baboons. In Guinea baboons mothering style did not have any noticeable effect on infant growth and survival since a rejecting mothering style did not predict higher mortality and slower growth trajectories.

Can we determine protective and rejecting as *good* and *bad* mothering style? Is it one *better* than the other? Jeanne Altmann (1980) mentions that a protective mothering style might imply a better mothering for infant yellow baboons, since survival is higher in infants from these mothers. However, in the sense that infants of protective mothers reach independence later, protective might be a bad style of mothering, as they might be less able to survive the death of their mothers at an age in which infants of rejecting mothers would have been able to survive. Altmann suggests that a protective style is a "strategy that achieves a short-term gain at the cost of a long-term loss" (Altmann, 1980; p. 188). Our results do not seem to indicate that a protective or a rejecting style is better than the other; however, differences in mothering style in Guinea baboons appear less pronounced than in yellow baboons, and behaviours of protection (i.e., retrieving, restraining), cradle, and rejection (i.e., mock bite, push away, nipple contact and carry rejection) are very infrequent, which overall suggests a more permissive and relaxed mothering style as a consequence of the tolerant social system of guinea baboons. Further, in Guinea baboons, females form linear and steep hierarchies within a unit, the most basal entity of the multi-level society, but there are no matriclans and rank does not depend on kin (Faraut et al., 2019; Fischer et al., 2017). Therefore, adopting a protective or rejecting mothering style can be seen as a strategy that is beneficial depending on which factors might be affecting the individuals of a population or a given species, such as dominance relationships, rank, food availability, increased competition due to group density, transfer of new males, etc. Generally, in species forming strict hierarchies, mothers need to be more protective, except if they are higher-ranking (e.g., rhesus macaques). In tolerant societies, mothers are typically more permissive, since other individuals do not pose a risk for the infants (e.g., Tonkean macaques [Hawkes et al., 2017; Thierry, 2013]). Therefore, the covariation between mothering style, maternal caregiving behaviour, and dominance style might be the result of the need for infant protection in a given society (reviewed in Hawkes et al., 2017).

4.3 On the evolution of the mother-infant bond

The course of mammal evolution has been characterised by placentation, foetal internal development, and lactation. Gestation, pre-natal investment, and post-natal investment in the form of lactation can only be supplied by mothers. Moreover, to ensure offspring survival, a period of extended maternal care is common in mammals (Clutton-Brock, 2016). It is not unexpected, therefore, that the strongest bond is the one between mothers and offspring. However, some aspects of the bonding separate primates from the rest of mammals (Broad et al., 2006).

In early mammals, information from the external environment was integrated through sensory detection and brain processing. In order to regulate homeostasis, early mammalian brains also processed internal information. Organisms would, therefore, behave in response to their internal and external needs. For instance, thirst would trigger a drinking response, and pregnancy hormones would trigger maternal care (Broad et al., 2006; Keverne, 2001). This is still the case for most mammalian species, in which maternal care is not spontaneous, since it is triggered as a consequence of the effect of pregnancy, parturition and lactation hormones (Broad et al., 2006; Keverne, 2001). In most mammals, bond formation and regulation are mostly mediated through hormonal responses elicited by odour recognition, tactile stimulation, and reward stimulus (Broad et al., 2006; Curley & Keverne, 2005; Keverne, 2001); specific hormones and expression changes in neuropeptides such as ß-endorphin and oxytocin mediate maternal care and other social behaviours, and maternal care ceases at weaning (Broad et al., 2006; Curley & Keverne, 2005; Keverne, 2001; Keverne & Curley, 2004).

The evolution of small to large brains in anthropoid primates produced a transition from olfactory to complex visual processing and recognition, which was promoted by the selective pressures on vision, and the subsequent development of trichromatism, derived from the change from a nocturnal to a diurnal lifestyle (Broad et al., 2006; Curley & Keverne, 2005). In similar ways as in other mammals, the appearance of maternal behaviours in primates is mediated by hormonal and neuropeptide changes promoted by pregnancy, parturition, and lactation. For instance, in primates, pregnancy oestrogen stimulates responsiveness to infant stimuli, placental lactogen and prolactin promote the expression of maternal behaviour, and oxytocin at the brain level increases affiliation and interest in infants (Saltzman & Maestripieri, 2011). Further, maternal attachment appears to be mediated by the endogenous opioid system, and serotonin at brain level acts on impulsivity and anxiety, and can affect behaviours such as infant retrieval and rejections to the infant's attempts to establish contact with the mother (Saltzman & Maestripieri, 2011). However, in monkeys and apes, the evolutionary expansion of the brain and the increasing complexity of social interactions and social systems seems to have promoted an emancipation of the mother-infant bonding away from exclusively hormonal pathways, even though hormones still play a role in enhancing maternal behaviours and bonding (Broad et al., 2006; Curley & Keverne, 2005; Maestripieri & Zehr, 1998; Saltzman & Maestripieri, 2011). In primates, recognition is based on vision instead of olfaction, caregiving and bonding can occur outside the context of pregnancy, parturition, and lactation, and seem to be highly promoted by physical interaction; caregiving behaviour can, in fact, be elicited in females other than the mother, in the father, and in other males (Broad et al., 2006; Curley & Keverne, 2005; Saltzman & Maestripieri, 2011). In humans, infant-bonded relationships take place with fathers, siblings, aunts, grandparents, adoptive parents, and can occur with other non-family members (Broad et al., 2006) (see section 4.4). The emancipation from hormonal regulation in bonding and maternal care in anthropoid primates has made possible the extended parental and allomaternal care beyond weaning (Broad et al., 2006). The observed post-mortem caretaking behaviours in our population of Guinea baboons displayed by individuals other than the mother described in study 2 (chapter 3) reflect the consequences of the emancipation from pregnancy, gestation, and lactation hormones in anthropoid primates, which causes the ability to elicit maternal behaviours in non-mothers, and the importance of mutual feedback for maintaining a social bonds, since the cessation of such responses seem to occur when there is no reciprocity from the infant side.

4.4 Variability in mother-infant relationships and relationships beyond the mother in human and non-human primates

Both humans and non-human primates show variability in the mother-infant relationships, but also in their interaction with other group members. In non-human primates, relationships beyond the mother will depend on several factors, such as social system, dominance style, mothering style, mother parity, dispersal pattern, and number and age of co-resident siblings (Hawkes et al., 2017).

In non-human primate species in which kinship plays a main role in determining steep dominance hierarchies, mothers exert a strong control on the social relationships of their infants. Protective mothers restrict the movements of infants, who not only interact less with other individuals, but also experience more severe consequences should their mother die or disappear. This control of the mother on her infant's social relationships is more exacerbated in species that are socially intolerant, like it is the case of rhesus and Japanese macaques (Hawkes et al., 2017; Thierry, 2007, 2013). In contrast, in species with tolerant social systems, like it is the case of Tonkean macaques, infants frequently interact with other social members, and the absence of the mother does not imply serious outcomes, since other members of the group buffer the consequences of maternal absence and the disruption of the mother infant bond (Drago & Thierry, 2000). Furthermore, social systems with high tolerant social interactions allow for social learning from individuals other than the mother (Coussi-Korbel & Fragaszy, 1995). In colobines there is a high affiliation between infants and allomothers (Kumar et al., 2005; Kumar & Solanki, 2014; McKenna, 1979, 1981), and allomothering has been observed to start after three hours of the infant's birth (capped langur, *Trachypithecus pileatus* [Kumar et al., 2005]). Allomothering in colobines allows for socially coordinated infant growth and development (Kumar et al., 2005), and increases infants' survival chances should their mothers die (McKenna, 1981). Therefore, infant relationships beyond the mother have the potential to act as a social buffer and as a role for social learning in non-human primates.

Similar social-buffering and social learning mechanisms occur in humans, in which cultural and social diversity manifest in the way of an extensive variation in mother-infant relationships and child relationships beyond the one with mother. In contrast to the rest of primates, humans have shortened gestation with respect to neural maturation, and reach weaning earlier (Hawkes et al., 2017; Keller & Chaudhary, 2017), and maternal investment can be reduced as long as care is shared with fathers, grandparents, older siblings, or unrelated kin (Hrdy, 2009). In many societies around the world, mothers and children live within larger communities and kinship groups, and children-rearing is shared with other members of the community (Seymour, 2013). For instance, allomaternal care by kin and non-kin is extensive in the ethnic groups of people Aka (Meehan & Hawks, 2013) and Hadza, (Crittenden & Marlowe, 2013; Hawkes et al., 1997). Studies so far have shown that allomaternal care in humans increases infant growth and survival, and that strong relationships with other individuals increase the sense of security in children (Hawkes et al., 1997; Meehan & Hawks, 2013).

4.5 Conclusions and outlook

In this thesis, I conducted the first study on mother-infant relationships in wild Guinea baboons. Using behavioural data, data on demography, and Parallel Laser Photogrammetry data, I was able to describe the development of behaviours between mothers and infants throughout infancy and characterize mothering styles in Guinea baboons. Further, I was able to determine that mothering style and mother inexperience does not have a noticeable effect on infant growth and survival in Guinea baboons, although I critically evaluated a possible lack of effect due to sparsity in the data and methodological issues derived from Parallel Laser Photogrammetry (see section 3.5).

I showed that mothers in Guinea baboons are characterized by fewer overall behaviours of protection and rejection (including rejection of nipple contact and carry rejection), and that differences in protective-rejecting mothering style are less pronounced compared to other species of the genus *Papio*, such as yellow baboons. Further, I revealed that Guinea baboons mothers and infants associate for longer than yellow baboons. Overall, Guinea baboons adopt a more permissive and relaxed style of mothering, as a consequence of their tolerant social system and their safe social environment. I added to the mother-infant relationship and growth assessment in non-human primates with a new statistical approach.

In this thesis I contributed to the ongoing debate on the awareness of death in non-human primates. Using data collected opportunistically, and data on demography, I reported the cases of post-mortem caretaking behaviours and cannibalism over the course of nine years in our population of Guinea baboons. I critically evaluated the hypotheses that until present try to elucidate the behavioural responses towards dead infants in non-human primates, and I declared the *grief-management hypothesis* as non-testable. I called for caution when hypotheses that only explain variation in post-mortem behaviours are used to assign causation, and when lightly attributing non-human primates the ability to understand death. I interpreted the proximate mechanism of the occurrence of post-mortem behaviours as a result of the high significance of the mother-infant bond along with the releaser potential of the infant's appearance, and the ultimate mechanism from the perspective that abandoning a non-responsive infant is non-adaptive, and mothers show over-care-taking because their “erring” behaviour is selected for. I further ascribed the termination of post-mortem caretaking behaviours to the fading of the mother-infant bond and lack of infant reciprocity. Overall, it is of utmost importance to exert rigour and to develop testable predictions for the advancement of the hypotheses and in the field.

Altogether, my thesis contributes to increasing the current knowledge on mothers and infants in primates, and also raises new research questions. Further research should now turn to investigating if other characteristics of the mother, such as maternal condition, might affect aspects of the infant development in Guinea baboons. New investigation should now shed light into the dynamics of the mother-infant relationships from the perspective of the infant, and their role in maintaining contact and proximity, and overall contribution to the bond with the mother.

My results also open new questions about the potential effect of forming and maintaining early social bonds with other conspecifics for the development and survival of individuals, which might prove advantageous in a social system with female-biased dispersal in which mothers might leave their offspring behind. In species with high tolerant social interactions, immatures can greatly benefit from social learning from other individuals than the mother (Coussi-Korbel & Fragaszy, 1995), which, along with the potentially high social buffering of tolerant species (see section 4.4) could further disentangle why rejecting mothering style and mother inexperience were not major determinants of infant survival and growth in Guinea baboons in study 1 (chapter 2). Further research is needed to unravel these open questions.

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