Sibling competition in two social primate species, chacma baboons and mandrills

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Sibling competition in two social primate species, chacma baboons and mandrills

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Scampi's piercing scream

Bring's the wrath of J-troop's mob.

Helen's trousers ripped.

Baboon Haiku, Esa Ahmad

ABSTRACT

Parental care is widespread in the animal kingdom and refers to any parental trait that enhances an offspring fitness. Yet, the amount of parental care that can be devoted to each offspring is limited, conflicts may therefore arise between the different family members with diverging evolutionary interests. Sibling competition has been extensively studied by behavioural ecologists who focused on competition over parental resources between same-age offspring in species producing broods or litters, or by psychologists who focused on children from Western societies. Hence, little is known on competition between different-age siblings in non-human species producing one offspring at a time (i.e. monotocous). In this thesis, we investigated the causes and mechanisms of sibling competition in two social primate species, chacma baboons (*Papio ursinus*) and mandrills (*Mandrillus sphinx*). These two species both produce one offspring at a time and share many similarities in their social organization but mandrills are seasonal breeders living in equatorial, food-rich forests while chacma baboons reproduce non-seasonally and live in a challenging arid environment. In the first two chapters, I investigate the dynamics of maternal care and mother-offspring relationships during an intriguing milestone, the birth of a younger sibling, in both species. I show that young chacma baboons solicit their mother more often and show more signs of anxiety after the birth of their younger sibling although they are already weaned and do not suffer from reduced maternal investment. This result suggests a discrepancy between the amount of maternal care provided by the mother and the amount requested by the juvenile (*manuscript 1*). In contrast, in mandrills, the birth of a younger sibling induces an abrupt decrease in maternal care toward the older sibling which, yet, does not trigger any detectable signs of conflicts. In addition, juvenile mandrills show sex-specific reactions, with females increasing their affiliations toward the mother while males become more rapidly independent than females (*manuscript 2*). Finally, as sibling competition in humans is often characterized by children's attempts to disrupt affiliative interactions between their mother and their siblings, the last chapter investigates offspring interferences in grooming interactions between the mother and a sibling. I show that grooming interferences occur in contexts eliciting sibling competition, are most frequent against siblings with whom competition is more intense, and are generally unsuccessful at granting access to maternal grooming (*manuscript 3*). These results suggest that grooming interferences may reflect spontaneous emotional reactions to affiliation between the mother and a sibling rather than strategic attempts to gain maternal grooming. This work extends our understanding of sibling competition in long-lived, monotocous social mammals by showing that sibling conflict can extend beyond nutritional dependency, over post-weaning maternal resources such as maternal grooming and attention, and can take subtle forms. In addition, this thesis provides new insights on the potential emotional aspect of sibling competition and the evolution of secondary emotional states in non-human primates.

Keywords: sibling competition; parental investment; post-weaning maternal care; transition to siblinghood; jealousy

RESUME

Les soins parentaux sont très répandus dans le règne animal et désignent tout trait parental qui améliore la santé de la progéniture. Cependant, la quantité de soins parentaux qui peut être consacrée à chaque enfant est limitée. Des conflits peuvent donc survenir entre les différents membres de la famille dont les intérêts évolutifs divergent. La compétition entre frères et sœurs a été largement étudiée par les écologistes comportementaux qui se sont concentrés sur la compétition pour les ressources parentales entre enfants de même âge chez les espèces produisant des couvées ou des portées, ou par les psychologues qui se sont concentrés sur les enfants dans les sociétés occidentales. Par conséquent, on sait peu de choses sur la compétition entre frères et sœurs d'âges différents chez les espèces non humaines produisant un seul enfant à la fois (c.à.d. espèces monotoques). Dans cette thèse, nous avons étudié les causes et les mécanismes de la compétition entre frères et sœurs chez deux espèces de primates sociaux, les babouins chacma (*Papio ursinus*) et les mandrills (*Mandrillus sphinx*). Ces deux espèces produisent un seul petit à la fois et partagent de nombreuses similitudes dans leur organisation sociale, mais les mandrills sont des reproducteurs saisonniers vivant dans des forêts équatoriales riches en nourriture, tandis que les babouins chacma se reproduisent de manière non saisonnière et vivent dans un environnement aride difficile. Dans les deux premiers chapitres, j'étudie la dynamique des soins maternels et des relations entre la mère et sa progéniture lors d'une étape intrigante, la naissance d'un petit frère ou d'une petite sœur, chez les deux espèces. Je montre que les jeunes babouins chacma sollicitent plus souvent leur mère et montrent plus de signes d'anxiété après la naissance de leur petit frère ou petite sœur, bien qu'ils soient déjà sevrés et ne souffrent pas d'une diminution de l'investissement maternel. Ce résultat suggère un décalage entre la quantité de soins maternels fournis par la mère et la quantité demandée par le juvénile (*manuscrit 1*). En revanche, chez les mandrills, la naissance d'un frère ou d'une sœur plus jeune induit une diminution abrupte des soins maternels envers le frère ou la sœur plus âgé(e) mais, pourtant, ne déclenche aucun signe de conflit détectable. De plus, les mandrills juvéniles montrent des réactions spécifiques au sexe, les femelles augmentant leurs affiliations envers la mère tandis que les mâles deviennent plus rapidement indépendants que les femelles (*manuscrit 2*). Enfin, comme la compétition entre frères et sœurs chez les humains est souvent caractérisée par les tentatives des enfants de perturber les interactions affiliatives entre leur mère et leurs frères et sœurs, le dernier chapitre étudie les interférences de la progéniture dans les interactions de toilettage entre la mère et un frère ou une sœur. Je montre que les interférences de toilettage se produisent dans des contextes suscitant la compétition entre frères et sœurs, qu'elles sont plus fréquentes contre les frères et sœurs avec lesquels la compétition est plus intense, et qu'elles ne réussissent généralement pas à donner accès au toilettage maternel (*manuscrit 3*). Ces résultats suggèrent que les interférences de toilettage peuvent refléter des réactions émotionnelles spontanées à l'affiliation entre la mère et un frère ou une sœur plutôt que des tentatives stratégiques pour obtenir le toilettage maternel. Ce travail élargit notre compréhension de la compétition entre frères et sœurs chez les mammifères sociaux monotoques à longue durée de vie en montrant que le conflit entre frères et sœurs peut s'étendre au-delà de la dépendance nutritionnelle, sur des ressources maternelles post-sevrage telles que le toilettage maternel et l'attention, et peut prendre des formes subtiles. En outre, cette thèse fournit de nouvelles perspectives sur l'aspect émotionnel potentiel de la compétition entre frères et sœurs et sur l'évolution des états émotionnels secondaires chez les primates non humains.

Mots-clés : compétition entre frère et sœur ; investissement parental ; ressources maternels post-sevrage ; transition vers la fratrie ; jalousie

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General Introduction

Parental care is intrinsically associated with the evolution of sociality in the animal kingdom and is found in various social systems, from simple social structures, such as temporary associations between parents and offspring, to much complex social systems, such as cooperative breeders. Parental care allocation can induce conflicts between the different family members, who may have diverging interests. Sibling competition over parental care has been extensively studied in evolutionary biology, but most of the research to date have focused on species producing broods or litters, and particularly in birds. In humans, sibling competition is a major concern for most parents and has attracted interests from researchers in multiple disciplines. However, little is known on sibling competition in long-lived non-human animals producing single young, hence limiting our understanding of this evolutionary conflict.

This thesis attempts to fill this gap by investigating the causes and mechanisms of sibling competition in two long-lived, social primates, chacma baboons (*Papio ursinus*) and mandrills (*Mandrillus sphinx*). In the first section, I define parental care and give a brief overview of the different evolutionary conflicts that can arise within families. In the second section, I review our current understanding of the causes, mechanisms and consequences of sibling competition in non-human animals. The third section summarises multidisciplinary knowledge on the causes, mechanisms and consequences of sibling competition in humans. The fourth section addresses why sibling competition has been overlooked in long-lived non-human animals producing single young, and justify why studying such systems would broaden our understanding of family conflicts and ecology. Finally, the fifth section describes the study questions and the organisation of the present manuscript.

1. Parental investment and intrafamilial conflicts

Parental investment is expressed through parental care (Box 1), which includes a wide variety of traits: provisioning eggs with yolk, provisioning young before birth, preparing nests/burrows, attending and brooding eggs or young, provisioning young before and after nutritional independence and, in some species, such as primates, caring for sexually mature offspring (Clutton-Brock, 1991; Royle et al., 2012). Parental care has evolved in many taxa, including invertebrates (insects, molluscs) and vertebrates (fishes, amphibians, reptiles, birds and mammals) and the diversity of forms of care provided by the parents varies across and

within species. Some forms of parental care can be facultative, such as in the burying beetle (*Nicrophorus vellispoides*) where parents can provide post-hatching provisioning via regurgitating food to their young, but where larvae can also survive in the absence of their parents (Eggert et al., 1998; Smiseth et al., 2003). In addition, the extent to which both sexes are involved in parental care is extremely diverse across taxa, although largely female-biased, especially in mammals (Kokko & Jennions, 2012). In invertebrates, female care is most common but some species exhibit biparental or male-only care; in fishes, male care is much more common than female or biparental care; in birds, the three forms of care occur but biparental care is generally the norm; and in mammals, most species exhibit female-only care with a few exceptions of bi-parental care also reported (Clutton-Brock, 1991).

Parental investment was first formalised in an evolutionary framework by Trivers in 1972, who defined it as "any investment by the parent in an individual offspring that increases the offspring's chances of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (Trivers, 1972). Parental investment includes **any parental trait** that can improve offspring's fitness (generally referred as parental care, Box 1), and is measured through fitness benefits in offspring and costs in a parent's ability to raise other offspring, be it through reduced fecundity in the current breeding attempt, reduced parental survival to the next breeding attempt, or reduced mating and reproductive success in the next breeding attempt(s) (Royle et al., 2012). As parental investment refers to the costs incurred by caring for an **individual offspring** (rather than the costs incurred by raising an

Box 1: Definitions

Parental investment: any investment by a parent in an individual offspring that increases offspring's survival and reproductive success at the cost of parent's ability to invest in other current or future offspring (Clutton-Brock, 1991; Royle et al., 2012; Trivers, 1972).

Parental care: any parental trait that enhances an offspring's fitness, likely to originate and/or be maintained for this function (Royle et al., 2012).

Parental behaviour: any behavioural forms of parental care (e.g. brooding eggs, provisioning young, Royle et al., 2012).

entire progeny), it generally also includes costs on other offspring's fitness and parent's reduced ability to improve the fitness of other related individuals via e.g. nepotistic behaviours (Clutton-Brock, 1991).

Because the amount of parental investment that can be devoted to each offspring is, by definition, limited (Stearns, 1992; Trivers, 1972), the classical perspective that family members cooperate to raise the maximum number of surviving offspring (Lack, 1947, 1954), has been questioned by Trivers (1972, 1974) who pointed out that the evolutionary interests of parents and offspring are diverging, likely inducing conflicts within the family. In a seminal paper, building up on Hamilton's kin selection theory (1964), Trivers argues that the optimal quantity of parental investment a parent is willing to provide to its offspring differs from the optimal quantity this offspring wishes to receive (Trivers, 1974). This difference in optima stands from an asymmetry in genetic relatedness between family members: a parent is equally related to all of its offspring ($r = 0.5$) while an individual offspring is two to four times more related to itself than to its sibling ($r = 1$ with itself, $r = 0.5$ or 0.25 with its sibling in case of full- *vs.* half-sibling, respectively). Thus, natural selection should favour traits in the offspring that allow to monopolise parental investment until the costs for its siblings are two (for full-siblings) to four (for half-siblings) times higher than its own benefits. This genetic conflict of interests is expected to trigger conflicts over parental investment between the different family members (Fig. 1). Parent and offspring should disagree over the amount and duration of parental investment (**parent-offspring conflict**), and offspring should monopolise investment to the detriment of their siblings (**sibling competition**). In addition, in species where both parents provide care, parents should compete over the quantity of parental investment each of them provide, maximising the investment provided by the other parent, and minimising their own (**sexual conflict**). These three mechanisms are difficult to disentangle because they are intertwined. Thus, actual parental investment observed in nature likely reflects the resolution of these three conflicts between family members (Parker

et al., 2002).

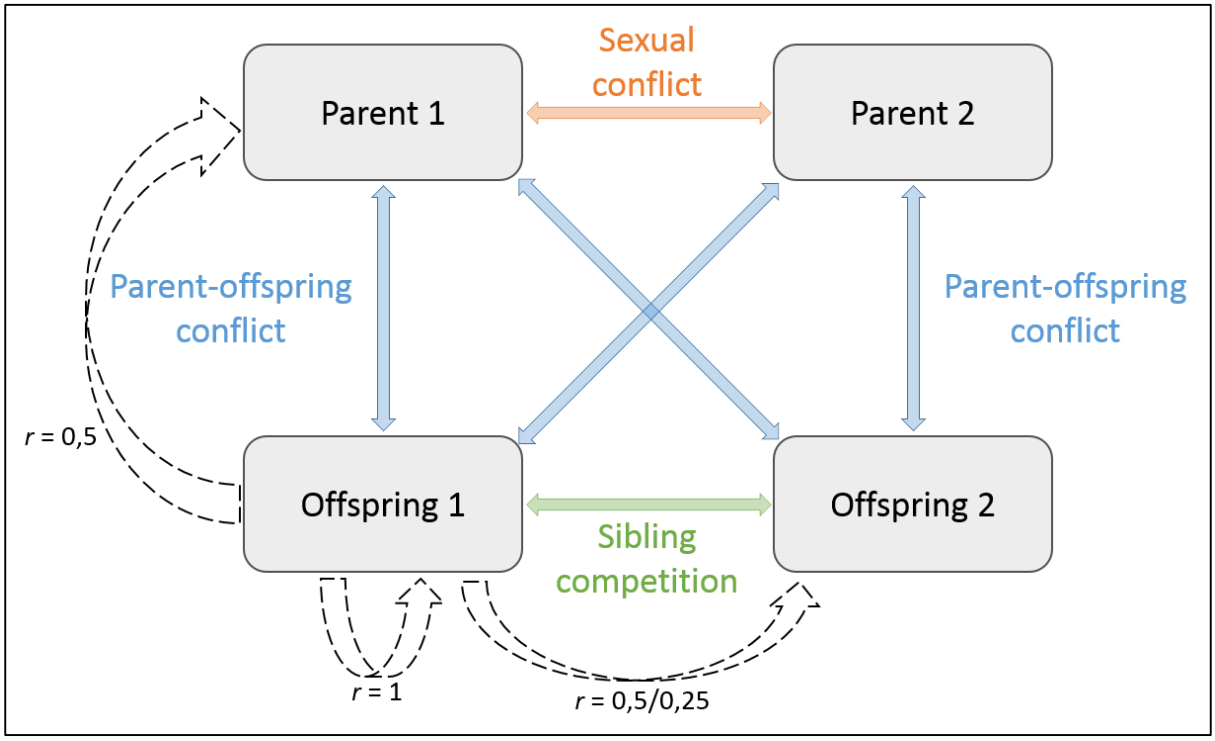

Figure 1: Summary of the intrafamilial conflicts over parental investment in a theoretical family. Parents' and offspring's interests diverge over parental investment (parent-offspring conflict, blue arrows), siblings compete over parental investment (sibling competition, green arrow), and parents compete over the quantity of investment each of them should provide (sexual conflict, orange arrow). Dashed white arrows indicate theoretical degree of relatedness between the different family members.

Sibling competition can be divided in two categories (Parker et al., 2002). Sibling competition, as originally defined by Trivers (1974) refers to competition over parental investment between an offspring and its future sibling, where the offspring's demands for increased parental investment decreases the parent's future reproductive success, referred as **interbrood conflict** (Parker & Macnair, 1979; Trivers, 1974). This is the narrowest definition, as it only applies to species were offspring reach independence before younger siblings are born. In its broader definition, interbrood conflict refers to competition between siblings born in successive reproductive events (Roulin & Dreiss, 2012; Trillmich & Wolf, 2008), which includes cases were siblings from successive cohorts can be simultaneously dependent from parental care and compete directly. **Intrabrood conflict** can be defined as competition between siblings resulting from the same reproductive attempt (Roulin & Dreiss, 2012). Parker & Macnair (1979) proposed a slightly different definition, based on which siblings bear

the cost of sibling conflict: interbrood competition refers here to the costs of parental investment borne by future (but not contemporary) siblings, while intrabrood competition refers to the costs borne by contemporary (but not future) siblings. Inter- and intrabrood competition may take the form of **scramble competition**, where siblings consume non-monopolisable but finite parental resources that run out faster as the number of siblings increases, or of **contest competition**, where the most competitive sibling will monopolise most of a (monopolisable) resource via physical contests, thus depriving defeated siblings (*sensus* Nicholson, 1954). Sibling competition can occur in a wide range of taxa expressing parental investment. Yet, studies have mainly focused on intrabrood competition in non-human animals in the fields of behavioural and evolutionary ecology, with a large bias toward bird species (Roulin & Dreiss, 2012), or on sibling competition in humans across multiple disciplines (psychology, anthropology). Here, I review the causes, mechanisms and consequences of sibling rivalry in both non-human and human animals.

2. *Sibling competition in non-human animals*

2.1. Forms of sibling competition

Sibling competition has been extensively studied in the field of behavioural ecology, across a wide variety of taxa (e.g. insects, fishes, amphibians, birds and mammals). Most studies in this field have focused on brood- or litter-rearing species, and the dynamics of sibling competition over parental resources provided at one specific developmental stage, namely before nutritional independence, such as provisioning and thermoregulation. In these species, siblings can use a broad range of tactics to compete with each other, with high inter-specific variations (reviewed in Mock & Parker, 1998; Roulin & Dreiss, 2012). For instance, sibling competition can be limited to mere scramble competition, where siblings do not physically compete with each other. Begging to attract parental attention and secure provisioning is found in invertebrates, such as in the burying beetle where larvae touch their parents mouthparts to beg for food (Smiseth & Moore, 2002), in birds, where nestlings vocalize loudly upon their parents' arrival in the nest (e.g. reviewed in Mock & Parker, 1998) and in mammals, such as meerkats (*Suricata suricatta*) where pups actively follow and vocalize to their care-givers to get fed (Manser et al., 2008). Another non-aggressive form of competition is to jostle in order to reach a position in the brood or litter huddle that is

favourable to secure parental provisioning (e.g. great tit, *Parus major*: Kölliker et al., 1998) or thermally advantageous positions (e.g. domestic rabbit, *Oryctolagus cuniculus*: Bautista et al., 2008, 2013). Competition can also translate into physical aggression between siblings. Agonistic behaviours can serve to establish a dominance hierarchy between siblings (reviewed in Drummond, 2006), which will determine priority of access over parental resources throughout the developmental period. In cattle egret (*Bubulcus ibis*) for instance, an age-related linear hierarchy is pre-established via hatching asynchrony, and reinforced through violent attacks by older (and stronger) siblings toward younger ones during the first weeks of life. Aggressions decrease markedly after three weeks once the dominance hierarchy is stable (Mock & Lamey, 1991; Ploger & Mock, 1986). Similarly, in spotted hyenas (*Crocuta crocuta*), twin cubs start fighting intensely a few hours after birth, and keep doing so until one of them enforces dominance over the other one (Frank et al., 1991). The dominant cub can later exclude the subordinate one from accessing maternal nipples (Hofer & East, 2008). Aggressions can also be used to monopolise access to particular teats, as found in pigs (*Sus scrofa*), hyraxes or felids (reviewed in Drummond, 2006), where pups defend access to their "personal" teat against their siblings throughout the developmental period, or access to care-givers, as in some cooperative breeders where pups defend access to a long-term (banded mongoose, *Mungos mungo*: Gilchrist, 2008) or temporary (meerkats: Hodge et al., 2007) care-giver. In extreme cases, sibling competition can take the form of siblicide, where one offspring (the dominant/stronger/older one) kills its sibling (the subordinate/weaker/younger one), either through forced starvation and/or repeated aggressions. Siblicide (also referred to as "brood reduction") has been reported in several bird and mammal species, and can either be facultative (e.g. blue footed booby, *Sula nebouxii*: Drummond & Garcia Chavelas, 1989; cattle egret: Fujioka, 1985; spotted hyena: Hofer & East, 1997), depending on food availability, or obligate (e.g. Verreaux eagle*, Aquila verreauxii*: Edwards & Collopy, 1983; American white pelican, *Pelecanus erythrorhyncos*: Cash & Evans, 1986).

Sibling competition is, however, not always resolved through behavioural conflicts. As competition often entails energetic costs and can sometimes lead to physical injuries, siblings may try to reduce such costs by negotiating with each other priority of access over parental resources. For example, in barn owls (*Tyto alba*), nestlings vocalise in the absence of their

parents to signal each other their intention to compete for the next food item delivered by the parents, and individuals refrain from vocalising upon parents arrival when their nestmates are hungrier than themselves or in larger broods, when sibling competition is more intense and competing for the next food item could be costlier (Roulin et al., 2000).

2.2. Causes and factors modulating sibling competition

A big question in behavioural ecology has been to understand which factors modulate the intensity of sibling competition. Within-species, environmental and individual causes can both play a role. For instance, one of the ultimate factors modulating the intensity of sibling competition is the intensity of parental provisioning (i.e. food availability). This "Food Amount Hypothesis" (Mock et al., 1987) has received empirical support across many taxa: siblings beg more when food availability is low (e.g. in burying beetle: Botterill-James et al., 2017; in birds: reviewed in Mock & Parker, 1998) and may also show more agonistic behaviours (e.g. black guillemot, *Cepphus grylle*: Cook et al., 2000; meerkat: Hodge et al., 2009; spotted hyena: Golla et al., 1999). In facultative siblicidal species, food shortage often triggers brood reduction (e.g. black-legged kittiwakes, *Rissa tridactyla*: Braun & Hunt, 1983; blue-footed booby: Drummond & Garcia Chavelas, 1989). Similarly, a larger brood often increases sibling competition because the food provided by parents is shared, and the total amount received *per* individual depends on the number of siblings present (e.g. burying beetle: Smiseth et al., 2007; great tit: Neuenschwander et al., 2003; meerkat: Madden et al., 2009). In line with Trivers' original prediction, genetic relatedness also influences the intensity of sibling competition: in several bird species, nestlings beg louder when the degree of relatedness between siblings is lower (e.g. barn swallow, *Hirundo rustica*: Boncoraglio et al., 2009; see Briskie et al., 1994 for a comparative analysis). In a marine gastropod (*Crepidula fornicata*), larvae show a greater variation in growth rates when their degree of relatedness is lower (Le Cam et al., 2009). In addition, within-brood sexes' combination may also play a role: competition is more intense in mixed-sex broods with an older brother and a younger sister in blue-footed boobies, because of a female-biased sexual dimorphism emerging in ontogeny (Drummond et al., 2022). Younger sisters outgrow their older brother after a few weeks, consuming more food, and older brothers sometimes violently attempt to suppress their sister's growth (Drummond et al., 2022). Similarly, in the female-dominated spotted hyenas, competition is more intense in litters where females are the dominant pups (Benhaiem et al., 2012). Finally, variation in

competitive abilities, often induced by age difference due to hatching asynchrony in birds, can also modulate the intensity of sibling competition (Roulin & Dreiss, 2012).

The mode and intensity of sibling competition is highly variable between species, and may be associated with species' life history traits, ecology and morphology. In a comparative analysis on sibling aggression in seven avian families, Gonzalez-Voyer and colleagues (2007) showed that aggression was both more common and more intense in species with a long nestling period and with an indirect feeding method (i.e. when the food is deposited on the nest floor and is accessible to all broodmates *vs.* direct provisioning, when the food passes directly from beak to beak). Aggression was also more intense in species with small broods, perhaps because it is more difficult to enforce dominance in larger broods. In addition, offspring's ability to escape aggression and/or display submissive behaviours could modulate the intensity of sibling competition in species with aggressive interactions, being more violent in species where subordinate siblings cannot physically escape (e.g. in birds nesting on cliffs) compared to species where offspring are more mobile (Drummond, 2006). Other factors such as the presence of effective weaponry to inflict injuries (as found in spotted hyenas or pigs) may also play a role (Roulin & Dreiss, 2012), as it has been proposed that sibling competition could have selected for the evolution of teeth in pigs (Fraser & Thompson, 1991).

2.3. Consequences of sibling competition

Sibling competition can have both short and long-term consequences. Historically, studies on sibling competition were motivated by the puzzling observation of siblings violently attacking and killing each other in species with facultative siblicide. In these species, low food availability increases sibling competition, which reduces survival chances for the subordinate sibling because siblicide events generally occur when the dominant sibling's growth rate decreases below a critical level (e.g. blue footed booby: Drummond & Garcia Chavelas, 1989; spotted hyena: Hofer & East, 2008). Siblicide generally allows the surviving sibling to achieve normal growth rate later on (e.g. Hofer & East, 2008), if parents do no readjust their provisioning rate (e.g. brown pelican, *Pelecanus occidentalis*: Ploger, 1997). In non-siblicidal species as well, offspring face higher mortality risks when sibling competition is more intense, for instance in larger brood or in environments with lower food availability (e.g. burying beetle: Sieber et al., 2017; domestic rabbit: Drummond et al., 2000; pig: Andersen et al.,

2011). Besides the immediate fitness cost of reduced survival, sibling competition can also impact offspring's development and physiology: offspring growing up in larger broods show reduced growth (e.g. burying beetle: Sieber et al., 2017; European starling, *Sturnus vulgaris*: Nettle et al., 2013; pig: Andersen et al., 2011; meerkat: English et al., 2014), increased cortisol levels (e.g. guinea pig, *Cavia aperea*: Fey & Trillmich, 2008; blue-footed booby: Mora et al., 1996), decreased immunocompetence (e.g. rat, *Rattus norvegicus*: Prager et al., 2010), and shorter telomere lengths (e.g. meerkat: Cram et al., 2017; black-tailed gull, *Larus crassirostris*: Mizutani et al., 2016). Such effects can vary with offspring's dominance rank within the brood/litter, with more subordinate siblings incurring more costs in general than dominant ones. For instance, in cavies, the smallest pup shows higher level of cortisol at the end of the rearing period than heavier ones (Guenther & Trillmich, 2015), and subordinate European starling chicks suffer from greater telomere loss (Nettle et al., 2013). As subordinate individuals typically face a competitive disadvantage compared to dominant ones, they might need to trade-off self-maintenance and immune functions against growth (Stier et al., 2015). Finally, interactions between siblings during early-life could further shape the development of behavioural syndromes and personality in mammals (Hudson et al., 2011; Hudson & Trillmich, 2008). Evidence from cavies and laboratory rats shows that body size – hence, dominance rank within the litter – is associated with some personality traits: heavier pups are generally bolder and show more exploratory behaviours (Guenther & Trillmich, 2015; Rödel & Meyer, 2011). However, it is unclear whether these differences arise from interactions with siblings during the developmental period, or are due to maternal effects, such as differential investment towards offspring (Rödel & Meyer, 2011).

Importantly, most studies so far have focused on the effects of sibling competition during ontogeny, and at best, around weaning, fledging or dispersal. Even though some of the costs examined in these studies might have consequences extending into adulthood, such as shorter telomeres, which might affect ageing rates and longevity later in life (e.g. Heidinger et al., 2012), few studies to date have attempted to measure the long-term effects of sibling competition (except the obvious fitness cost of increased pre-weaning/fledging/dispersal mortality). This gap might be partly due to the historical bias in the literature toward bird species, where juveniles in the wild disperse after fledging hampering long-term investigations of sibling competition. However, a couple of studies from long-term projects or

in laboratory settings report contrasting results. In blue-footed boobies, younger sisters raised with (thus, subordinate to) an elder brother (where competition is most intense during the developmental period compared to other sex and status combination) have a lower hatching success than those raised with an older sister (Drummond et al., 2022). Offspring produced by subordinate siblings during their early reproductive life are also less likely to later recruit in the breeding population (Drummond & Rodríguez, 2013), although subordinate and dominant siblings show similar breeding success and lifespan (Drummond et al., 2003, 2011). In Seychelles warblers (*Acrocephalus shechellensis*), subordinate chicks have a lower probability to survive until adulthood, but those who do reproduce at the same age, have equivalent breeding tenure duration and live as long as dominant siblings (Bebbington et al., 2017). Experimental manipulation of brood size in zebra finches (*Taeniopygia guttata*) allowed to show that individuals raised in large broods remain smaller and lighter throughout their life, males are less attractive to females and females show increased mortality during adulthood than individuals raised in small broods (De Kogel, 1997; De Kogel & Prijs, 1996; Verhulst et al., 2006). In mammals, female spotted hyenas that faced higher sibling competition during early life survive less to adulthood but do not show any difference in age at first reproduction, longevity, and lifetime reproductive success (Gicquel et al., 2022), while female rabbits raised in small or large litters show lower survival to adulthood and lower lifetime reproductive success than those raised in medium-size broods (Rödel, Holst, et al., 2009).

As emphasized in this section, the literature in behavioural ecology has mainly focused on polytocous (i.e. species producing several offspring *per* breeding event), altricial species, measuring competition and its consequences during the developmental period. Lifelong consequences remain to be investigated, although recent efforts have been made toward this direction. Moreover, the focus so far has been much more on competitive interactions compared to cooperative ones, and little is known regarding the potential benefits of growing up with siblings. For instance, in many altricial species, pups or chicks' thermal requirements can only be met if they huddle with their siblings (e.g. Bautista et al., 2003), which has led to the evolution of a medium, optimal litter size in rabbits, balancing the costs and benefits of scramble competition and thermoregulation (Rödel, Starkloff, et al., 2009). Siblings could also

cooperate to extract more resources from their care-givers, as observed in banded mongoose (Bell, 2007). In social species, interacting with siblings during early-life could influence the development of social skills in adulthood (e.g. earwigs, *Forficula auricularia*: Van Meyel & Meunier, 2022). Finally, most of our knowledge concerns intrabrood competition (i.e. competition between same-age siblings, see section 1),and little is known on the potential effects of subsequent litters on each other (but see Rödel et al., 2008), or of different-age siblings in long-lived species.

3. Sibling rivalry in humans

Sibling competition, often termed rivalry in the human literature, has been extensively studied in our species, where squabbles between siblings have attracted interests from several disciplines, including evolutionary psychology, developmental and family psychology, and anthropology. Importantly, in humans, sibling rivalry has not only been studied within the framework of the parent-offspring conflict theory (Trivers, 1974), but also within the attachment theory (Ainsworth, 1979; Bowlby, 1969). The attachment theory states that human infants are predisposed to form emotional bonds with a primary caregiver because such "attachment" improves survival (Bowlby, 1969). Observations that attachment forms vary from one individual to another led to the identification of three main attachment styles: secure (characterized by high level of autonomy and ability to get comfort from the mother), avoidant (generally avoiding interactions with the mother and not seeking comfort from her) and ambivalent (characterised by both comfort-seeking and resistance behaviours toward the mother). These three styles have been proposed to result from differences in maternal responsiveness to infants' needs (Ainsworth, 1979). Psychologists have then linked attachment styles to various health and social outcomes during the developmental period and across various life stages (Gustison & Phelps, 2022), including sibling relationships (Whiteman et al., 2011). This section is an attempt to summarise multidisciplinary knowledge on the mechanisms, factors of variation, and consequences of sibling rivalry in humans.

3.1. Causes and mechanisms of sibling rivalry in humans

Sibling rivalry in humans is likely to differ in its causes and mechanisms from non-human, polytocous species because humans are characterized by a long developmental period and short inter-birth intervals (Sear, 2011) (compared to great apes for instance, e.g. Jones, 2011;

Wells, 2012), and extensive paternal care (Balshine, 2012; Marlowe, 2000; Sear, 2011). Parents often have to care simultaneously for several dependent children at different developmental stages (Sear, 2011), who likely do not compete over the same resources at the same time (Schlomer et al., 2011). For instance, a young child likely does not compete with its younger sibling for maternal milk, but the time spent by the mother nursing the baby might reduce her ability to provide other forms of care to the older sibling, such as preparing food for him (Schlomer et al., 2011). In addition, humans are characterized by an extremely long period of parental investment, as parents provide care throughout the developmental period until sexual maturity, and often keep supporting their offspring when they start their own reproductive career (Balshine, 2012; Sear, 2011). Consequently, parental investment in humans covers a wide range of parental resources, including provisioning, protection or teaching skills, but also material/financial resources (e.g. inheritance), or emotional support (Balshine, 2012; Sear, 2011). In particular, parental attention and parental love are widely considered as resources *per se*, for which siblings can compete (Thomas et al., 2015; Volling et al., 2010).

Competition between siblings – or at least as it is measured – often takes the form of quarrels and disputes, which can include physical violence or not, and often has an emotional dimension (Cicirelli, 1995; Pollet & Hoben, 2011; C. A. Salmon & Hehman, 2014). It is difficult to draw conclusions from studies in psychology as it seems that there is much debate over what constitutes a conflict between siblings (Pollet & Hoben, 2011), and because measures of sibling rivalry are most of the time self- or parentally-reported instead of relying on objective behavioural observations. This might create biases such as underreporting conflicts as they are often considered a normal dimension of siblings relationships (Pollet & Hoben, 2011; C. A. Salmon & Hehman, 2014; Whiteman et al., 2011). Moreover, many proximate cues can trigger conflict between siblings, and it is not clear whether it always relates to sibling competition over parental resources. For instance, the most commonly cited source of conflict between siblings involve the sharing of personal items and the least commonly cited is competition over parental attention (Dunn & Munn, 1987; McGuire et al., 2000). When sibling conflict includes physical violence, it rarely escalates further than pushing, biting, slapping or hitting, and declines with age (Straus et al., 2017). Siblicide is extremely rare in humans, and in contrast with non-human animals, mainly occurs between adult siblings (C. A.

Salmon & Hehman, 2014), and generally over power and/or status struggles, when the pay-offs are really high (e.g. in Vikings: Dunbar et al., 1995).

So far, a unique characteristic of sibling rivalry in humans is its emotional dimension, as it can be mediated by jealousy at the proximate level (Volling et al., 2010). Jealousy is a complex socioemotional state that arises in a social triangle when an individual (e.g. a sibling) perceives its relationship with a beloved partner (e.g. the mother) as threatened by or lost to a rival third-party (e.g. another sibling) (Hart, 2016; Volling et al., 2010). As such, sibling jealousy refers to rivalry over parental love and attention (Volling et al., 2010). Jealousy can include a blend of emotions such as anger, fear or sadness, and can trigger attempts to separate the beloved and rival individuals, and divert and/or regain the beloved's attention from the rival (Hart, 2010). Despite being a universal concern for parents, which is often time-consuming and energy-draining (Elise Huchard, *pers. com.*), sibling jealousy has been largely overlooked so far, and very few studies have investigated jealous reactions within the appropriate social context. Studies on infants as young as 6-months old reported negative reactions when their mother directed her attention to a social rival (Hart, 2016; Hart et al., 2004), which suggests that some forms of jealousy can already be felt and expressed at this age. The birth of a younger sibling is often seen as the starting point of sibling jealousy for the older child, as (s)he now has to share maternal attention with the newborn (Volling, 2012; Volling et al., 2010). Older children often react to the arrival of a younger sibling with aggressive and attention-seeking behaviours toward the mother and attempts to disrupt mother-infant interactions, which are often interpreted as jealous reactions (Dunn et al., 1981; Kendrick & Dunn, 1980, 1982; Legg et al., 1974; Volling et al., 2010, 2014). Sibling jealousy can last throughout life, from early childhood to adulthood, and is generally induced by the loss of parental attention to a sibling, and maintained by a differential parental treatment between siblings (reviewed in Volling et al., 2010).

3.2. Factors influencing sibling rivalry across populations and individuals

In anthropology, a primary focus has been to examine the link between resource availability and sibling rivalry. However, it seems much harder to measure in human than in non-human animals, where the intensity of sibling competition in relation to the amount of parental provisioning has been extensively studied. Some studies on rural populations have used an

indirect approach, using interbirth interval duration as a proxy of sibling competition intensity, and showed that shorter interbirth interval increased mortality risks for both the younger and older sibling (Alam, 1995; Cleland & Sathar, 1984). Conversely, a modelling approach across five populations (Ache, Gambia, Sweden, Taiwan and Tsimane) showed that increased sibling competition lengthens interbirth intervals, but only in population with low infant mortality (Thomas et al., 2015). Other studies have investigated the effect of the number of siblings on parental investment *per* offspring, and showed that individual share of parental investment decreases as sibship size increases (e.g. in Gabbra pastoralist men: Mace, 1996; in modern western population: Lawson & Mace, 2009). Interestingly, Lawson and Mace (2009) measured the joint effects of parents' socioeconomic status and sibship size on investment *per* offspring (investment included childcare activities such as preparing food, cleaning, helping with schoolwork, and social and affective interactions such as playing, cuddling or chatting with the child), and showed that contrary to their predictions, higher socioeconomic status does not alleviate the costs of larger sibship but exacerbates it.

In the psychology literature, studies have mainly focused on the influence of individual traits on the intensity of sibling rivalry (reviewed in Brody, 1998; Pollet & Hoben, 2011; Salmon & Hehman, 2014; Volling et al., 2010). First, despite the fact that genetic relatedness between siblings lies at the heart of Trivers' theory, it has largely been neglected in humans until recently. Surprisingly, studies consistently reported more frequent and more intense conflicts (along with higher levels of cooperation) between full-siblings compared to half-siblings (Khan et al., 2020; C. A. Salmon & Hehman, 2021; C. Salmon & Hehman, 2015; Tanskanen et al., 2017). A potential explanation for these findings could be that parental investment is only partly overlapping between half-siblings (since they only share one parent) while full-siblings compete for the same parental investment (Khan et al., 2020; Tanskanen et al., 2017). Second, age difference and sibship size also mediate the intensity of sibling rivalry, with greater conflicts reported between closer in age siblings (Pollet, 2007; C. A. Salmon & Hehman, 2021; C. Salmon & Hehman, 2015; Tanskanen et al., 2017), and in larger sibships (e.g. Lawson & Mace, 2009; Tanskanen et al., 2017), in line with parent-offspring conflict predictions. Third, siblings' gender also influences sibling rivalry, but has contrasted effects: more frequent and more intense conflicts are generally found in male dyads (e.g. C. Salmon & Hehman, 2015, reviewed in C. A. Salmon & Hehman, 2014), while higher conflicts are

sometimes observed within opposite-sex dyads (e.g. Tanskanen et al., 2017). More rarely, sibling conflicts are not explained by gender (Khan et al., 2020). In most studies, dyads where the older sibling is a female, and particularly sister dyads, generally show the lowest levels of conflicts, in line with the idea that sisters are more likely to take care of siblings. A recent study found that conflicts were highest in sister dyads though(C. A. Salmon & Hehman, 2021), perhaps because other forms of conflicts, such as arguing, were considered, while previous studies focused solely on physical aggressions. Several other individual traits might impact siblings' relationships, such as temperament or attachment style with the mother, with insecurely attached children experiencing poorer sibling relationships (reviewed in Brody, 1998; Volling et al., 2010).

Finally, siblings' relationships can also be shaped by family processes, such as relationships between the parents (e.g. conflicts) and parental differential treatment (hereafter, PDT) (Brody, 1998; Volling et al., 2010). The latter reflects differences in parental behaviours between siblings, such as differential parental positivity (e.g. hugging, laughing or praising children), negativity (e.g. threatening, physical violence or negative facial expression), control (e.g. requesting children to behave in certain ways) or responsiveness (e.g. teaching, answering questions) (e.g. Brody et al., 1992; Volling et al., 2010). Measures of PDT vary between studies because different parental behaviours are considered (e.g. Brody et al., 1992 considered five parental behaviours while Jenkins et al., 2012 only two), which makes it difficult to compare conclusions across studies. However, there is consistent evidence that PDT is associated with more intense sibling conflicts and jealousy across all life stages (childhood: Brody et al., 1987; Kowal & Kramer, 1997; Volling & Elins, 1998; adolescence: A. K. Kowal et al., 2006; Richmond et al., 2005; adulthood: Gilligan et al., 2015; Jensen et al., 2013), and that it can have long-term consequences on individuals wellbeing in adulthood (e.g. Padilla et al., 2021; Peng et al., 2018). Some studies have shown that the negative effects of PDT can be mediated by offspring's appraisal of its fairness, with siblings judging PDT biased in favour of their younger sibling as fair reporting more positive relationships with them than those who perceived PDT as unfair (e.g. A. K. Kowal et al., 2006; A. K. Kowal & Kramer, 1997).

3.3. Consequences of sibling rivalry

Measuring all the consequences of sibling rivalry in humans can be challenging. Across all fields, there is a lack of longitudinal studies, meaning that consequences of sibling relationships can only be studied over the short-term, or by relying on indirect proxies of sibling competition, such as age difference, sibship size or birth order. Drawing strong conclusions is rather difficult because measures of sibling competition vary between disciplines. For instance, anthropologists tend to focus on proxies of sibling competition, such as age difference or sibship size and their effects on mortality or reproductive success (e.g. reviewed in Pollet & Hoben, 2011). On the other hand, psychologists focus more on the nature of sibling relationships (i.e. relatively conflicting or supportive ties) but tend to investigate its short-term consequences, such as social competences (Brody, 1998), because of the difficulty of longitudinal follow-ups.

So far, one of the most studied aspect in the human literature has been the long-term effects of birth order. For instance, Sulloway (1996, 2001) contributed an influential and controversial work on the effect of birth order on personalities, arguing that the strategies used by individuals to compete with siblings over parental investment determine the family niche in which an individual grows up and shapes her or his personality. Birth order has been linked to various personality traits, such as leadership, sociability, cooperative and innovative behaviours, but results are often contrasted (e.g. see Black et al., 2017; Courtiol et al., 2009; Pollet et al., 2010; Sulloway, 2001 and references therein). Birth order can also impact development, with, for instance, firstborns acquiring language faster during early childhood than laterborn children (Keller et al., 2015; Wellen, 1985). Finally, birth order may have long-term consequences, with e.g. laterborn children showing better mental health than firstborn ones (Lawson & Mace, 2010), and impact fitness *via* differential survival or reproductive success (Faurie et al., 2009; Modin, 2002). However, disentangling the effects of birth order from sibship size is challenging, as middleborns and laterborns are typically found in larger families, and sibship size is not always controlled for when testing birth order effects (see Pollet & Hoben, 2011).

Similarly to non-human animals, sibship size and birth intervals may also have short and long-term effect in humans. Large sibships also appear to be costly, as offspring growing up in larger families experience reduced nutritional status and growth (e.g. in Ngandu horticulturalists: Helfrecht & Meehan, 2016; in Maya agriculturalists: Kramer et al., 2016; in

modern British: Lawson & Mace, 2008), lower educational attainment (e.g. modern Americans: Downey, 1995, 2001), and lower reproductive success (e.g. pre-industrial Finnish: Nitsch et al., 2013). Rather than the overall number of siblings, the number of older or younger siblings only can also have different effects: for instance, growth rate is negatively impacted by the number of younger siblings only in Maya agriculturalists (Kramer et al., 2016), while reproductive success of males decreases with the number of older brothers only in pre-industrial Finnish (Nitsch et al., 2013). Similarly, close interbirth intervals negatively impact development and educational attainment, and decrease offspring's survival (e.g. in rural Pakistan: Cleland & Sathar, 1984; in modern Americans: Powell & Steelman, 1993; see Conde-Agudelo et al., 2006 for a meta-analysis). Finally, psychologists reported that siblings' relationships can impact children's psychosocial skills: children who experience more sibling conflicts have more negative relationships with peers, and poorer emotional regulation (reviewed in Brody, 1998).

As discussed in this section, sibling rivalry in humans is an important component of child development, can extend into adulthood, with far-reaching consequences at multiple levels. However, the results presented above need to be considered with caution, most come from studies on western, modern populations (except where specified), and populations with a different cultural background could show different patterns (Pollet & Hoben, 2011). Importantly, the interplay between sibling competition and sibling cooperation has attracted much more interest in human than in non-human animals, and results largely show that growing up with siblings brings many benefits despite competition (e.g. improving social skills, providing emotional support, or increasing reproductive success or survival, see Brody, 1998; Pollet & Hoben, 2011 for reviews, and studies on the "helper-at-the-nest" hypothesis). In addition, as sibling relationships are the most enduring relationships in humans (as parents and children belong to different generations, and spouse often divorce, Cicirelli, 1995), the extent to which siblings compete or cooperate might change depending on their life stage, and traits that promote competition at one stage might promote cooperation at another one (e.g. short interbirth intervals could trigger more intense competition during childhood but closer relationships in adulthood, Pollet & Hoben, 2011). Sibling rivalry in long-lived non-human animals where offspring remain with their kin throughout their life might show similar temporal dynamics.

4. Potential for sibling competition in monotocous species

4.1. Why has sibling competition been overlooked in monotocous species?

Monotocous mammals, which produce and raise one offspring at a time, represent a perfect study system to study interbrood competition without the confounding effect of intrabrood competition (Hudson & Trillmich, 2008). Yet, very few studies to date have investigated sibling competition[1] in such species (but see e.g. Trillmich & Wolf, 2008). A potential explanation for this bias is that offspring are generally weaned before the birth of their younger sibling and thus may not compete for maternal milk (but again, see Lee et al., 2019; Trillmich & Wolf, 2008). More generally, these different-age siblings also are at different developmental stages and may not require the exact same maternal resources at the same time, which may hinder sibling competition. This age difference also induces an asymmetry in competitive abilities between siblings, meaning that any overt behavioural competition (i.e. aggression) might lead rapidly to substantial costs to the younger sibling (e.g. Trillmich & Wolf, 2008). In addition, the overwhelming importance of lactation on development in mammals may have diverted the focus from sibling competition to mother-offspring conflicts over milk provisioning (e.g. the conspicuous tantrums over weaning observed in many primate species, reviewed in Maestripieri, 2002). Therefore the scope for sibling competition in monotocous mammals may be limited compared to mother-offspring conflict (Hudson & Trillmich, 2008).

The study of sibling competition in monotocous mammals also raises a challenging question: over which maternal resources may siblings of different age compete? Studies on polytocous species traditionally focused on competition over parental resources provided before nutritional independence (hence, mostly on parental provisioning) (Mock & Parker, 1998), most likely because parental care after nutritional independence is rare in these species (e.g. birds, Clutton-Brock, 1991). However, in longer-lived vertebrates – such as monotocous mammals – parental care commonly extends beyond weaning (hereafter, post-weaning maternal care, Clutton-Brock, 1991). Although competition for maternal milk between different-age siblings can occasionally occur in some species around the birth of the younger sibling (e.g. Galapagos fur seals, *Arctocephalus galapagoensis*, and sea lions,

[1] Note that throughout this section, "siblings" refers to maternally related siblings (full- or maternal half-siblings), but exclude paternal half-siblings.

Zalophus wollebaeki: Trillmich & Wolf, 2008; rhesus macaques, *Macaca mulatta*: Lee et al., 2019), these post-weaning forms of maternal care could also be the stake of sibling competition – as in humans (see section 3). Post-weaning maternal care may include protection against predators, social support, facilitated access to food or information transfer (Clutton-Brock, 1991; Crockford et al., 2020; Royle et al., 2012), and several recent studies suggested that it may improve offspring growth (e.g. chimpanzees, *Pan troglodytes*: Samuni et al., 2020; reindeers, *Rangifer tanrandus*: Holand et al., 2012) and future reproductive success and longevity (chimpanzees: Crockford et al., 2020; Stanton et al., 2020; bonobos, *Pan paniscus*: Surbeck et al., 2011; yellow baboons, *Papio cynocephalus*: Tung et al., 2016; Zipple et al., 2019; killer whales, *Orcinus orca* : Foster et al., 2012; red deers, *Cervus elaphus*: Andres et al., 2013, Asian elephants, *Elephas maximus*: Lahdenperä et al., 2016). However, these studies investigated the effect of maternal presence (*vs.* absence) during the post-weaning period and proposed the provisioning of post-weaning care as the most likely mechanism at play, but it remains unclear how much it results from active maternal involvement and care, and whether other resources could also play a role (Crockford et al., 2020). Finally, an important criterion for sibling competition to arise is the limitation of parental resources, and it remains unclear whether post-weaning forms of maternal care are limited: for instance, if information transfer mostly occurs passively through maternal tolerance of offspring in close proximity, siblings would not need to compete to benefit from it.

4.2. Evidence that sibling competition may occur in monotocous species

Recent empirical studies suggest that sibling competition may incur fitness costs in non-human monotocous mammals. Similarly to humans, short interbirth interval with a younger sibling is associated in the older sibling with lower juvenile body mass (chimpanzees: Emery Thompson et al., 2016), decreased juvenile survival (rhesus macaques: Lee et al., 2019), decreased survival in adult females (yellow baboons: Tung et al., 2016), weaker social bonds in adult females (yellow baboons: Lange et al., 2022) and decreased offspring survival in females (yellow baboons: Zipple et al., 2019). For younger siblings, short interbirth intervals with an older sibling also increased infant mortality in rhesus macaques (D. S. Lee et al., 2019) but did not influence juvenile body mass in chimpanzees (Emery Thompson et al., 2016). Costs incurred by small interbirth intervals have been generally attributed to an early weaning for

the older sibling, and to depleted maternal physiological condition for the younger sibling (e.g. Lee et al., 2019). However, in red deer, early-weaned calves who experienced the birth of a younger sibling during the following birth season did not show decreased survival and growth compared to calves whose mother did not reproduce during the next breeding season (Clutton-Brock et al., 1983), which suggests that early weaning might not be the only mediator of the detrimental effect of short interbirth intervals in monotocous mammals. In Galapagos fur seals and sea lions, mothers can sometimes give birth to their subsequent offspring while the older sibling is still dependent. Newborns with a dependent older sibling show a decreased birth weight and growth rate, and an increased mortality, often due to siblicide (Trillmich & Wolf, 2008). Another anecdotal case of siblicide has been reported in false vampire bats (*Megaderma lyra*), where a weaned juvenile killed its newborn younger sibling a few days after birth (Leippert et al., 2000). Finally, to another degree, a recent study in wild bonobos investigating juveniles' reactions to the birth of their younger sibling reported that, independently from weaning, having a younger sibling induced an increase in cortisol level and a decrease in neopterin level that lasted several months (Behringer et al., 2022). These sudden physiological changes were not associated to any changes in the relationship with the mother, which suggests that they were triggered by the presence of a competing younger sibling rather than an increase in mother-offspring conflict. Hence, while diluting maternal care between different-age siblings clearly appears costly, little is known about the mechanisms at work, and whether the underlying genetic conflict translates into behavioural conflicts (except for the now well-known from the reader example of Galapagos fur seals and sea lions, see Trillmich & Wolf, 2008).

4.3.Sibling relationships in monotocous species

Sibling relationships have been best studied within the framework of kin-biased social bonds and cooperation during adulthood, and their associated fitness benefits in monotocous species, where siblings are among the most valuable social partners (Lynch et al., 2019; Rendell et al., 2019; Silk, 2007, 2009). Sibling relationships during the juvenility period in such species have been much less studied, so that siblings' influence on each other's development and siblings' social relationships thus largely remain to be investigated (Lonsdorf & Ross, 2012). In addition, immature siblings' social bonds have been mainly investigated through the lens of affiliative interactions and cooperation, but competition has been rarely examined.

For instance, in several primate species, immatures form the strongest bonds with their maternal siblings (Amici et al., 2019; Charpentier et al., 2007; Grebe et al., 2022), especially those of the philopatric sex (e.g. Amici et al., 2019; Lonsdorf et al., 2018). Older siblings may represent an important socialization agent toward infants by playing a helper role (e.g. chimpanzees: Brent et al., 1997; Lonsdorf et al., 2018 but see Murray et al., 2014; orang-utans, *Pongo* spp.: Fröhlich et al., 2020), and can even support their younger sibling following maternal loss (e.g. chimpanzees: Hobaiter et al., 2014; Reddy & Mitani, 2019; yellow baboons: Altmann, 1980; chacma baboons, *Papio ursinus*: Engh et al., 2009; African elephants, *Loxodonta africana*: Goldenberg & Wittemyer, 2017), by strengthening their relationships and adopting a "parent-like" role (Reddy & Mitani, 2019).

Much less is known on competitive interactions between siblings (except for sisters' agonistic interactions over rank acquisition in matrilineal primates, see e.g. Chapais et al., 1994; Datta, 1988; Engh et al., 2009). First, agonistic interactions between immature siblings have been rarely investigated. In wild mountains gorillas (*Gorilla beringei beringei*), immature maternal half-siblings engaged in competitive behaviours at the same rate than paternal half-siblings or non-siblings, except for mixed-sex dyads, where non-siblings have higher aggression rates than siblings (Grebe et al., 2022). Similarly, juvenile rhesus macaques and vervet monkeys (*Cercopithecus aethiops*) showed similar rates of aggression with their siblings than with their peers (Janus, 1991; P. C. Lee, 1987). Second, siblings' competitive interactions might arise in different contexts than between non-siblings. In both rhesus macaque and vervet monkey, siblings appeared to compete much more in a grooming context while non-siblings competed more often in a feeding context (Janus, 1991; P. C. Lee, 1987). Unfortunately, both studies did not investigate patterns of aggression in relation to maternal care specifically: indeed, if siblings' aggression reflects sibling competition over maternal care, it might arise in specific contexts, in relation to maternal presence or maternal care allocation such as maternal grooming for instance. To the best of my knowledge, this has never been investigated in monotocous mammals.

To sum up, sibling competition seems to be the most likely hypothesis to explain the high costs associated to the presence of siblings in monotocous mammals but the ultimate and proximate causes that can trigger it, as well as the mechanisms at play, are yet to be

uncovered. Long-lived monotocous mammals, where close kin such as maternal siblings often stay in the same group for life (e.g. primates: Langergraber, 2012, ungulates: e.g. Clutton-Brock et al., 1982, elephants: Archie et al., 2006, cetaceans: Rendell et al., 2019) also offer a unique opportunity to investigate lifelong dynamics of siblings' relationships, and the interplay between sibling competition and cooperation across different life stages and contexts. On the one hand, lifelong maternal support positively influences offspring's fitness in many ways, meaning that maintaining a strong relationship with the mother and monopolizing her support (if monopolisable) against siblings might be beneficial. On the other hand, siblings are also valuable social partners throughout life or long life segments, and kin cooperation may bring substantial fitness benefits as well.

Monotocous primates, like apes or cercopithecines, represent ideal model species to investigate sibling competition. Indeed, they are long-lived organisms, with relatively low reproductive rates and slow life-histories. Offspring have a slow developmental pace, with extended periods of lactation, and siblings are often several years apart. For instance, interbirth interval ranges from one year on average in macaques (D. S. Lee et al., 2019), two years in baboons (Cheney et al., 2004), five years in chimpanzees (Clark, 1977) and up to eight years in orang-utans (van Noordwijk & van Schaik, 2005). Offspring also exhibit a period of juvenility, defined as the period spanning from weaning to sexual maturation, during which they keep benefiting from post-weaning maternal care. Siblings of different ages co-reside for several years and interact preferentially with each other throughout their developmental period (Lonsdorf & Ross, 2012), and same-sex siblings from the philopatric sex can remain strong social partners for life (Silk, 2007). In addition, their shared evolutionary history with humans as well as the similarities of their life-history make them an ideal model to better understand the evolutionary roots of sibling rivalry in humans. Specifically, studying sibling competition in primates might benefit from an interdisciplinary approach, bringing together psychology, anthropology and behavioural ecology, as the dynamics of sibling relationships in these species might resemble those of humans much more than other species such as rabbits. For instance, they may represent an ideal model to study the evolution of the emotional mechanisms of sibling competition that are ubiquitous in humans. And finally, because one has to consider practical aspects before starting a PhD, primate behaviour, sociality and ecology have been extensively studied over the last 50 years in comparison to other

mammals, with many long-term projects collecting data spanning over several decades and generations (e.g. the Amboseli baboon project with data spanning over five generations of yellow baboons), making non-human primates a rich source of comparative data.

5. Study aims

This study is an attempt to investigate the extent to which siblings compete over maternal care, one behavioural aspect of sibling competition, and to identify the potential maternal resources at stake in two wild primate populations, chacma baboons (*Papio ursinus*) in Namibia, and mandrills (*Mandrillus sphinx*) in Gabon. These two species both live in large and stable multimale-multifemale groups, forming matrinilineal societies where females are philopatric and males disperse upon sexual maturity. Offspring form strong bonds with their mother, which can extend into adulthood for females. Although being closely related and showing similarities in their social organization, chacma baboons and mandrills differ in several aspects particularly relevant for this study: mandrills have a faster developmental pace than baboons, and reproduce seasonally while chacma baboons breed year-round which induces different distributions of interbirth intervals. Mandrills also live in an equatorial environment where food is relatively abundant year-round, while chacma baboons live in a semi-desertic environment where food is generally scarce.

In the first chapter, I provide details on the two study species, describing their similarities and differences, and their relevance for my questions. I also describe the two study sites and populations, and give a brief overview of the nature of the data collected in these two projects within the framework of my PhD.

In the second chapter, I investigate changes in mother-juvenile relationships following the birth of a younger sibling (i.e. also referred as the “transition to siblinghood” period) in chacma baboons. In this species, where offspring are already weaned for several months by the time their mother gives birth again, I test whether the birth of a younger sibling induces a decrease in maternal care toward the older juvenile, a weakening in the mother-juvenile relationship, and if the transition to siblinghood is stressful for the older sibling.

The third chapter examines the same developmental milestone in mandrills, investigating changes in maternal care, mother-offspring relationships and mother-offspring

conflicts between the mother and the older juvenile upon the birth of a younger sibling, with a particular focus on offspring age during the transition given the seasonal reproduction of mandrills.

Finally, the fourth chapter investigates whether siblings can strategically interfere in their siblings' maternal grooming in chacma baboons, investigating whether siblings compete over maternal grooming and attention, whether such competition targets specific siblings, and the potential emotional underpinnings of such behaviours.

Chapter 1: Study species and populations

1. Study species

Chacma baboons (*Papio ursinus*) and mandrills (*Mandrillus sphinx*) are two relatively closely related primate species, both belonging to the *Cercopithecidae* family. Chacma baboons are one of the six species from the genus *Papio*, which are closer to the *Lophocebus* genus, while mandrills and drills (the other species from the genus Mandrillus, *Mandrillus leucophaeus*) have been recently found to be closer to mangabeys (genus *Cercocebus*) than to the *Papio* genus (Schroeder et al., 2022; Zinner et al., 2009) (Fig. 1a).

Chacma baboons and mandrills share many similarities in their ecology and social organization. First, both species are mainly terrestrial, with an omnivorous diet. Second, they are among the largest primates in the *Cercopithecidae* family, with a strong sexual dimorphism. Mandrill and chacma baboon males weigh on average 30-35 kg, and are respectively almost 3.5 and two times heavier than adult females, respectively, who weight ~8-10 kg in mandrills (Setchell et al., 2002) and ~15kg in baboons (Fig. 2). Adult males exhibit large canine teeth, and bright facial and hindquarters colours in mandrills (Setchell & Jean Wickings, 2005, Fig.2). Third, both species live in large multimale-multifemale groups, ranging from 20-80 individuals for chacma baboons and can go up to several hundred for mandrills (Abernethy et al., 2002). Females are philopatric and remain in their natal group for life, forming matrilines, while males often disperse in neighbouring groups upon sexual maturity (Abernethy et al., 2002; Bulger, 1993; Seyfarth, 1976) (although several male mandrills seem to come back after a few years to reproduce in their natal group, *M.J.E.C. pers. obs.*) . Both sexes form a linear hierarchy within groups: adult males hierarchy is unstable and generally established through frequent fights and aggressions (Bulger, 1993), while adult females form stable hierarchies in which daughters inherit the rank of their mother (Setchell et al., 2002; Seyfarth, 1976; J. Silk et al., 1999). Younger daughters typically outrank their older sisters before reaching adulthood, thanks to familial support from their mother and older sisters (Cheney, 1977; Engh et al., 2009). Individuals show strong affiliative bias toward maternal and paternal kin, in particular with their mother and sisters (M. J. E. Charpentier et al., 2007, 2012; J. B. Silk, Alberts, et al., 2006; J. B. Silk, Altmann, et al., 2006), which can extend into adulthood for females (M. J. E. Charpentier et al., 2020). These strong affiliative bonds between closely related females later translate into fitness benefits (M. J. E. Charpentier et al., 2012; J. B. Silk et al., 2003, 2010). Both species are polygynandrous. Males compete intensely to access

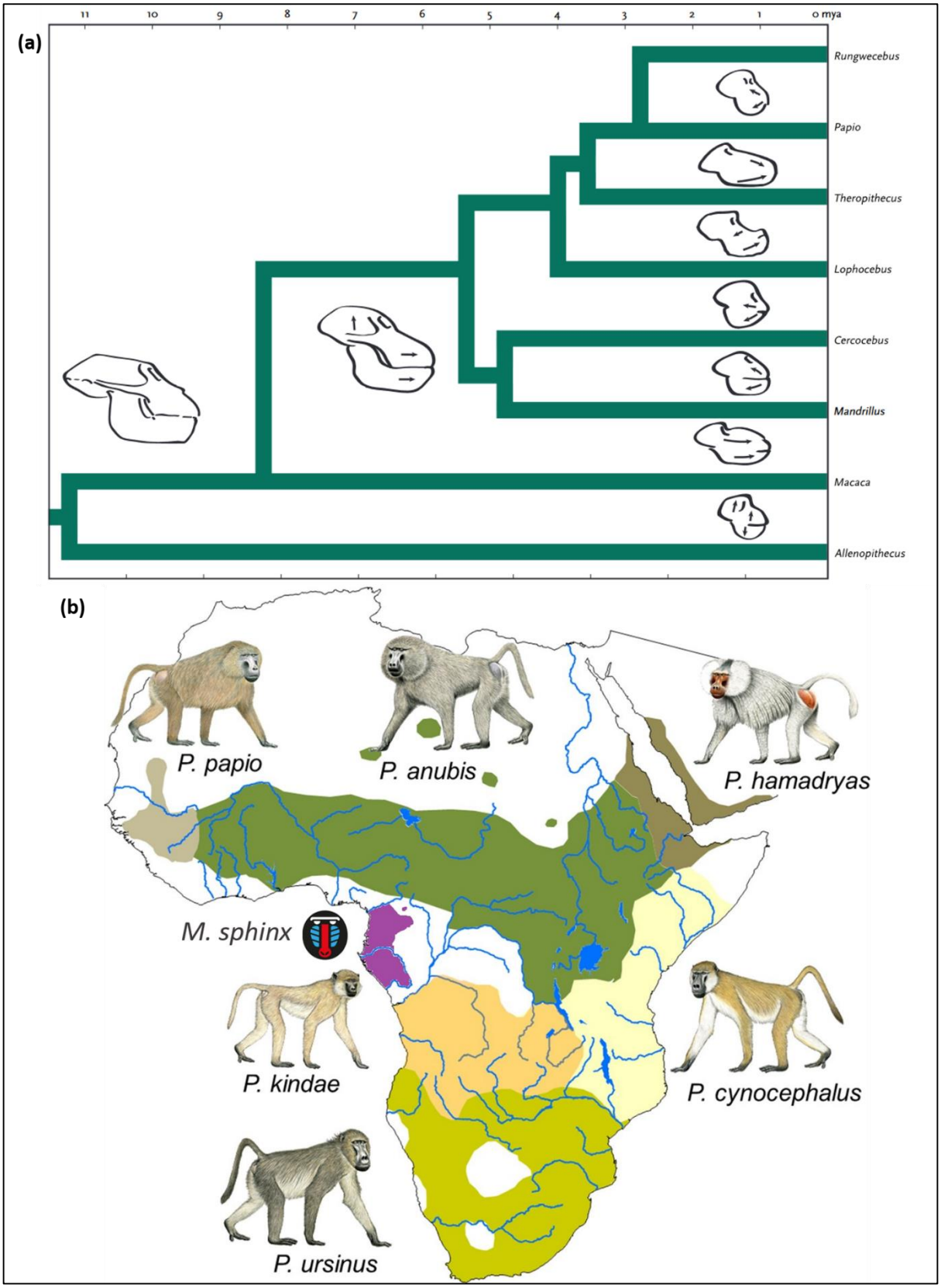

Figure 1: (a) Phylogenetic tree of the Cercopithecidae family (from Kingdon, 2012), and (b) geographical distribution of the six species the Papio genus and mandrills (redrawn from Fischer et al. 2019)

receptive females, and mate-guard them around the ovulation period (Bulger, 1993; Dixson

et al., 1993; Seyfarth, 1978). During these mate-guarding episodes, also called “consortships”, the male maintains close spatial proximity with the female and monopolises sexual access to her. Dominant males usually monopolise most breeding opportunities in a group, resulting in high reproductive skew toward the alpha male (M. Charpentier et al., 2005; Huchard et al., 2010). Females in both species have a roughly similar gestation length (175 days on average for mandrills (Setchell et al., 2002), and 190 days for chacma baboons (Barrett et al., 2006) and give birth to a single offspring.

However, mandrills and chacma baboons also differ in various aspects of their ecology, social system and life history traits. First, mandrills are endemic to dense equatorial forests from central Africa (Abernethy et al., 2002), while chacma baboons are found in southern Africa, and inhabit a wide range of environments, such as woodlands, mountains, savannahs, or arid areas (Cowlishaw, 1997a; Jolly, 1993) (Fig. 1b). Second, perhaps due to their size difference, mandrills tend to have faster life histories than chacma baboons, as they start to reproduce at younger ages (age at first birth = 5.0 years in mandrills *vs.* 6.9 in chacma baboons Cheney et al., 2004), show shorter post-partum amenorrhea (median = 8.1, range 2.6-19.1 months in mandrills *vs.* 11.2, 7.3-18.1 months in baboons) and inter-births interval on average (median = 18.6 months for mandrills *vs.* 22.3 months in baboons) (Dezeure, 2021). Infant mandrills also show a faster developmental pace, with an average weaning age around 8 months-old in semi-captive mandrills (Setchell & Wickings, 2004) *vs.* 12 months-old in chacma baboons (Carboni et al., 2022). Third, mandrills are seasonal breeders while chacma baboons breed year-round (Dezeure et al., 2021, 2022). In mandrills, the reproductive season occurs throughout the dry season (Jun-Sept), with a peak in conceptions in July and August, and the birth season peaks in December and January (Dezeure et al., 2022). Consequently, a female not reproducing during a given year will have to wait until the next reproductive season to start a new reproductive attempt. Interbirth intervals in mandrills therefore show a bimodal distribution, with a first peak centred on 13.8 ± 1.6 months (mean ± SD) for females giving birth the consecutive year, and around 22.6 ± 1.9 months for females skipping one reproductive season (Fig. 3). In contrast, in chacma baboons, interbirth interval are roughly normally distributed, with an average length of 23.0 ± 4.6 months. Mandrill offspring whose mother skips the consecutive reproductive season might benefit from this extended period of care in comparison to offspring whose mother reproduces one year after their birth, while

Figure 2: Mandrills (A, C, E) and chacma baboons (B, D, F) living their life. (A) a mandrill mother resting while nursing her infant, her older juvenile affiliating with her; (B) a chacma baboon alpha female resting while maintaining her newborn infant on her belly and being groomed by her older daughter; (C) two mandrill siblings spending time together – note that the older one is not trying to suffocate the younger one; (D) chacma baboon siblings doing the same; (E) adult male mandrill being groomed by an adult female with her infant, and a juvenile female at the same time – note the extreme sexual dimorphism, and (F) chacma baboon adult male and female resting together on the first day of life of their baby – note the cuteness. Photo credit: Berta Roura Torres (A, C and E), Ndapandula Shihepo (B), and me (D and F).

in baboons, mothers' reproductive pace might be more flexible depending on offspring's

developmental pace and resource availability. As a consequence of this strong reproductive seasonality, in mandrills, most males are only temporary resident in the group, immigrating massively into the group at the beginning of the mating season and, for half of them, emigrating at the end (M. J. Charpentier et al., 2022). The social or parental role of those male mandrills who are still in the group at the time of their offspring's birth is largely unknown. This seasonal social dynamic likely impacts many aspects of mandrills' socio-ecology. In contrast, adult male chacma baboons generally stay in the same group for several years, meaning that they are most of the time still present in the group when the offspring they sired are born, and might remain throughout their developmental period (Huchard et al., 2013; Moscovice et al., 2009). Adult males can form 'friendships' with lactating and pregnant females (Huchard et al., 2010; Moscovice et al., 2009), characterized by a strong grooming relationship and high spatial proximity (Baniel et al., 2016). These friendships' main function seems to be infant protection against infanticide (Moscovice et al., 2010; Palombit et al., 1997), but male-infant association during ontogeny also facilitates access to better food quality during weaning and juvenility (Huchard et al., 2013; Lynch et al., 2020), limits aggression from conspecifics (Lemasson et al., 2008; Nguyen et al., 2009), and can therefore increase offspring's developmental pace and fitness (M. J. E. Charpentier et al., 2008). In mandrills, infanticide has never been formally documented (but is the most plausible scenario for several infant deaths recorded in our study population, *M.J.E.C. pers. obs.*) and whether such forms of paternal care as the ones observed in baboons exist in mandrills is unknown, although the potential for such associations and long-term effects seems reduced given their socio-ecology. Finally, baboons are one of the most-studied primate genus and are often used as model species to understand early-human evolution (Fischer et al., 2019), while mandrills remain a charismatic yet unknown primate, with most of our knowledge on their ecology and social system coming from a semi-captive population (Setchell, 2016).

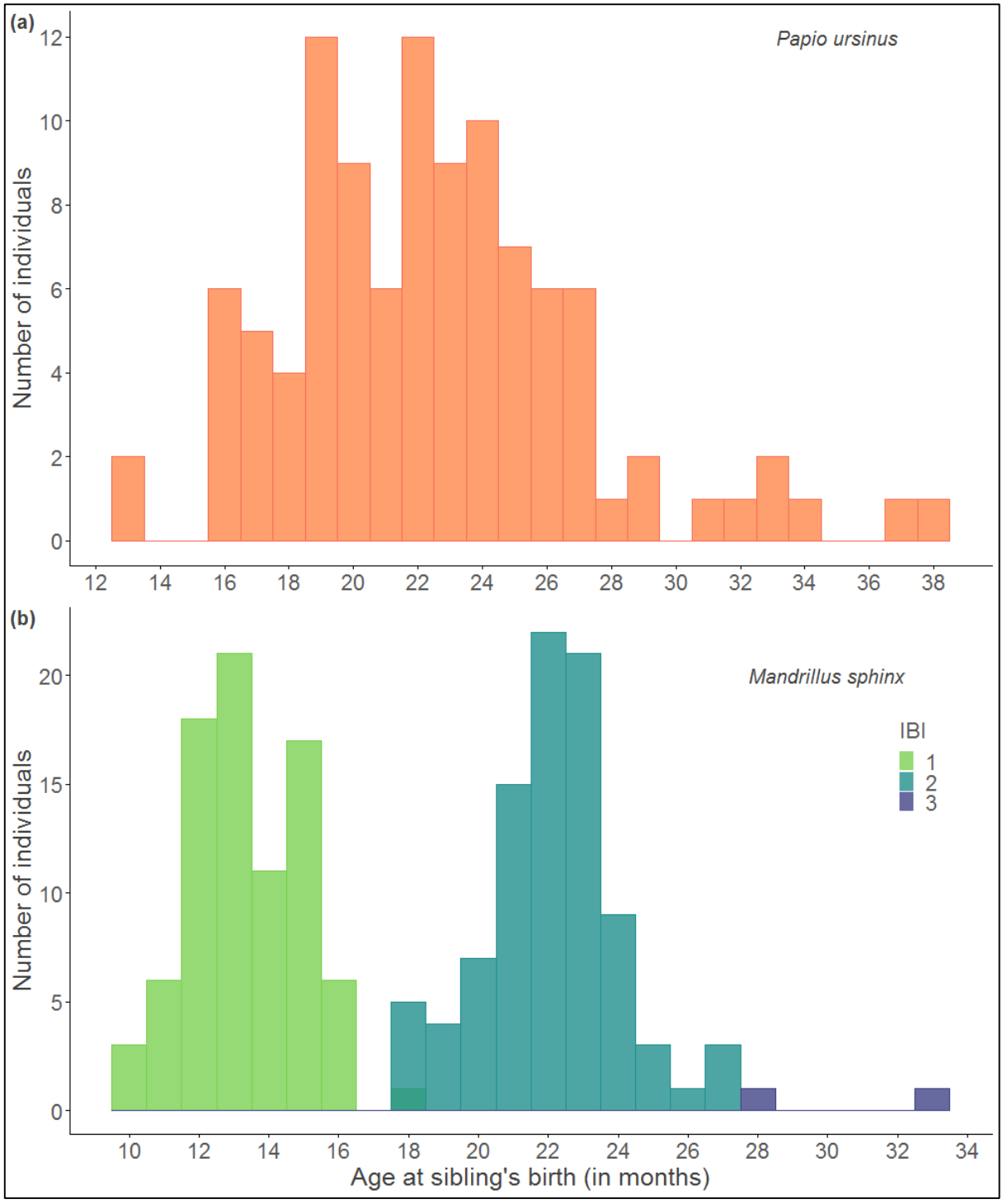

Figure 3: Distribution of interbirth intervals. Panel (a) shows interbirth intervals in chacma baboons using 104 individuals for which birth date accuracy was ≤2 months. Panel (b) shows the interbirth intervals in mandrills using 175 individuals with birth date accuracy ≤2 months. Colours in (b) corresponds to the number of reproductive seasons between the birth of the individual and the birth of its younger sibling (1: the younger sibling was born the next birth season, 2: the younger sibling was born 2 birth seasons later, etc.)

2. *Study sites and populations*

The study population of chacma baboons has been followed for more than 20 years by the **Tsaobis Baboon Project**, which was funded by Guy Cowlishaw in 2000 and is now co-directed by Alecia J. Carter, Guy Cowlishaw and Elise Huchard. This population lives in the Tsaobis Nature Park (22°23'S, 15°45'E), a natural reserve located in the Erongo region in central Namibia. Tsaobis is located in a semi-desertic environment, characterized by steep rocky mountains and ravines descending toward alluvial plains, separated by the ephemeral Swakop River (Cowlishaw & Davies, 1997). It is a strongly seasonal environment, with a long dry (and hot) season throughout most of the year, and a short rainy (even hotter if possible) season from November to March (primarily in January and February). Annual rainfall is low (85mm measured during a period of five years), and highly variable between years, with frequent dramatic droughts lasting several years (two episodes since the beginning of the project). The Swakop River is dry most of the time but still supports permanent patches of trees and bushes where chacma baboons can forage year-round, such as *Acacia erioloba*, *Acacia tortilis*, *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica* (the latter also known as the fieldworker's nightmare) (Cowlishaw & Davies, 1997). Following rainfall episodes, they can also forage on the short perennial bushes and annual grasses that grow in hills and plains.

The project follows two troops of chacma baboons, 'L' and 'J', which have been habituated in 2000 and 2005 respectively. In addition, we followed 'M' troop, that fissioned from 'J' in 2016 before fusioning again in 2021. Troop size between 2005 and 2021 ranged from 18 to 81 individuals in L troop, 27 to 68 individuals in J, and 16 to 24 individuals in M between 2016 and 2020. Individuals from L and J were captured in 2005, 2006, 2012, 2016, 2018, 2019, and 2021, and M troop was captured in 2017. During these captures (see (Huchard et al., 2010) for details on the trapping process), individuals are marked with unique ear-notches so that they are all individually recognizable, including juveniles and infants. Small tissue samples taken from the ears are used for genetic analyses. In addition, dental examination were used at the onset of the project to determine individuals' age, using patterns of tooth eruption and molar wear patterns (Huchard, Benavides, et al., 2009). All troops are followed on a daily basis by field observers during field seasons, which usually take

place every year during austral winter (field season duration ranges from 3 to 8 months, from May to December).

The study mandrills are followed within the framework of the **Mandrillus Project**, which was created by Marie (J.E.) Charpentier in 2012, and is the only population of wild habituated mandrills followed by a long-term project. They live in the Lékédi Park and its vicinity (near Bakoumba, Haut-Ogooué, Gabon), an area composed of a mosaic of evergreen forests, grasslands and savannahs (Brockmeyer et al., 2015). Annual rainfall variations mark four distinct ecological seasons: a long-rainy season (February-May), a long-dry season (June-September), a short-rainy season (October-November) and a short-dry season (December-January). This population originated from 65 captive individuals, initially housed at the CIRMF (Centre International de la Recherche Médicale à Franceville, Gabon), who were released in two waves in 2002 and 2006 (Peignot et al., 2008). Wild males immigrated in the group and started to breed with females as early as 2003. The Mandrillus Project started in 2012, benefitting from the initial habituation of captive-born females, when the group counted ~120 individuals. Since then, the group has extended, counting ~250 individuals in Fall 2022, of which only 6 adult females were born in captivity. All individuals, including infants and juveniles, are now individually recognizable thanks to skilled field assistants and distinctive marks and features. Field assistants follow the group on a daily basis year-round, except occasionally when the mandrills vanish into the wild for several days or weeks (when the world need them most (↓).

3. Data collection

In both projects, trained fieldworkers collect a variety of data during daily observation on the troop they follow. First, precise demographic data are collected through censuses conducted every day to record all individuals that were seen in the field, as well as observed births, deaths or dispersal. Second, females' reproductive states (cycling, pregnant or lactating) are recorded non-invasively on a daily basis, as well as mate-guarding events. Chacma baboon and mandrill females both exhibit exaggerated sexual swellings when they are sexually receptive. Sexual swellings' size increases during the first phase (turgescent) of the oestrus cycle, reaches its maximum around ovulation and then decreases (deturgescent phase) until disappearing, when females are not receptive anymore (Higham et al., 2008; Huchard,

Courtiol, et al., 2009). Pregnancy is determined *a posteriori* when a female has not been seen cycling for a while, and some females exhibit small pregnancy swelling, that differ in shape and colour from sexual ones (*pers. obs.*). Finally, fieldworkers also collect behavioural data every day on individually recognizable individuals (Fig. 4A, 4B). These data consist mostly in *ad libitum* and focal observations (Altmann, 1974) with specific protocols in both projects.

1.1. Data collection at Tsaobis

I spent a total of seven months in Tsaobis, between May and December 2021, along with a team of ~8 field assistant and another PhD student. Every day, two teams of 2-3 people would follow each troop on foot, from dawn to dusk. Chacma baboons sleep on steep cliffs at night to limit predation risk and can travel 1-20km every day to forage (Cowlishaw, 1997b). As they can use different cliffs every night, we follow them before they leave in the morning until they climb up a (maybe new) cliff in the evening in order to locate them every next morning. Baboons are extremely well-habituated, allowing observers to approach within 5m from any individual without triggering any reaction, allowing us to collect detailed behavioural data. During this field season, we conducted two different protocols as part of my project, in addition to data collected as part of long-term protocols.

First, we collected a wide variety of data as part of the long-term protocols:

- Daily censuses monitoring the presence of every individual in the troop, new births or deaths, and females' reproductive states;
- Troop spatial location and activity: every 30 minutes, we take a GPS point and record the spread of the troop along with the habitat used, and the activities at the group level;
- *Ad libitum* collection of grooming and agonistic interactions, copulations, tantrums, and unusual events;
- *Ad libitum* collection and follow-up of injuries (these data were not used in this thesis);
- Monthly phenology surveys in the hills and riverbed to record food availability (these data were not used in this thesis);
- Two long-term focal observation protocol: a thanatology focal protocol, to investigate 'grieving' behaviours in the troop after the death of an individual, and maternal style

focal protocol, to determine the maternal style of each female with a dependent infant (these data were not used in this thesis).

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Figure 4: (A) data collection at Tsaobis – one field assistant is actually collecting observations while the other serves as focal individual for the juvenile baboon (©Jesse Jorna). (B) Berta Roura-Torres pretending to collect focal observations at the Mandrillus Project (©Nikos Smit).

Second, as part of my project, we conducted **focal observations** on all immature individuals younger than 4 years-old at the beginning of the field season. Individuals that were born during the field season were incorporated to the sample group. Focal observations lasted 20 minutes, and were at least 10 minutes long. Focal observations were spread equally across the day (split into four 3h time-blocks), and focal individuals were chosen randomly and sampled no more than once per half-day. We collected three different category of data:

- Focal individual's activity on a continuous basis: feeding and travelling-feeding (with the nature of the food item), drinking, travelling, resting/exploring the environment, solitary and social playing (along with the identity of the play partners and the identity of the initiator of the play bout for social play), grooming (along with the identity of the grooming partner, the direction of the grooming, and the identity of the individual that terminates the grooming bout), suckling (along with the mother's activity and the identity of the individual that terminates the suckling bout), and vigilance behaviours. In addition, we kept track of mother-focal individual proximity by recording on a continuous basis every close approach and leave (within 60cm) between the mother and the focal individual, with the identity of the initiator. For juveniles with an infant younger sibling, we also recorded the presence and activity of the infant for every approach (i.e. the mother is nursing or grooming the infant, or the infant is present or absent within a 60 cm radius around the mother, or out of sight).
- Point events: these data included every affiliative (e.g. lipsmack, come-here face, presenting, grunt, handling, etc.) and agonistic (e.g. displacement, supplant, threat, attack, etc.) interactions. We also recorded stress (e.g. nervous glances, barks, screaming etc.), anxiety (e.g. self-scratch, yawning etc.) and social learning behaviours (e.g. observe feeding, sniff-mouth, feeding on scraps etc.). As I was particularly interested in mother-offspring relationships, we also recorded detailed data on specific interactions such as offspring's requests of maternal care, maternal rejections in response to such requests, and tantrums.
- Scan observations every 5 minutes (5 scan observations *per* focal observation in total): we recorded focal individual's activity, its distance to its mother (along with the mother activity if she was within a 5m radius), and the number and identity of all individuals present within a 5m radius. If the focal individual was feeding during the

scan, we also recorded the nature and patch quality of the food item, and counted the number of bites during 30 seconds.

In total, we collected 1117.2 hours of focal observations from 53 individuals (mean ± SD = 21.1 ± 4.8 hours of observations *per* individual, across *N* = 63.2 ± 14.4 focal observations *per* individual). Unfortunately, these data were not used in the present thesis, but should be used in the coming months as I have several papers in mind that I would like to write using these data.

Third, we conducted a mini-focal observations' protocol to collect **grooming interferences** within the family context. We included every family (i.e. a mother and all her offspring) with at least 2 offspring living in the group during the study, resulting in a total of 16 families and 49 offspring. Family size ranged from 2 to 5 offspring, with offspring aged from 6 days up to 8.9 year-old. We conducted 5 minute-long focal observations on i) a mother-offspring dyad engaged in a grooming interaction (independently from the direction of the grooming), and ii) resting mothers. We collected two types of data:

- All behaviours directed at the grooming dyad or resting mother: these behaviours included any affiliative (e.g. body contact, play, lipsmack, come-here, presenting, etc.) and aggressive behaviours (e.g. threat, attack, displacement, etc.) directed to one or both groomers (or the resting mother), any maternal care solicitation (e.g. grooming or suckling request, tantrum), and close spatial proximity (e.g. approach or pass by within 1m around the grooming dyad/resting mother). We recorded the identity of the individual displaying the behaviour, and the identity of the receiver within the dyad if assignable. In addition, for observations on grooming dyads, we recorded the outcome of the behaviour, i.e. whether the grooming continued, whether it disrupted the grooming but did not allow the interferer to gain access to one of the groomer, or whether it disrupted the grooming and allowed the interferer to gain access to one of the groomer.
- Offspring spatial proximity within a 10m radius around the grooming dyad/resting mother on a continuous basis.

In total, we collected 89.3 hours of observations across 1330 focal observations performed on the 16 families, including 45.8 hours across 696 observations on grooming

dyads, and 43.5 hours across 632 observations on resting mothers. I used these data in the fourth chapter of this PhD.

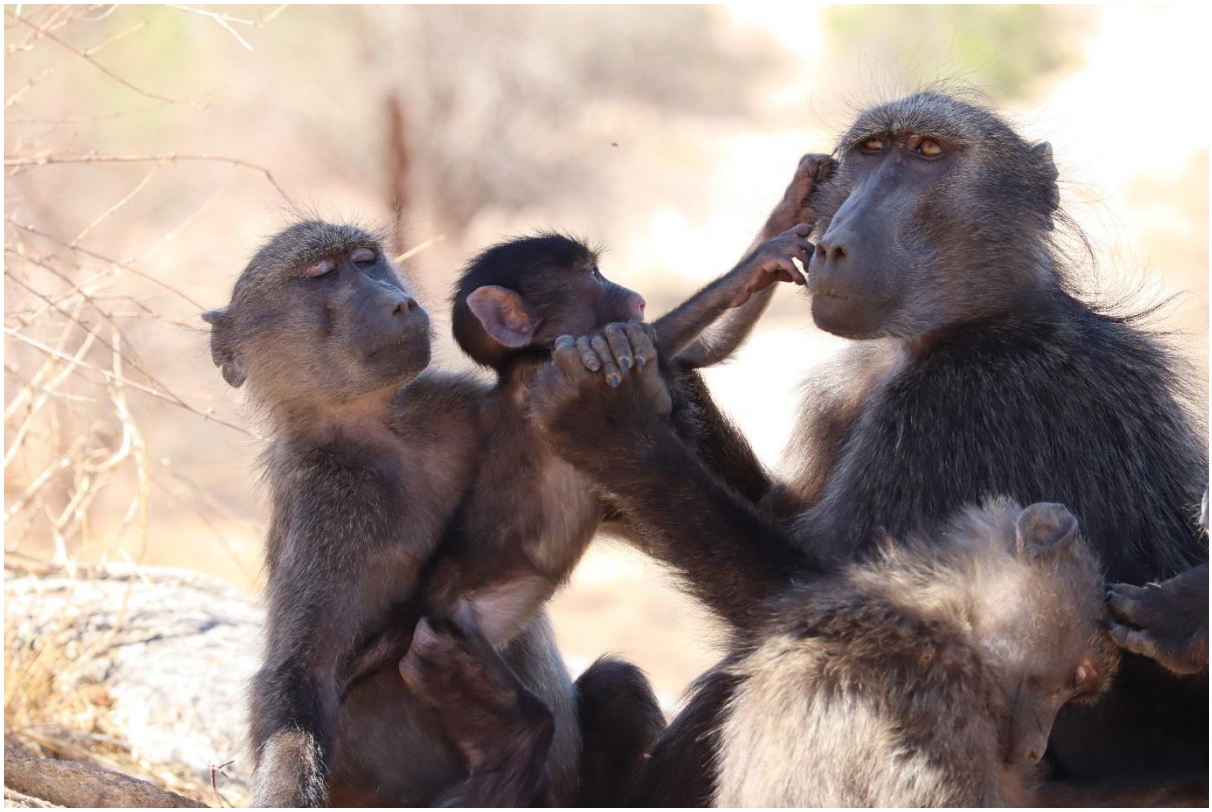
1.2. Data collection at the Mandrillus Project

I spent roughly four months and a half at the Mandrillus Project, between November 2019 and March 2020. This project runs year-round with a full-time field team of ~6-8 persons following the mandrills every day on foot. Mandrills sleep up in trees at night to reduce predation risk, and the team needs to follow them from dawn to dusk to find the group every day. Mandrills are all well-habituated, allowing observers to approach within 2m from some individuals without triggering any reaction, but some individuals are more elusive, and can be difficult to observe, especially in closed habitats. During my field season at the Mandrillus Project, I mainly enriched a pre-existing focal protocol on juveniles, and participated in the long-term data collection. Below is an overview of the main data collected by field assistants:

- Daily census of all individuals present in the group, births, deaths and dispersal events, as well as females' reproductive states;
- *Ad libitum* collection of grooming, agonistic and sexual interactions;
- *Ad libitum* collection of injuries;
- Focal observations on adult individuals;
- Focal observations on immature individuals (1 to 4 years old). Focal observation last 5 minutes maximum (often less due to the closed environment) and focal individuals are chosen randomly. This protocol is quite similar to the one used with baboons. We record on a continuous basis individual focal activity: travelling, foraging, resting/sleeping, drinking, playing (along with the identity of play partner(s)), grooming (along with the direction of the interaction, the identity of the partner, and the identities of the individuals that initiate and terminate the grooming bout), maternal carrying and suckling. Close spatial proximity between the mother and the offspring is continuously monitored, by recording every approach and leave within 1m, with the identity of the initiator. We also collect point events, including affiliative (e.g. affiliative contact, mounting, sniff mouth, etc.), aggressive and dominance interactions (e.g. displacement, supplant, threat, attack). Mother-offspring relationships are a particular focus of this protocol, so we record interactions such as

offspring requests of maternal care, comfort-seeking behaviours, maternal rejection and protection, and tantrums. As I was particularly interested in siblings' relationships, I also added specific behaviours on juvenile-infant siblings' interactions, such as infant manipulation, nursing interruption or infant kidnapping. Infant's distance and activity (if visible) are also recorded after each approach between a juvenile older sibling and its mother. Finally, we record scan observations twice *per* focal observation. Initially, we were recording the identity of all the individuals in body contact with the focal, and present within a 1m and 5m radius. Since 2020, we now also record the distance with the mother and her activity, and the distance with the infant younger sibling and its activity.

The length of this section reflects my personal contribution to the Mandrillus database: as I spent a good 3 months and a half trying to learn all the immature individuals by face, I collected an astonishing total of 23 focal observations. Luckily, full-time field assistants were much more efficient than me, and I was able to use focal data collected as part of the long-term protocol in the third chapter of this thesis (see chapter 3 for more details on the sample sizes).



Chapter 2: Transition to siblinghood in a wild chacma baboon population

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ABSTRACT

In monotocous mammals (i.e. where females produce one offspring at a time), most juveniles will experience the birth of a younger sibling in their life. Transition to siblinghood (TTS) has rarely been studied in primates, although it reflects the last step in the shift of maternal investment from one offspring to the next and could thus represent a critical moment for mother-offspring conflict and sibling competition. Here, we use behavioural data on juvenile primates who recently experienced, or not, the birth of a younger sibling to investigate changes in mother-juvenile relationships during TTS in a wild population of chacma baboons (*Papio ursinus*). We show that (1) mother-juvenile spatial association remained stable; (2) mothers did not decrease their probability to initiate proximity or affiliation with their juvenile; and (3) juveniles initiated proximity and affiliation more frequently toward their mothers, and showed more signs of anxiety after the birth of their younger sibling. Taken together, these findings suggest that juveniles with a younger sibling solicit their mother more often and seek more maternal attention than juveniles without. Overall, mother-offspring conflict could extend in the post-weaning period, during which more subtle maternal resources, such as maternal attention, could be at stake in sibling competitive relationships.

KEYWORDS

Maternal behaviour; mother-offspring bonds; mother-offspring conflicts; sibling birth; sibling rivalry; sibship

INTRODUCTION

Parental investment is defined as any type of investment a parent can provide to its offspring that will enhance the offspring's fitness at the cost of the parent's future reproduction (Trivers, 1972). In a seminal paper, Trivers argued that natural selection should favour, in offspring, the expression of traits favouring the monopolisation of parental resources, above the level that parents may be willing to provide (Trivers, 1974). This difference in the optimal amount of parental investment is triggered by an asymmetry in genetic relatedness between the different family members: an offspring is twice as related to himself as it is to its siblings, while a parent is equally related to all offspring. This genetic conflict of interest is predicted to trigger conflicts over the amount and duration of parental investment, not only between parents and offspring, but also between siblings, who should all try to maximize their share of parental investment until the costs for their siblings decrease their own inclusive fitness.

Sibling competition has found empirical support in a wide range of taxa from insects to mammals (see for reviews: Mock et Parker 1998; Drummond 2006) where it can largely impact offspring's development, with long-term consequences in three areas: morphology (e.g. insects: Schrader et al., 2018; birds: de Kogel and Prijs, 1996; mammals: Fisher et al., 2018; Hofer and East, 2008), physiology (e.g. birds: Drummond and Rodríguez, 2013; Nettle et al., 2015; Verhulst et al., 2006; mammals: Fey and Trillmich, 2008; Guenther and Trillmich, 2015; Stauffer et al., 2018) and behaviour (e.g. birds: Bebbington et al., 2017; Ekman et al., 2002; mammals: Guenther and Trillmich, 2015; Hudson et al., 2011) and even lead to siblicide (e.g. birds: Braun and Hunt, 1983; Fujioka, 1985; Lougheed and Anderson, 1999; mammals: Andersen et al., 2011; Hofer and East, 2008). However, our understanding of family competition suffers from a taxonomic bias: most studies have focused on brood or litter-rearing species (especially in mammals, see for reviews: Drummond 2006, Hudson et Trillmich 2008, Roulin et Dreiss 2012). Most of the theoretical models and evolutionary hypotheses have thus been developed for same-age siblings and within-brood competition (Hudson & Trillmich, 2008), leaving the competition between siblings of different ages virtually unstudied.

In long-lived species, such as monotocous mammals, which generally produce and nurse one offspring at a time (Altmann 1980, Clutton-Brock et al., 1983), siblings could compete for different resources than milk (Hudson & Trillmich, 2008), meaning that sibling competition can last beyond weaning age. In those species, offspring may form long and enduring bonds with mother that can extend far beyond independency (e.g. yellow baboons, *Papio cynocephalus*: Silk et al., 2006b, 2006a; Asian elephants, *Elephas maximus*: Lynch et al., 2019; red deer, *Cervus elaphus*: Clutton-Brock et al., 1982), and exhibit a period of post-weaning juvenility, during which they keep benefiting from maternal care such as social support, facilitated access to food, or protection against predators (Clutton-Brock, 1991). Maternal presence during the post-weaning developmental period improves offspring growth (e.g. chimpanzees, *Pan troglodytes*: Samuni et al. 2020), and increases future reproductive success and longevity (chimpanzees: Crockford et al., 2020, Stanton et al. 2020; bonobos, *Pan paniscus*: Surbeck et al., 2011; red deer: Andres et al., 2013), potentially through a prolonged access to such forms of maternal care. Monopolising such resources might be advantageous for offspring, and could thus induce competition between siblings.

In line with this, several empirical studies show that sibling competition can have substantial fitness consequences in monotocous species. In Galapagos fur seals (*Arctocephalus galapagoensis*) and sea lions (*Zalophus wollebaeki*), calves whose mother is still nursing the older sibling experience a reduced growth and increased mortality risk (Trillmich & Wolf, 2008). In rhesus macaques (*Macaca mulatta*), short interbirth intervals reduce the survival to adulthood for the older offspring and the survival to weaning for the younger one (Lee et al., 2019). In female yellow baboons, having a close-in-age younger sibling nearly doubles the mortality risk during adulthood (Tung et al., 2016). Moreover, this effect has intergenerational consequences because adult females whose mother had a close-in-age younger sibling further experienced higher offspring mortality (Zipple et al., 2019). In humans (*Homo sapiens*) as well, short interbirth intervals increase offspring mortality risk (Conde-Agudelo et al., 2006; Rutstein, 2005; Wendt et al., 2012). Overall, these studies show that the dilution of maternal care between different-age offspring has fitness costs, setting the conditions under which sibling competition over access to maternal resources should evolve.

Regarding the behavioural mechanisms at play, while many primate studies have focused on mother-offspring conflicts during the weaning period or around a mother's cycle

resumption (Barrett and Henzi, 2000; Bateson, 1994; reviewed in Maestripieri, 2002), the birth of a younger sibling has been somewhat overlooked. This is striking as the arrival of a younger sibling is the last step in the mother's shift from her current offspring to the next one, and could thus represent a critical moment for both mother-offspring conflict and sibling competition. A few studies led on captive or free-ranging cercopithecines showed that the birth of a younger sibling induces an abrupt decrease in time spent in contact or in proximity to the mother and in the rate of mother-offspring interactions, primarily driven by the juvenile itself (Devinney et al., 2001; DiGregorio et al., 1987; Holman & Goy, 1988; Schino & Troisi, 2001). Maternal rejection and aggression also increased, often associated with signs of stress and "depression" in the offspring (Bolwig, 1980; Devinney et al., 2001; DiGregorio et al., 1987; Holman & Goy, 1988). In bonobos, juveniles face an increase in cortisol and a decrease in neopterin levels that can last more than six months after the birth of their younger sibling (Behringer et al., 2022). The behavioural transition to siblinghood has been more thoroughly studied in humans: it is often characterized by a decrease in maternal care and in the rate of mother-offspring interactions, an increase in the rate of confrontational behaviour with the mother and a reversal in who initiates most interactions, with children (instead of mothers) becoming the primary initiators (Dunn et al., 1981; Dunn & Kendrick, 1980; Stewart et al., 1987; Volling, 2012). Children can also show signs of distress, and exhibit more demanding behaviours (Dunn et al., 1981; Volling, 2012). Finally, a striking aspect emerging from the human literature is the high inter-individual variability in children's behavioural adjustment to the birth of a sibling (Dunn et al., 1981; Volling, 2012, 2017). Poor behavioural adjustment (e.g. higher frequency of tantrums and jealousy events toward the younger sibling) is associated, possibly causally, with lower quality relationships between siblings later in life (Brody, 1998; Pike et al., 2005), which could potentially be costly as siblings' relationships and support during adulthood can promote fitness (Pollet & Hoben, 2011).

In this study, we investigated changes in mother-juvenile relationships following the birth of a younger sibling in a wild chacma baboon population (*Papio ursinus*). Baboons typically live in matrilineal, multimale-multifemale societies, where females are philopatric and males disperse from their natal group around the age of 7-8 years (Cheney et al., 2004). Females maintain hierarchical and differentiated social bonds and give birth to one offspring every two years on average (Cheney et al., 2004; Dezeure, Baniel, et al., 2021), an interbirth

interval somewhat closer to human traditional societies than to great apes (Kramer, 2005). Offspring have a long developmental period and weaning occurs gradually during the second year of life (Carboni et al., 2022; Dezeure, Baniel, et al., 2021), which is characterized by elevated infant mortality (Altmann & Alberts, 2003a). Unweaned infants are sometimes targets of infanticide in this species, with minimal risks to weaned, older offspring (Palombit et al., 2000). In baboons, like in most primates, mothers form long-lasting bonds with their offspring, which facilitate the transition to feeding autonomy (e.g. Lynch et al., 2020) and subsequently translate into preferential grooming relationships and occasional support during conflicts as long as offspring remain in their natal group. All these resources likely increase offspring survival, as observed in chimpanzees (Nakamura et al., 2014; Stanton et al., 2020), and may generate competition among siblings. Specifically, maternal support often allows younger sisters to outrank their older sisters, which suggests that, for a female, having a younger sister could induce lifetime costs through the loss of maternally-transmitted social capital (Pereira, 1989).

In three social groups of chacma baboons from Namibia, we investigated immediate changes in the mother-juvenile relationship during the transition to siblinghood (hereafter, TTS), by comparing mother-juvenile interactions among juveniles with no younger sibling and those of comparable ages who recently experienced the birth of a younger sibling. First, we predicted (P1.1) that the amount and quality of affiliative relationships, specifically grooming interactions, between the mother and the juvenile would decrease after the birth of a new infant, with (P1.2) a shift in patterns of initiations of such interactions, from mostly mother-initiated before the birth of the sibling, to mostly juvenile-initiated interactions afterwards, as found in humans. Second, we predicted that juveniles (P2.1) would associate less often with their mother, and (P2.2) would become primarily responsible for initiating and maintaining spatial proximity to their mother after the birth of a younger sibling. Third, we predicted (P3) that juveniles that had recently experienced the birth of a younger sibling would exhibit more self-directed behaviours, generally indicating anxiety (Castles et al., 1999; Maestripieri et al., 1992; Palagi & Norscia, 2011).

METHODS

Study site and population

We studied wild chacma baboons living in Tsaobis Nature Park, on the edge of the Namib Desert (22°23' S, 15°44' E), Namibia. We collected data on three well-habituated troops (J, L and M, the latter a fission group from J since 2016) over three observational periods: July-August 2017, September-December 2018, and April-July 2019. The groups were followed every day from dawn to dusk by observers on foot, collecting demographic, life history and behavioural data. All individuals, including infants, are individually recognizable (Huchard et al., 2013).

Individual data

Individual birth dates were assessed with certainty when field observers were present during the birth (*N* = 10 offspring), or were estimated using two different methods, depending on the available information: (i) infant's coloration using a standardized, validated protocol, when the infant was not fully grey when first observed (*N* = 16, median date uncertainty = 41 days, see (Dezeure, Dagorrette, et al., 2021)), (ii) mother's reproductive states in the previous months otherwise (*N* = 32, median date uncertainty = 18 days). Overall, age uncertainty in our sample ranged from 0 to 130 days (median = 10 days).

Female parity was known from life-history records and was defined as primiparous (between the birth of the first-born offspring and the second one), or multiparous (after the birth of the second offspring). Female dominance ranks were calculated separately for each group and each year, using *ad libitum* data and focal observations of agonistic and approach-avoidance interactions: supplants, displacements, attacks, chases and threats (Huchard et al., 2010). We computed a linear hierarchy using Matman 1.1.4 (Noldus Information Technology, 2013), and transformed it into a proportional hierarchy with relative ranks (i.e. absolute rank divided by number of adult females in a group), assigning each female one relative rank per year, ranging from 0 (low-ranking) to 1 (high-ranking). We used proportional ranks rather than simple ordinal ranks because they allow to control for group size across different social groups and/or observational periods. Proportional ranks have recently been shown to better predict some female traits associated with reproductive pace (Levy et al., 2020), and could thus better predict patterns of maternal care during the post-weaning period.

Behavioural observations and sample selection

We collected 1401 hours of focal observations from 71 offspring born to 37 females (mean ± SD = 19.7 ± 9.9 h of observation per individual, range 1.3-38.6 h) using 20-min long focal observations (*N* = 57.6 ± 27.9 focal observations per individual, *N* = 4086 in total). Focal individuals were aged from 1 to 34 months old (mean ± SD = 16.1 ± 8.7 months old). Focal observations were spread equally across the day (split evenly into four 3h time blocks), and focal individuals were chosen randomly and sampled no more than once per half-day. We recorded the duration and direction of grooming interactions with the mother and the occurrence of self-scratches, a self-directed behaviour generally indicating anxiety. Maintenance of spatial proximity was assessed by recording every close approach or leave (to and from 1m) between the focal individual and its mother. In addition, we collected scans during focal observations every five minutes (i.e., up to 5 scans for each 20-min focal observation, resulting in 20182 scans in total across 4086 focal observations), and recorded whether the mother was in sight, and if yes, her distance to the focal. If the mother was out of sight, observers indicated the number of meters around the focal individual for which they could guarantee that the mother was not in sight (range: 1-100 m). Other cases where visibility was too obstructed (e.g. when focal was in sight but in a dense bush) were recorded as missing data.

In this study, we aimed to characterize the immediate behavioural response to the birth of a younger sibling. To do so, we used a cross-sectional approach, comparing juveniles who recently experienced, within the last three months, the birth of a younger sibling to juveniles of similar ages who did not yet. Juveniles who had experienced the birth of a sibling in the more distant past were excluded from this study. This 3-months window was chosen to maximize our chances to detect changes in behaviour that immediately follow the birth of an infant, i.e. reasonably close to the birth event while still ensuring a decent sample size of observations. In our sample of focal observations, juveniles who had recently experienced the birth of a younger sibling were 17- to 29-month-old. Therefore, we restricted our dataset to any juvenile in this age range (17-29 months), who either had no younger sibling (*N* = 28), or a younger sibling born within the last three months (*N* = 18). Individuals who were followed both before and after the birth of their younger sibling were included in each group respectively. We collected a total of 1525 focal observations and 7581 scan observations on 38 individuals (8 individuals were observed both with and without a younger sibling).

Statistical models

Mother-juvenile grooming relationships

To test predictions P1.1 and P1.2, we used focal data during which we recorded the duration and direction of each grooming event. First, for each observation, we recorded whether the focal juvenile groomed its mother at least once (binary: yes/no – model 1), and whether it received grooming from its mother (binary: yes/no – model 2). The probability to give or to receive grooming from the mother during a focal observation (models 1 and 2, respectively) was modelled with two generalised linear mixed models (GLMMs) with a binomial error structure. Second, we extracted the total duration (in seconds) the juvenile spent grooming its mother (model 3), or being groomed by its mother (model 4) during a focal observation. We ran two GLMMs with a negative binomial distribution and a log-link function.

Mother-juvenile spatial proximity

To test prediction P2.1, we used scan data to estimate how often a juvenile was found in close proximity to the mother. For each scan observation (recorded every 5 minutes), we recorded whether the juvenile focal was in proximity (1) or not (0) to its mother. We considered two distinct ranges of proximity: within 1m (model 5) and 5m (model 6) of the mother. We ran two GLMMs with a binomial error structure.

Second, to test prediction P2.2 and characterize juveniles' responsibility in the maintenance of spatial association with their mother, we used focal observation data. For each focal observation, we established whether the juvenile initiated an approach to, or a leave from its mother within a circle of 1m-radius (1) or not (0) (models 7 and 8, respectively). We then determined whether the juvenile received an approach or a leave from its mother (1) or not (0) (models 9 and 10, respectively). We ran four GLMMs with a binomial error structure. In addition, we computed 'Hinde's Index' for each mother-juvenile dyad, calculated as the percentage of approaches minus the percentage of leaves initiated by the juvenile (Hinde & Atkinson, 1970). This index ranges from -100 (the mother is fully responsible for maintaining proximity) to +100 (the juvenile is fully responsible for maintaining proximity). We calculated one index per dyad for each observational period (i.e. field season) and for each 'sibling status' (i.e., experienced TTS or not). When the focal juvenile experienced TTS during the period, we computed the Hinde's index before and after the birth event. We then tested

if the average Hinde's Index for a given sibling status differed from zero using a one-sample Student's t-test (*N* = 13 indices on juveniles with a younger sibling, *N* = 22 on juveniles without a younger sibling). We also tested whether the average Hinde's Index differed between juveniles with or without sibling using a linear model (*N* = 34 indices across both groups). For each test, if a dyad had several indices (because it was observed during two different observational periods or because a sibling was born during a given period – *N* = 28 individuals with 1 index, *N* = 9 with 2 indices and *N* = 1 with 3 indices), we randomly selected one of them to avoid pseudoreplication.

Juvenile self-directed behaviour

To monitor the anxiety level of juveniles, we calculated the number of self-scratches per focal observation and ran a GLMM with a negative binomial distribution and a log-link function (model 11).

Fixed and random effects

For each GLMM, we tested the effect of having recently experienced the birth of a younger sibling (yes/no), as well as the following control variables: focal juvenile sex, age (in months), birth rank (first-born vs later-born), and maternal rank. We also tested the interaction terms between the recent birth of a younger sibling and the focal juvenile age and sex (except for model 3 because of a limited and unbalanced sample size). We further included three additional fixed effects as controls: (1) group identity, to account for potential differences between groups; (2) in binomial models, duration of the focal observation (in seconds) (except models 5-6 using scan data) or, in negative binomial models, the log-transformed duration of focal observation as an offset; and (3) in model 11, year of observation because preliminary analyses showed that this variable had a strong effect only on self-scratch frequency.

We included the focal juvenile identity as a random effect in all models to control for repeated focal observations within juveniles. In models 5 and 6, we initially fitted the focal observation identity as a random effect to account for the non-independence of multiple scan observations within a same focal observation. However, adding this random effect caused convergence problems. We therefore restricted our dataset to two scans per focal observation, which were separated by >15 minutes and for which the mother-focal juvenile

distance was documented ("out of sight" or "in sight" with the approximated distance; missing data were removed). We therefore assumed that such scans were independent from each other and omitted the "focal observation" random effect from our models to facilitate model convergence.

In the linear model analysing Hinde's Index, because of limited sample size (*N* = 34), we only included the three following explanatory variables to avoid over-parametrisation: presence of a younger sibling, focal juvenile's sex and age (average age in months across the observational period).

The structure of each model, the different fixed and random effects, and sample sizes are summarised in Table A1.

Note that several other variables could account for some variability in mother-juvenile relationships throughout the TTS, such as the mother's reproductive stage or the presence or number of older siblings. In the first case, pregnant mothers may reduce their level of care but it was impossible to test with this cross-sectional design because mother's reproductive stage was correlated with the presence of a younger sibling (i.e. mothers of juveniles with a younger sibling are all lactating, while mothers of those without are either cycling or pregnant). In the latter case, older non-adult siblings may represent potential compensatory social partners, or may alternatively contribute to dilute the level of maternal care received by each sibling. Therefore, we re-ran all models with the number of older immature siblings as an additional fixed factor, setting the maximum age threshold at 4 years old for older siblings, as some females can reach menarche at this age in our population, and results are presented in the Supplementary Materials (Tables A2 to A7). This additional control variable was never found to exert a significant effect on our response variables, and did not improve our model fits, so we present the results without it in the main text.

Statistical analysis

All statistical analyses were conducted using the R Studio software (version 4.0.2). We ran mixed models using the function "glmer" from the lme4 package (Bates et al., 2015) for binomial models and "glmmTMB" from the glmmTMB package (Brooks et al., 2017) for Poisson and negative binomial models. To control for the focal juvenile's age in all analyses, we started by investigating the developmental pattern of each response variable, i.e. the

shape of its relationship with age. To do so, we ran generalized additive mixed models (GAMMs), using the "gam" function of the mgvc package (Wood, 2003), and fitted univariate models using a smoothing function, a linear function, and a second- or third-degree polynomial function to model the effect of age (offsets and random effects were also included). We then compared model fits and selected the models with the lowest AIC (Zuur et al., 2009). Linear, first-order functions of age produced the best fit to all types of data analysed, so we subsequently used linear regression between the response variable and age. When we obtained singular fits, we confirmed the results by running a Bayesian approach, using the "bglmer" function from the blme package (Dorie et al., 2021). When a Poisson model was overdispersed, we compared its fit with a type-I negative binomial model and a type-II negative binomial model and selected the model with the lowest AIC (Zuur et al., 2009). Following this test, models 3 and 4 were run with a type-I negative binomial distribution and model 11 was run with a type-II negative binomial distribution. All quantitative variables were z-transformed (mean = 0; SD = 1) using the "scale" function from the car package (Fox & Weisberg, 2019) in order to facilitate model convergence, as well as to compare effect sizes across estimates (Harrison et al., 2018). To diagnose the presence of multicollinearities, we calculated the variance inflation factor (VIF) for each predictor in each model using the "vif" function from the car package (Fox & Weisberg, 2019). VIFs were inferior to 2 in all cases, suggesting that multicollinearities did not impact coefficients' estimation in our models. To test the significance of fixed factors for each model, we used the likelihood ratio test (LRT) and associated p-values computed by the "drop1" function, and calculated the 95% Wald confidence intervals. Non-significant interactions were removed from the full model to limit the risk of over-parametrisation and facilitate the interpretation of simple effects. Finally, we assessed the significance of our full model by comparing its fit to the equivalent null model (intercept only model, including the random effects) using a likelihood-ratio test. We further checked the distribution of the residuals using "simulateResiduals" from the DHARMa package (Hartig & Lohse, 2021).

Ethical Note

This study was strictly observational and relied on behavioural data collected noninvasively on animals well habituated to human observers. Our research procedures were evaluated and approved by the Ethics Committee of the Zoological Society of London and

adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. This research was carried out with the permission of the Namibian Ministry of Environment and Tourism (MET), the Ministry of Land Reform, and the National Commission on Research, Science and Technology. Our research was conducted under MET permit numbers 2303/2017, RPIV00392018/2019.

RESULTS

Mother-juvenile grooming relationships

We first investigated whether a juvenile's grooming relationship with the mother was affected by the birth of a younger sibling (P1.1 and P1.2). Both the probability and the duration of grooming received from the mother were independent from the birth of a younger sibling (probability: Odds Ratio – OR – = 0.89, duration: mean ± SD = 36.5 ± 13.8 seconds per observation; Tables 1 and 2, Fig. 1b, 1d). In contrast, juveniles with a younger sibling had a significantly higher probability (OR = 1.71; mean probability ± SD with a sibling: 0.10 ± 0.07 vs without a sibling: 0.05 ± 0.04), and spent significantly more time grooming their mother (20.9 ± 17.3 seconds per focal observation for juveniles with a sibling vs. 9.1 ± 7.2 for those without; Tables 1 and 2, Fig. 1a, 1c). Juvenile males had a significantly lower probability, and spent less time grooming their mother than juvenile females (OR = 0.22, Tables 1 and 2). In contrast, the probability and duration of grooming received from the mother was independent of juveniles' sex (Tables 1 and 2). The probability to groom the mother and its duration both significantly increased with age (an increase in one standard deviation in age increased grooming likelihood by 49%, OR = 1.49, Tables 1 and 2), while the probability to receive a grooming from the mother and its duration tended to decrease with juvenile age (OR = 0.84, Tables 1 and 2).

Mother-juvenile spatial proximity

Mother-juvenile proximity was not influenced by the birth of a younger sibling (P2.1): juveniles with or without a younger sibling had the same probability to be within 1m or 5m of their mother during a scan observation (OR = 0.92 and 1.12 respectively, Table 3). Males were significantly less likely to be within 1m or 5m of their mother than females (OR = 0.53 and 0.72 respectively, Table 3). Juveniles born to higher-ranking females were significantly more likely to be within 5m of their mother (OR = 1.21, Table 3). Overall, juveniles were significantly less

likely to be within 1m or 5m of their mother as they grew older (OR = 0.81 and 0.80 respectively, Table 3).

Juveniles who had recently experienced the birth of a younger sibling were, however, significantly more likely to approach (OR = 1.74, mean probability ± SD = 0.24 ± 0.06 for juveniles with a sibling vs. 0.18 ± 0.05 for juveniles without) and leave (OR = 1.71, 0.20 ± 0.05 for juveniles with a sibling vs. 0.14 ± 0.05 for juveniles without) their mother than juveniles who did not yet have a younger sibling (P2.2, Table 4, Fig 2a, 2b). Males were significantly less likely to leave their mother than females (OR = 0.66), while juveniles born to high-ranking females were significantly more likely to approach and leave their mother (OR = 1.19 and 1.21 respectively, Table 4). Overall, the probability to approach and to leave the mother decreased with age (OR = 0.81 and 0.83, Table 4).

The probability of receiving an approach from the mother (P2.2) was also influenced by the interaction between the sex of the focal juvenile and the birth of a younger sibling: juvenile females with a younger sibling were less likely to be approached by their mother (mean probability ± SD = 0.05 ± 0.02) than those without a sibling (0.08 ± 0.04), while males with a younger sibling were more likely to be approached by their mother (0.08 ± 0.02) than those without a sibling (0.05 ± 0.04,Table 5, Fig. 2c). Juveniles born to high-ranking females were also significantly more likely to be approached by their mother than those born to low-ranking females (OR = 1.74, Table 5). The probability to be left by the mother was not influenced by the birth of a younger sibling, and our model did not differ from the null model (Chi^2 = 13.90, P= 0.084, Table 5, Fig. 2d).

Finally, average Hinde's indices were positively and significantly different from zero both for juveniles with a younger sibling (one-sample t-test, N = 13, t = 6.2, P < 0.001) and without (one-sample t-test, N = 22, t = 3.8, P < 0.001), indicating that juveniles were more responsible than their mother for maintaining their close spatial proximity. The average Hinde's index was not different between both groups (N = 34, t = 1.131, P = 0.267), meaning that juveniles were equally primarily responsible for maintaining close spatial proximity with their mother whether they had a younger sibling or not (P2.2).

Juvenile self-directed behaviour

Finally, juveniles' self-scratch frequency was significantly influenced by the interaction between sibship status and age (P3). Self-scratch frequency generally decreased with age but less so for juveniles who had a younger sibling compared to those with no younger sibling (Table 6, Fig. 3). Juveniles born to higher-ranking females tended to have a lower self-scratch frequency than juveniles born to lower-ranking females (Table 6).

DISCUSSION

This study investigated changes in mother-juvenile relationships during the transition to siblinghood in young chacma baboons. First, we showed that, contrary to our predictions, mothers did not reduce their investment in terms of grooming and proximity following the birth of a new infant, as their grooming probability and duration (P1.1), and their probability to initiate and stay in close spatial proximity with their older juveniles remained stable (P2.1 and P2.2). Second, we showed that juveniles with a younger sibling increased their responsibility in the maintenance of grooming and spatial relationships with their mother. Indeed, they groomed two times more often and two times longer (P1.2), and approached and left their mother a third more often (P2.2), even though they spent on average the same amount of time in close spatial proximity with her than juveniles with no younger sibling. Third, signs of anxiety decreased more slowly with age for juveniles with a younger sibling compared to juveniles of similar age without a sibling (P3). Here, we discuss the implications of our findings for the understanding of mother-offspring conflict and sibling competition in primates.

Baboon mothers did not reduce their level of maternal investment in terms of grooming and proximity following the birth of a new infant, while their older offspring initiated interactions more often. These results contradict previous studies on TTS in macaques, which reported an abrupt decrease in maternal grooming, time spent in close spatial proximity and maternal approaches (Devinney et al., 2001; Holman and Goy, 1988; Schino and Troisi, 2001; Singh and Sachdeva, 1977 but see DiGregorio et al., 1987). In these macaques, these changes were also driven by the juveniles themselves, who decreased the rate at which they initiated interactions with their mother (Devinney et al., 2001; Holman & Goy, 1988; Schino & Troisi, 2001; Singh & Sachdeva, 1977). These differences with our findings could relate to several, non-mutually exclusive factors. First, the macaque studies were conducted on captive

populations (from free-ranging to laboratory housing). Captivity and provisioning could affect mother-offspring relationships and specifically accelerate maternal reproductive pace (Altmann & Alberts, 2003b). Second, and perhaps because of their different environments, young macaques were on average 12 months old at the birth of their younger sibling, while young chacma baboons were on average 23 months old in this study. Although this age difference is partly due to species differences in reproductive pace, it may also reflect differences in juveniles' independence. Indeed, juvenile macaques were still nursing in the few months preceding the birth of their siblings, while our study subjects had stopped suckling long before their sibling was born (Dezeure, Baniel, et al., 2021). In addition, isotopic analyses showed that milk intake ceases around 12 months in our study population (Carboni et al., 2022). Subsequently, weaning and the birth of a younger sibling were simultaneous and impossible to disentangle in the macaque studies, while we were able to measure the effects of TTS on mother-offspring relationships independently of weaning.

Our results recall previous findings in human studies. Indeed, in western industrialised societies, children became more responsible for initiating interactions with their mother, including more demanding and clinging behaviour and more signs of anxiety (Dunn et al., 1981; Dunn & Kendrick, 1980; Stewart et al., 1987; Volling, 2012), following the birth of a sibling. Yet, in humans – as in captive macaques – this pattern was associated with a decrease in maternal care and an increase in maternal rejections. The lack of changes in maternal behaviour we observe in our study may be expected in natural populations, as mothers may space births in a way that allows them to provide the care needed by their offspring at different stages of their lives. When a newborn arrives, older juveniles are fully weaned and lactation may not substantially affect mothers' ability to maintain their relationship with their juvenile offspring via proximity, grooming, co-feeding, and occasional acts of social support. Thus, adjustments in maternal behaviour after the birth of new infants may be relatively small, contrasting with patterns reported in (at least some) human societies, where mothers care for multiple dependent offspring at the same time. Overall, studies across species and populations may reveal how flexible maternal strategies are, and the associated range of juveniles' behavioural reactions to TTS, widening our understanding of family ecology.

Although juvenile baboons with and without a younger sibling received as much care from their mother, juveniles with a younger sibling approached, left and initiated

grooming with their mother more often than those without. These results may first reflect their attraction to the newborn, which is commonly observed across primate species, where non-mother individuals, mainly females, frequently touch or handle newborns (Dunayer & Berman, 2018; Hrdy, 1976; Meredith, 2015). Non-mother females often access the infant by initiating grooming with the mother, resulting in new mothers receiving increased levels of grooming and attention (Caselli et al., 2021; Frank & Silk, 2009; Henzi & Barrett, 2002; Jiang et al., 2019). However, if the increase in juveniles' initiation of interactions with their mother was exclusively triggered by infant attraction, we would expect juvenile females to initiate more interactions with their mother than males following the birth of a younger sibling, which was not supported by our results. Moreover, when approaching their mother, juveniles immediately interacted with their younger sibling in only 13% of cases, while they interacted with their mother in 35% of cases (see Appendix 1). Overall, these results suggest that infant handling was not the primary motivation for juveniles to approach their mother.

Second, such behavioural changes driven by juveniles may reflect changes in mother-offspring relationship following TTS, which may contribute to accelerate a juvenile's developmental trajectory. They may develop greater independence and autonomy following their sibling's birth, thus increasing their own responsibility in maintaining the mother-offspring spatial and grooming relationships. TTS may also translate into a rescheduling of mother-juvenile interactions, where juveniles would be conditioned to request maternal care only in convenient times so that it does not interfere with infant care (in a similar manner to the rescheduling during the weaning period proposed by (Altmann, 1980; Bateson, 1994)). Finally, juveniles may solicit their mother more frequently to seek maternal attention and obtain the same 'pre-sibling arrival' level of care, if the birth of a younger sibling leads to lower maternal responsiveness and greater mother-offspring conflict over maternal care. Although most studies on primates have focused on mother-offspring conflicts during weaning or when mothers resume cycling (Maestripieri, 2002), which often manifest through highly conspicuous tantrums (Barrett & Henzi, 2000), conflicts can arise at other developmental stages (Bateson, 1994) and over any type of maternal investment that can be monopolised. As infants grow older and stop throwing tantrums (as was the case of our study baboons), mother-offspring conflict could be expressed through more subtle behaviours, such as who

takes the responsibility in maintaining spatial proximity, or other signs of anxiety, such as self-directed behaviours (Maestripieri, 2002).

This increased mother-offspring conflict likely translates into sibling rivalry, which could be mediated, at a proximate level, by jealousy, and may explain the increase in juveniles' initiation of association and grooming with the mother. Jealousy is a complex emotional state that arises in a social triangle that consists of the jealous individual (here, the older sibling), a beloved (here, the mother), and a rival (here, the younger infant), and is elicited when the jealous individual perceives the relationship between their beloved and a rival as a threat to their own bond with the beloved one (Volling et al., 2010, 2014). Children undergoing TTS display two main types of jealous reactions when their mother interacts with their sibling: negative/distress behaviours (protesting, disrupting the interactions, directing aggression at the mother), and social approach behaviours (e.g. watching, maintaining proximity and seeking comfort) (Volling et al., 2014). The latter category—social approach— could match the behavioural patterns observed in this study. In humans, sibling jealousy is generally considered as a form of competition for parental attention (Volling et al., 2010), a behaviour that is generally not recognized as a form of parental care *per se* in other species but could be adaptive where parental attention improves offspring survival by preventing risks such as accidents or predation, or by promoting information transmission. In non-human primates, maternal attention could be a form of maternal care that siblings could compete over, but this would require testing whether juveniles who attract more maternal attention experience fitness benefits, such as a greater probability to secure maternal support during conflicts, protection against predators, etc.

Finally, further dimensions of TTS should be investigated to foster its description in monotocous species. In modern societies, children's adjustment to TTS is highly variable and is associated with several traits such as children's sex, age, personality or their attachment style (Dunn et al., 1981; Volling, 2012, 2017; Volling et al., 2014). Insecurely attached or younger children typically show more negative reactions to the birth of a younger sibling (Dunn et al., 1981; Volling, 2017). Maternal traits, such as maternal style, could also influence how juvenile primates cope with TTS (Fairbanks, 1996; Maestripieri, 2018). Moreover, throughout this transition, mother and offspring are generally part of a larger social system not restricted to their dyad. In humans, which are often described as communal or cooperative

breeders (Mace & Sear, 2005), the presence of other kin such as the father, grandmother and older siblings can also influence how children cope with this transition by developing strong bonds with others to compensate for the weakening of the maternal bond (Gottlieb & Mendelson, 1990; Legg et al., 1974; Stewart et al., 1987; Volling et al., 2014). This could also be the case in baboons to some extent, as juvenile primates primarily associate with their siblings, and can keep benefitting from their father's presence as long as they co-reside (Charpentier et al., 2008; Lynch et al., 2020).

Our study is among the first to investigate behavioural changes in mother-juvenile relationships following the birth of a new sibling in wild nonhuman primates. In chacma baboons, the birth of a newborn does not translate into decreased maternal affiliation or association towards the older sibling but it does push juveniles to increase solicitations towards their mother and seems to generate anxiety, which overall suggests that juveniles have to make more effort to maintain the same level of attention and care from their mother. From an ultimate perspective, these results raise the important question of the adaptive significance of maternal attention that siblings seem to compete over. From a proximate perspective, the juveniles' behavioural changes reported here may resemble the jealous reactions commonly observed in young humans during TTS, and may thus offer a relevant context to study emotional development in young primates. Finally, our results, which are distinct from findings in captive primates, show both similarities and differences to human patterns. As such, they emphasize the need to investigate broader aspects of this intriguing developmental milestone in the wild, and across populations and species showing a diversity of life histories and ecologies.

DATA AVAILABILITY

Data sets and scripts used in this study are available on the following public repository: https://gitlab.com/AxelleDelaunay/transition-to-siblinghood-in-a-wild-chacma-baboon-population

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TABLES

Table 1: Determinants of the occurrence of grooming between the mother and the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	*P-value*
				2.5 %	97.5 %		
Model 1: Probability to groom the mother	Intercept		-2.524	-3.063	-1.985	-	-
	Presence of a younger sibling (No)	Yes	**0.539**	**0.023**	**1.054**	**4.107**	**0.043**
	Juvenile's age		**0.397**	**0.117**	**0.678**	**9.026**	**0.003**
	Juvenile's sex (Female)	Male	**-1.476**	**-2.106**	**-0.846**	**20.622**	**<0.001**
	Juvenile's birth rank (Later-born)	First-born	0.184	-0.534	0.901	0.246	0.620
	Mother's rank		0.060	-0.222	0.342	0.171	0.679
	Troop (J)	L	0.133	-0.491	0.758	3.294	0.193
		M	-0.889	-2.035	0.257		
	Focal observation duration		0.065	-0.137	0.266	0.394	0.530
Full –Null model comparison: $X^2_2 = 46.605$, $P < 0.001$ (AIC full = 711.11, AIC null = 741.71)							
Model 2: Probability to be groomed by the mother	Intercept		-1.632	-1.993	-1.270	-	-
	Presence of a younger sibling (No)	Yes	-0.114	-0.495	0.268	0.350	0.554
	Juvenile's age		-0.179	-0.371	0.013	3.693	0.055
	Juvenile's sex (Female)	Male	-0.234	-0.601	0.133	1.828	0.176
	Juvenile's birth rank (Later-born)	First-born	-0.189	-0.679	0.301	0.603	0.437
	Mother's rank		-0.017	-0.199	0.166	0.042	0.838

	Troop (J)	L	0.099	-0.306	0.504	5.373	0.068
		M	-0.638	-1.291	0.016		
	Focal observation duration		0.141	-0.009	0.292	3.515	0.061
Full-Null model comparison: $X^2_2 = 17.211$, $P = 0.028$ (AIC full = 1252.8, AIC null = 1254.0)							

Table 1: Results of the mixed models analyzing the probability for a juvenile to groom (model 1) or to receive (model 2) a grooming from its mother during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table 2: Determinants of the grooming time exchanged between the mother and the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model 3: Time spent grooming the mother	Intercept		-4.460	-5.147	-3.773	-	-
	Presence of a younger sibling (No)	Yes	**0.519**	**0.032**	**1.007**	**4.284**	**0.038**
	Juvenile's age		**0.394**	**0.128**	**0.660**	**9.957**	**0.002**
	Juvenile's sex (Female)	Male	**-1.454**	**-2.068**	**-0.840**	**21.161**	**<0.001**
	Juvenile's birth rank (Later-born)	First-born	0.147	-0.540	0.834	0.172	0.678
	Mother's rank		0.061	-0.212	0.334	0.187	0.665
	Troop (J)	L	0.152	-0.448	0.752	3.544	0.170
		M	-0.879	-2.002	0.244		
Full-Null model comparison: $X^2_2 = 48.106$, $P < 0.001$ (AIC full = 2135.7, AIC null = 2169.8)							
Model 4: Time spent being groomed by the mother	Intercept		-3.357	-3.793	-2.922	-	-
	Presence of a younger sibling (No)	Yes	-0.126	-0.459	0.207	0.552	0.458
	Juvenile's age		-0.167	-0.338	0.003	3.650	0.056

	Juvenile's sex (Female)	Male	-0.229	-0.546	0.087	1.902	0.168
	Juvenile's birth rank (Later-born)	First-born	-0.171	-0.589	0.247	0.667	0.414
	Mother's rank		-0.015	-0.171	0.142	0.033	0.855
	Troop (J)	L	**0.142**	**-0.209**	**0.493**	**6.098**	**0.047**
		M	**-0.615**	**-1.206**	**-0.024**		
Full-Null model comparison: $X^2_2 = 14.867$, P = 0.038 (AIC full = 4368.7, AIC null = 4369.6)							

Table 1 : Results of the mixed models analyzing the grooming time (in seconds) given to the mother (Model 3) or received from the mother (Model 4) by the juvenile during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table 3: Determinants of the spatial proximity between the mother and the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model 5: Probability to be within 1m from the mother	Intercept		-1.913	-2.238	-1.588	-	-
	Presence of a younger sibling (No)	Yes	-0.080	-0.427	0.266	0.405	0.524
	Juvenile's age		**-0.208**	**-0.383**	**-0.033**	**5.480**	**0.019**
	Juvenile's sex (Female)	Male	**-0.629**	**-0.970**	**-0.288**	**13.242**	**<0.001**
	Juvenile's birth rank (Later-born)	First-born	-0.240	-0.693	0.213	1.161	0.281
	Mother's rank		0.103	-0.064	0.271	1.810	0.179
	Troop (J)	L	-0.015	-0.397	0.367	2.623	0.269
		M	-0.412	-0.978	0.154		
Full-Null model comparison: $X^2_2 = 27.008$, $P < 0.001$ (AIC full = 1607.7, AIC null =1620.7)							
Model 6: Probability to be within 5m from the mother	Intercept		-1.695	-1.967	-1.423	-	-
	Presence of a younger sibling (No)	Yes	0.115	-0.175	0.405	0.632	0.427
	Juvenile's age		**-0.223**	**-0.365**	**-0.081**	**10.120**	**0.001**

	Juvenile's sex (Female)	Male	**-0.331**	**-0.598**	**-0.064**	**5.432**	**0.020**
	Juvenile's birth rank (Later-born)	First-born	0.036	-0.320	0.392	0.040	0.842
	Mother's rank		**0.189**	**0.055**	**0.323**	**6.408**	**0.011**
	Troop (J)	L	0.034	-0.283	0.352	5.178	0.075
		M	0.443	0.074	0.812		
Full-Null model comparison: $X^2_2 = 25.398$, $P < 0.001$ (AIC full = 2195.2, AIC null =2206.6)							

Table 2 : Results of the mixed models analyzing the probability for a juvenile to be within 1 meter (model 5) or within 5 meters (model 6) from its mother during a scan observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 2562 and 2532 scan observations respectively, on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table 4: Determinants of proximity maintenance by the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model 7: Probability to approach the mother	Intercept		-1.572	-1.906	-1.237	-	-
	Presence of a younger sibling (No)	Yes	**0.552**	**0.225**	**0.879**	**10.628**	**0.001**
	Juvenile's age		**-0.207**	**-0.374**	**-0.039**	**5.864**	**0.015**
	Juvenile's sex (Female)	Male	-0.160	-0.479	0.159	0.973	0.324
	Juvenile's birth rank (Later-born)	First-born	-0.099	-0.540	0.342	0.197	0.657
	Mother's rank		**0.175**	**0.019**	**0.330**	**4.430**	**0.035**
	Troop (J)	L	**-0.123**	**-0.502**	**0.257**	**7.373**	**0,025**
		M	**0.571**	**0.113**	**1.029**		
	Focal observation duration		**0.139**	**0.003**	**0.275**	**4.148**	**0.042**
Full-Null model comparison: $X^2_2 = 26.202$, $P < 0.001$ (AIC full = 1505.2, AIC null = 1515.4)							
Model 8: Probability to leave the mother	Intercept		-1.726	-2.087	-1.365	-	-
	Presence of a younger sibling (No)	Yes	**0.538**	**0.186**	**0.891**	**9.402**	**0.002**

	Juvenile's age		**-0.185**	**-0.366**	**-0.003**	**4.534**	**0.033**
	Juvenile's sex (Female)	Male	**-0.421**	**-0.770**	**-0.072**	**6.168**	**0.013**
	Juvenile's birth rank (Later-born)	First-born	-0.089	-0.565	0.388	0.099	0.753
	Mother's rank		**0.194**	**0.024**	**0.364**	**5.493**	**0.019**
	Troop (J)	L	**-0.119**	**-0.521**	**0.284**	**9.065**	**0.011**
		M	**0.665**	**0.173**	**1.157**		
	Focal Observation duration		0.069	-0.075	0.213	0.916	0.338
Full-Null model comparison: $X^2_2 = 25.193$, P = 0.001 (AIC full = 1340.8, AIC null = 1350.0)							

Table 3 : Results of the mixed models analyzing the probability for a juvenile to approach (model 7) or to leave (model 8) its mother within 1 meter during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table 5: Determinants of proximity maintenance by the mother

Response variable	Fixed factors	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model 9: Probability to be approached by the mother	Intercept		-3.177	-3.758	-2.596	-	-
	Presence of a younger sibling (No)	Yes	-0.512	-1.201	0.177	-	-
	Juvenile's age		0.050	-0.211	0.311	0.100	0.752
	Juvenile's sex (Female)	Male	-0.557	-1.189	0.075	-	-
	Juvenile's birth rank (Later-born)	First-born	0.233	-0.448	0.914	0.484	0.486
	Mother's rank		**0.556**	**0.286**	**0.827**	**18.123**	**<0.001**
	Troop (J)	L	**0.792**	**0.203**	**1.382**	**17.726**	**<0.001**
		M	**1.430**	**0.743**	**2.117**		
	Focal observation duration		0.156	-0.062	0.373	1.943	0.163
	Presence of a younger sibling (No)*Juvenile's sex (Female)	Yes, Male	**1.138**	**0.156**	**2.119**	**6.070**	**0.014**
Full-Null model comparison: $X^2_2 = 30.352$, $P < 0.001$ (AIC full = 712.29, AIC null = 724.65)							
	Intercept		-1.919	-2.295	-1.544	-	-

Model 10: Probability to be left by the mother	Presence of a younger sibling (No)	Yes	0.254	-0.121	0.629	1.751	0.186
	Juvenile's age		-0.134	-0.325	0.056	1.943	0.163
	Juvenile's sex (Female)	Male	-0.273	-0.638	0.093	2.034	0.154
	Juvenile's birth rank (Later-born)	First-born	-0.370	-0.893	0.153	2.066	0.151
	Mother's rank		0.011	-0.169	0.190	0.014	0.907
	Troop (J)	L	0.171	-0.260	0.602	1.531	0.465
		M	0.339	-0.203	0.882		
	Focal observation duration		**0.188**	**0.028**	**0.347**	**5.557**	**0.018**
Full-Null model comparison: $X^2_2 = 13.902$, P = 0.084 (AIC full = 1197.5, AIC null = 1195.4)							

Table 4 : Results of the mixed models analyzing the probability for a juvenile to be approached (model 9) or left (model 10) within 1 meter by its mother during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values *for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.*

Table 6: Determinants of the juvenile's anxiety

Fixed factor	Levels	Estimate	CI		LRT	P-value
			2.5 %	97.5 %		
Intercept		-5.814	-5.966	-5.661	-	-
Presence of a younger sibling (No)	Yes	0.040	-0.102	0.183	-	-
Juvenile's age		-0.110	-0.197	-0.023	-	-
Juvenile's sex (Female)	Male	0.050	-0.082	0.182	0.536	0.464
Juvenile's birth rank (Later-born)	First-born	-0.105	-0.286	0.075	1.266	0.260
Mother's rank		-0.065	-0.132	0.001	3.498	0.061
Troop (J)	L	**0.008**	**-0.138**	**0.154**	**10.806**	**0.005**
	M	**-0.358**	**-0.565**	**-0.150**		
Year (2017)	2018	**-0.317**	**-0.518**	**-0.115**	**14.086**	**0.001**
	2019	**0.085**	**-0.059**	**0.228**		
Presence of a younger sibling (No)*juvenile's age	Yes	**0.166**	**0.036**	**0.296**	**5.873**	**0.015**

Full-Null model comparison: $X^2_2 = 26.07$, P = 0.004 (AIC full = 7158.1, AIC null = 7164.1)

Table 5 : Results of the mixed models analyzing the frequency of self-scratches during a focal observation (model 11). Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1523 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values *for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.*

FIGURES

*Figure 1: Influence of the birth of the younger sibling on mother-juvenile grooming interactions. In all panels, "Sibling status" refers to whether juveniles have recently experienced the birth of a younger sibling ("With"), or not ("Without"). (a) Predicted probability that a juvenile grooms its mother during a focal observation depending on its "sibling status". (b) Predicted probability that a juvenile is being groomed by its mother depending on its "sibling status". (c) Predicted grooming time (in seconds) given by a juvenile to its mother during a focal observation depending on its "sibling status". (d) Predicted grooming time (in seconds) received by a juvenile from its mother during a focal observation depending on its "sibling status". The violin plots show the distribution of the fitted values and the boxplots show the median of the distribution of the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively) and the whiskers include a maximum of 1.5 times the interquartile range. The effect of the predictor "Presence of a younger sibling" and the associated p-values are shown. "ns": not significant (P>0.05); * : P<0.05; ** : P <0.01; *** : P <0.001*

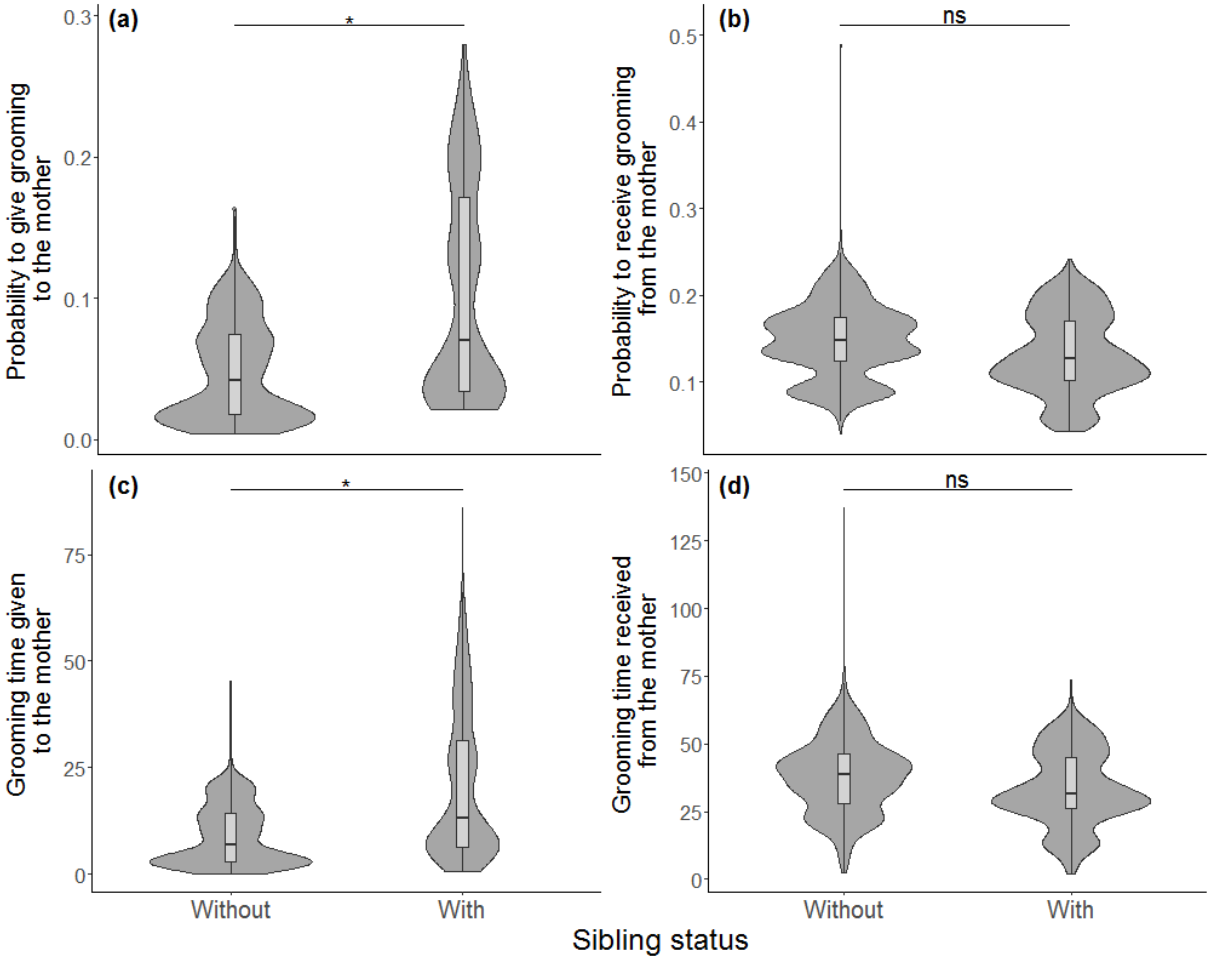

*Figure 2: Influence of the birth of the younger sibling on mother-juvenile spatial association (within 1m). In all panels, "Sibling status" refers to whether juveniles have recently experienced the birth of a younger sibling ("With"), or not ("Without"). The four panels show the effect of sibling status on (a) the predicted probability that a juvenile approaches its mother during a focal observation; (b) the predicted probability that a juvenile leaves its mother; (c) the predicted probability that a juvenile is approached by its mother in interaction with juvenile's sex; and (d) the predicted probability that a juvenile is left by its mother. The violin plots show the distribution of the fitted probabilities. The boxplots show the median of the distribution of the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively) and the whiskers include a maximum of 1.5 times the interquartile range. The effect of the predictor "Presence of a younger sibling" and the associated p-values are shown. "ns": not significant (P>0.05); * : P <0.05; ** : P <0.01; *** : P <0.001. Note that panel C shows the predicted values of the model including a significant interaction between sibling status and juvenile's sex (model 8), but post-hoc pairwise mean comparisons were not significant*

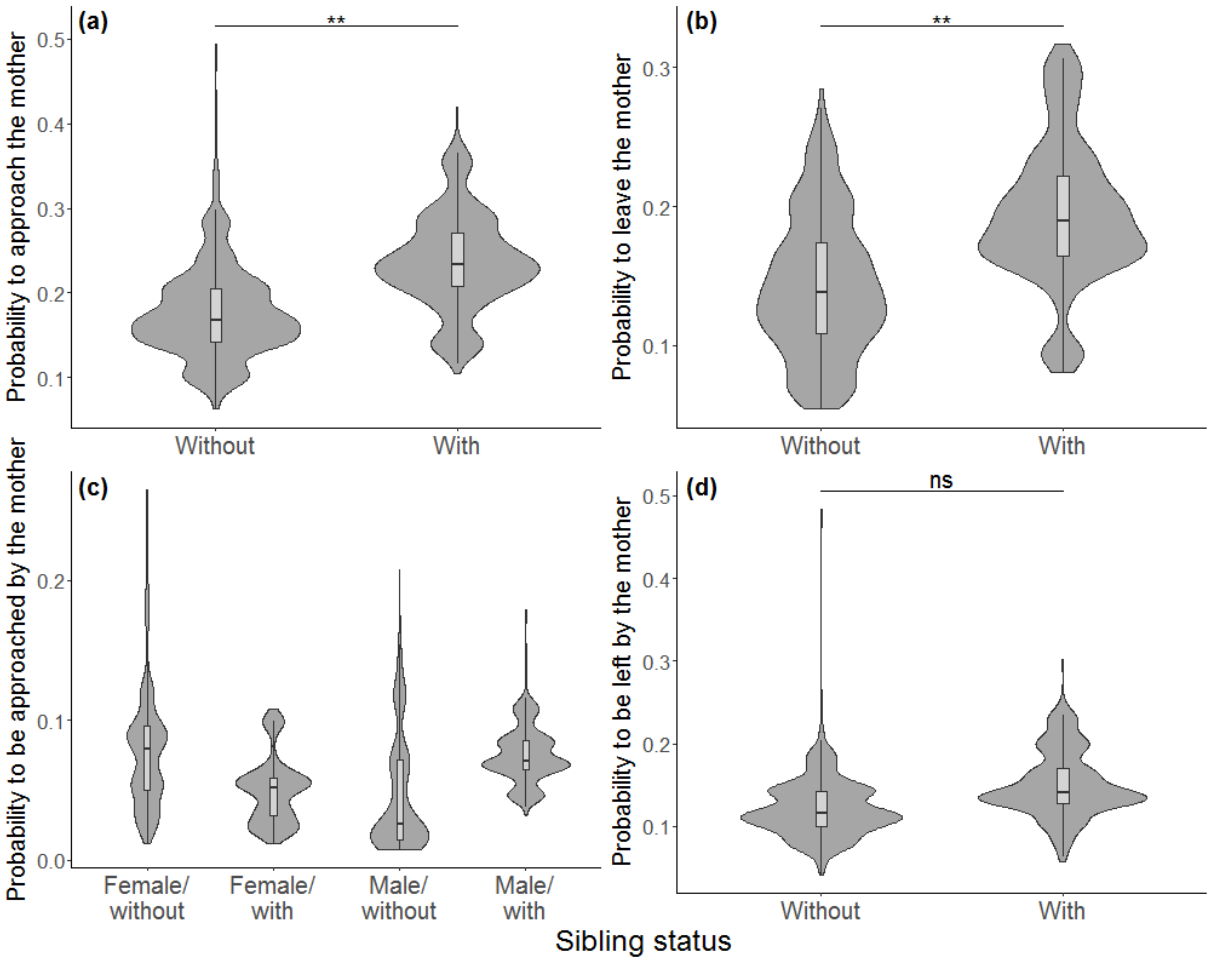

Figure 2: Variation in the frequency of self-scratches according to juvenile's age and the birth of a younger sibling. "With" refers to juveniles who recently experienced the birth of a younger sibling, "Without" refers to juveniles who did not experience the birth of a younger sibling yet. Dots represent the model's adjusted predicted values and the curves show the linear predicted fit from the corresponding mixed model. Predicted values were computed using the function "ggeffect" from the ggeffect package, averaging the values of all the other variables in the model. The darker area around each curve represents the confidence interval of the fitted curve

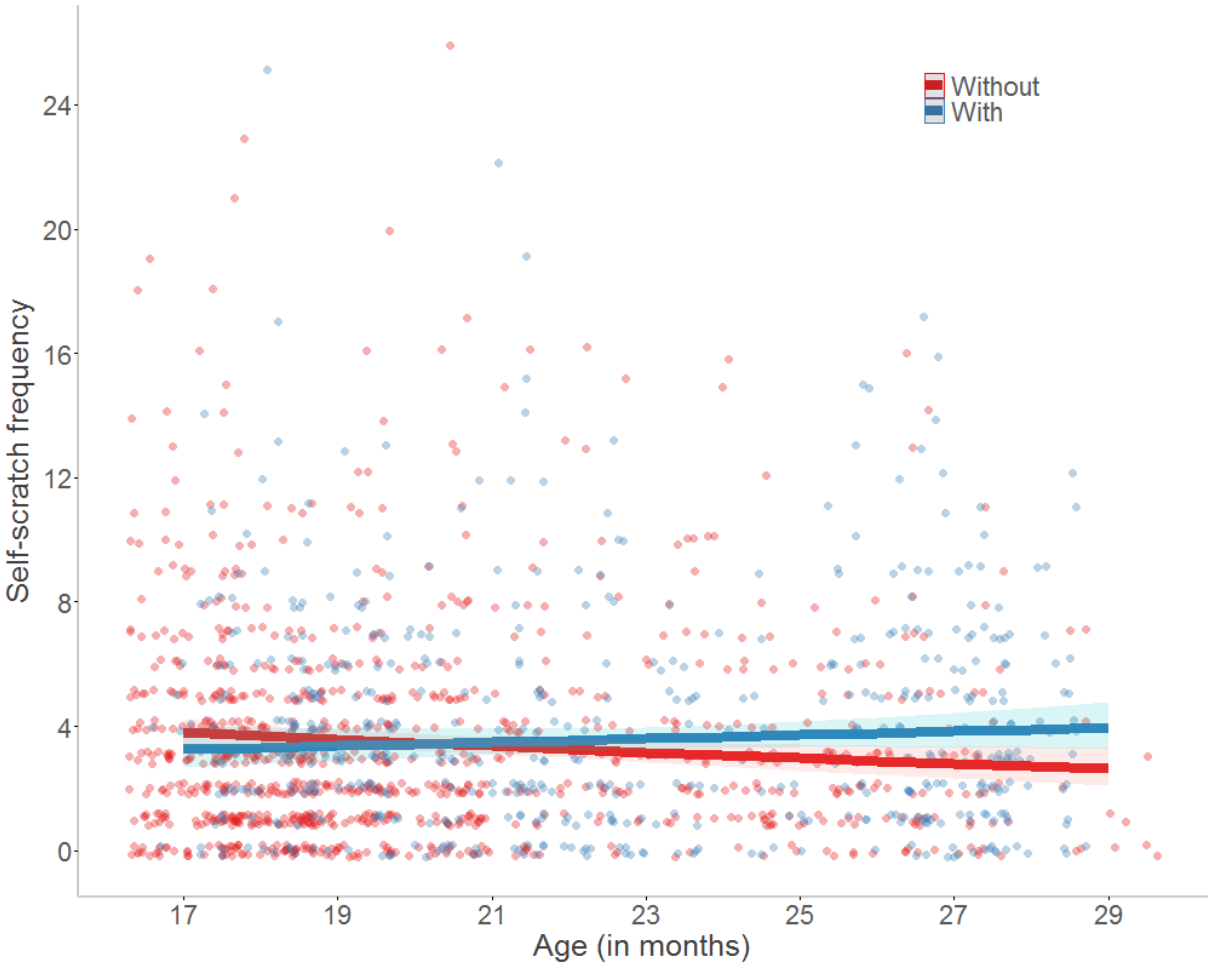

Table A1: Summary of all models included in the study

Model Number	Response variable	Model type	Sample size (number of observations/number of juveniles)	Fixed effects	Random effects	Offset
1	Probability to groom the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
2	Probability to be groomed by the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
3	Total time grooming the mother	Negative binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	Focal duration
4	Total time being groomed by the mother	Negative binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	Focal duration

5	Probability to be within 1m from the mother	Binomial GLMM	2562/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
6	Probability to be within 5m from the mother	Binomial GLMM	2532/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	NA
7	Probability to approach the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
8	Probability to leave the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
9	Probability to be approached by the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal	Juvenile identity	NA

				duration, presence of a younger sibling*juvenile's sex		
10	Probability to be left by the mother	Binomial GLMM	1525/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop, focal duration	Juvenile identity	NA
11	Frequency of self-scratch	Negative binomial GLMM	1523/38	Presence of a younger sibling, juvenile's age, sex and birth rank, maternal rank, troop	Juvenile identity	Focal duration

Table A2: Determinants of the occurrence of grooming between the mother and the juvenile

Response variable	**Fixed factor**	**Levels**	**Estimate**	**CI**		**LRT**	***P-value***
				2.5 %	**97.5 %**		
Model S1: Probability to groom the mother	Intercept		-2.522	-3.071	-1.973	-	-
	Presence of a younger sibling (No)	Yes	0.542	0.001	1.082	3.829	0.050
	Juvenile's age		**0.395**	**0.077**	**0.712**	**6.344**	**0.012**
	Juvenile's sex (Female)	Male	**-1.477**	**-2.109**	**-0.845**	**20.623**	**<0.001**
	Juvenile's birth rank (Later-born)	First-born	0.175	-0.690	1.039	0.153	0.695
	Mother's rank		0.060	-0.222	0.343	0.172	0.678
	Number of immature older siblings		-0.006	-0.357	0.344	0.001	0.971
	Troop (J)	L	0.132	-0.495	0.759	3.228	0.199
		M	-0.893	-2.059	0.273		
	Focal observation duration		0.065	-0.137	0.266	0.391	0.532
Full-Null model comparison: $X^2_2 = 46.607$, $P < 0.001$ (AIC full = 713.11, AIC null = 741.11) Model 1-Model S1 comparison: $X^2_2 = 0.0013$, $P = 0.971$ (AIC Model 1 = 711.11, AIC Model S1 = 713.11)							
Model S2: Probability to be groomed by the mother	Intercept		-1.648	-2.018	-1.277	-	-
	Presence of a younger sibling (No)	Yes	-0.137	-0.537	0.263	0.476	0.490
	Juvenile's age		-0.154	-0.387	0.079	1.854	0.173
	Juvenile's sex (Female)	Male	-0.229	-0.596	0.137	1.770	0.183
	Juvenile's birth rank (Later-born)	First-born	-0.118	-0.734	0.498	0.125	0.723
	Mother's rank		-0.021	-0.205	0.162	0.066	0.798

	Number of immature older siblings		0.048	-0.209	0.305	0.168	0.682
	Troop (J)	L	0.107	-0.299	0.512	4.428	0.109
		M	-0.596	-1.285	0.093		
	Focal observation duration		0.142	-0.009	0.292	3.545	0.060
Full-Null model comparison: $X^2_2 = 17.379$, $P < 0.043$ (AIC full = 1254.6, AIC null = 1254.0) Model 2-Model S2 comparison: $X^2_2 = 0.168$, $P = 0.682$ (AIC Model 2 = 1252.8, AIC Model S1 = 1254.6)							

Table A2: Results of the mixed models analyzing the probability for a juvenile to groom (model 1) or to receive (model 2) a grooming from its mother during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table A3: Determinants of the grooming time exchanged between the mother and the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model S3: Time spent grooming the mother	Intercept		-4.459	-5.153	-3.765	-	-
	Presence of a younger sibling (No)	Yes	**0.521**	**0.009**	**1.032**	**3.978**	**0.046**
	Juvenile's age		**0.393**	**0.094**	**0.691**	**7.097**	**0.008**
	Juvenile's sex (Female)	Male	**-1.455**	**-2.071**	**-0.838**	**21.161**	**<0.001**
	Juvenile's birth rank (Later-born)	First-born	0.143	-0.683	0.969	0.112	0.738
	Mother's rank		0.061	-0.213	0.335	0.188	0.665
	Number of immature older siblings		-0.003	-0.335	0.329	0.000	0.985
	Troop (J)	L	0.152	-0.451	0.754	3.466	0.177
		M	-0.881	-2.024	0.262		
Full-Null model comparison: $X^2_2 = 48.106$, $P < 0.001$ (AIC full = 2137.7, AIC null = 2169.8) Model 3-Model S3 comparison: $X^2_2 = 0.0003$, $P = 0.986$ (AIC Model 3 = 2135.7, AIC Model S3 = 2137.7)							
Model S4: Time spent being groomed by the mother	Intercept		-3.375	-3.814	-2.936	-	-
	Presence of a younger sibling (No)	Yes	-0.153	-0.500	0.194	0.749	0.387
	Juvenile's age		-0.137	-0.342	0.067	1.730	0.188
	Juvenile's sex (Female)	Male	-0.226	-0.540	0.088	1.869	0.172
	Juvenile's birth rank (Later-born)	First-born	-0.084	-0.613	0.445	0.098	0.754
	Mother's rank		-0.020	-0.176	0.137	0.063	0.803
	Number of immature older siblings		0.058	-0.164	0.280	0.262	0.609

	Troop (J)	L	0.151	-0.197	0.499	5.062	0.080
		M	-0.566	-1.181	0.048		
Full-Null model comparison: $X^2_2 = 15.129$, P = 0.057 (AIC full = 4370.4, AIC null = 4369.6) Model 4-Model S4 comparison: $X^2_2 = 0.262$, P = 0.609 (AIC Model 4 = 4368.7, AIC Model S4 = 4370.4)							

Table A3: Results of the mixed models analyzing the grooming time (in seconds) given to the mother (Model 3) or received from the mother (Model 4) by the juvenile during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as a random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table A4: Determinants of the spatial proximity between the mother and the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model S5: Probability to be within 1m from the mother	Intercept		-1.896	-2.227	-1.566	-	-
	Presence of a younger sibling (No)	Yes	-0.049	-0.417	0.319	0.182	0.670
	Juvenile's age		**-0.240**	**-0.453**	**-0.027**	**4.948**	**0.026**
	Juvenile's sex (Female)	Male	**-0.636**	**-0.979**	**-0.292**	**13.418**	**<0.001**
	Juvenile's birth rank (Later-born)	First-born	-0.325	-0.879	0.230	1.368	0.242
	Mother's rank		0.106	-0.062	0.274	1.854	0.173
	Number of older immature siblings		-0.061	-0.288	0.166	0.251	0.617
	Troop (J)	L	-0.021	-0.407	0.364	2.875	0.237
		M	-0.461	-1.057	0.134		
Full-Null model comparison: $X^2_2 = 27.259$, $P < 0.001$ (AIC full = 1609.4, AIC null = 1620.7) Model 5-Model S5 comparison: $X^2_2 = 0.251$, $P = 0.617$ (AIC Model 5 = 1607.7, AIC Model S5 = 1609.4)							
Model S6: Probability to be within 5m from the mother	Intercept		-1.682	-1.961	-1.403	-	-
	Presence of a younger sibling (No)	Yes	0.155	-0.164	0.474	0.968	0.325
	Juvenile's age		**-0.256**	**-0.432**	**-0.080**	**9.135**	**0.003**
	Juvenile's sex (Female)	Male	**-0.338**	**-0.610**	**-0.065**	**5.508**	**0.019**
	Juvenile's birth rank (Later-born)	First-born	-0.046	-0.485	0.394	0.042	0.838
	Mother's rank		**0.190**	**0.054**	**0.326**	**6.387**	**0.011**
	Number of immature older siblings		-0.064	-0.256	0.128	0.439	0.508

	Troop (J)	L	0.024	-0.303	0.351	3.255	0.196
		M	0.388	-0.023	0.800		
Full-Null model comparison: $X^2_2 = 25.837$, P = 0.001 (AIC full = 2196.7, AIC null = 2206.6) Model 5-Model S5 comparison: $X^2_2 = 0.439$, P = 0.508 (AIC Model 6 = 2195.2, AIC Model S6 = 2196.7)							

Table A4: Results of the mixed models analyzing the probability for a juvenile to be within 1 meter (model 5) or within 5 meters (model 6) from its mother during a scan observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 2562 and 2532 scan observations respectively, on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table A5: Determinants of proximity maintenance by the juvenile

Response variable	Fixed factor	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model S7: Probability to approach the mother	Intercept		-1.606	-1.943	-1.270	-	-
	Presence of a younger sibling (No)	Yes	**0.503**	**0.163**	**0.844**	**8.293**	**0.004**
	Juvenile's age		-0.161	-0.356	0.034	2.655	0.103
	Juvenile's sex (Female)	Male	-0.149	-0.463	0.165	0.874	0.350
	Juvenile's birth rank (Later-born)	First-born	0.036	-0.490	0.562	0.018	0.894
	Mother's rank		**0.170**	**0.016**	**0.323**	**4.257**	**0.039**
	Number of immature older siblings		0.096	-0.123	0.315	0.734	0.392
	Troop (J)	L	**-0.104**	**-0.477**	**0.270**	**8.063**	**0,018**
		M	**0.662**	**0.168**	**1.157**		
	Focal observation duration		**0.141**	**0.005**	**0.277**	**4.275**	**0.039**
Full-Null model comparison: $X^2_2 = 26.936$, P = 0.001 (AIC full = 1506.5, AIC null = 1515.4) Model 7-Model S7 comparison: $X^2_2 = 0.0003$, P = 0.734 (AIC Model 7 = 1505.2, AIC Model S7 = 1506.5)							
Model S8: Probability to leave the mother	Intercept		-1.778	-2.144	-1.413	-	-
	Presence of a younger sibling (No)	Yes	**0.468**	**0.101**	**0.835**	**6.758**	**0.009**
	Juvenile's age		-0.116	-0.327	0.096	1.426	0.232
	Juvenile's sex (Female)	Male	**-0.407**	**-0.752**	**-0.062**	**5.915**	**0.015**
	Juvenile's birth rank (Later-born)	First-born	0.120	-0.452	0.692	0.223	0.637
	Mother's rank		**0.187**	**0.019**	**0.356**	**5.244**	**0.022**

	Number of immature older siblings		0.152	-0.088	0.393	1.691	0.194
	Troop (J)	L	**-0.100**	**-0.497**	**0.296**	**10.745**	**0.005**
		M	**0.803**	**0.269**	**1.338**		
	Focal Observation duration		0.073	-0.071	0.217	1.039	0.308
Full-Null model comparison: $X^2_2 = 26.884$, P = 0.002 (AIC full = 1341.1, AIC null = 1350.0) Model 8-Model S8 comparison: $X^2_2 = 1.691$, P = 0.196 (AIC Model 8 = 1340.8, AIC Model S8 = 1341.1)							

Table A5: Results of the mixed models analyzing the probability for a juvenile to approach (model 7) or to leave (model 8) its mother within 1 meter during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.

Table A6: Determinants of proximity maintenance by the mother

Response variable	Fixed factors	Levels	Estimate	CI		LRT	P-value
				2.5 %	97.5 %		
Model S9: Probability to be approached by the mother	Intercept		-3.163	-3.749	-2.577	-	-
	Presence of a younger sibling (No)	Yes	-0.498	-1.191	0.195	-	-
	Juvenile's age		0.017	-0.292	0.325	0.006	0.941
	Juvenile's sex (Female)	Male	-0.585	-1.234	0.064	-	-
	Juvenile's birth rank (Later-born)	First-born	0.145	-0.659	0.949	0.155	0.694
	Mother's rank		**0.565**	**0.290**	**0.840**	**18.241**	**<0.001**
	Number of immature older siblings		-0.075	-0.438	0.289	0.141	0.707
	Troop (J)	L	**0.807**	**0.210**	**1.404**	**15.725**	**<0.001**
		M	**1.378**	**0.645**	**2.111**		
	Focal observation duration		0.154	-0.064	0.372	1.893	0.169
	Presence of a younger sibling (No)*Juvenile's sex (Female)	Yes, Male	**1.190**	**0.171**	**2.210**	**6.184**	**0.013**
Full-Null model comparison: $X^2_2 = 30.493$, $P < 0.001$ (AIC full = 714.15, AIC null = 724.65) Model 9-Model S9 comparison: $X^2_2 = 0.141$, $P = 0.707$ (AIC Model 9 = 712.29, AIC Model S9 = 714.15)							
Model S10: Probability to be left by the mother	Intercept		-1.977	-2.355	-1.599	-	-
	Presence of a younger sibling (No)	Yes	0.175	-0.213	0.563	0.779	0.377
	Juvenile's age		-0.055	-0.281	0.172	0.225	0.636
	Juvenile's sex (Female)	Male	-0.253	-0.612	0.107	1.788	0.181

	Juvenile's birth rank (Later-born)	First-born	-0.147	-0.763	0.470	0.222	0.638
	Mother's rank		0.000	-0.178	0.178	0.000	0.998
	Number of immature older siblings		0.157	-0.096	0.411	1.482	0.223
	Troop (J)	L	0.204	-0.214	0.623	2.578	0.276
		M	0.481	-0.095	1.057		
	Focal observation duration		**0.190**	**0.031**	**0.349**	**5.726**	**0.017**
Full-Null model comparison: $X^2_2 = 15.384$, P = 0.081 (AIC full = 1198.0, AIC null = 1195.4) Model 10-Model S10 comparison: $X^2_2 = 1.482$, P = 0.223 (AIC Model 10 = 1197.5, AIC Model S10 = 1198.0)							

Table A6: Results of the mixed models analyzing the probability for a juvenile to be approached (model 9) or left (model 10) within 1 meter by its mother during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1525 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values *for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.*

Table A7: Determinants of the juvenile's anxiety

Fixed factor	Levels	Estimate	CI		LRT	P-value
			2.5 %	97.5 %		
Intercept		-5.813	-5.971	-5.656	-	-
Presence of a younger sibling (No)	Yes	0.041	-0.113	0.194	-	-
Juvenile's age		-0.110	-0.209	-0.012	-	-
Juvenile's sex (Female)	Male	0.050	-0.083	0.182	0.529	0.467
Juvenile's birth rank (Later-born)	First-born	-0.106	-0.325	0.112	0.880	0.348
Mother's rank		-0.065	-0.132	0.001	3.476	0.062
Number of older immature siblings		-0.001	-0.090	0.089	0.000	0.989
Troop (J)	L	**0.008**	**-0.140**	**0.156**	**9.775**	**0.008**
	M	**-0.358**	**-0.578**	**-0.138**		
Year (2017)	2018	**-0.316**	**-0.519**	**-0.114**	**13.809**	**0.001**
	2019	**0.085**	**-0.060**	**0.230**		
Presence of a younger sibling (No)*juvenile's age	Yes	**0.166**	**0.036**	**0.296**	**5.866**	**0.015**
Full-Null model comparison: $X^2_2 = 26.07$, P = 0.006 (AIC full = 7160.1, AIC null = 7164.1)						
Model 11-Model S11 comparison: $X^2_2 = 0.0002$, P = 0.989 (AIC Model 11 = 7158.1, AIC Model S11 = 7160.1)						

Table A7: Results of the mixed models analyzing the frequency of self-scratches during a focal observation (model S11). Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 1523 focal observations on 38 juveniles (N=18 with a younger sibling, N=28 without). Juvenile identity was included as random effect. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values *for the simple predictors are not shown. We provided AIC values to clarify which model performed best in case the full-null model comparison was significant.*

Appendix 1: Test of the newborn attraction hypothesis

To estimate if juveniles were approaching their mother to access the newborn, we used focal data on the 18 juveniles who experienced the birth of a younger sibling within the last three months. Each time the juvenile approached their mother within 1m, we calculated whether the juvenile initiated an interaction with the newborn and/or the mother (yes=1, no=0) within one minute following the approach, or until one of them left if a leave happened less than one minute after the approach. We considered the following interactions: grooming, playing (with the newborn only), affiliative and aggressive interactions. For interactions with the newborn, we considered only the interactions initiated by the juvenile because young baboon infants tend to touch or climb on individuals interacting with their mother. For interactions with the mother, we considered interactions initiated both by the juvenile and its mother. We then calculated the percentage of approach followed by an interaction with the newborn (whether the juvenile interacted with the newborn only or both with the mother and the newborn) or with the mother (the juvenile interacted with the mother only.

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Chapter 3: An unexpected journey: becoming an older sibling in wild mandrills

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(Article in preparation)

ABSTRACT

In monotocous mammals, the birth of a younger sibling has always been considered as a stressful period, although an event that almost every individual will experience in its life. From a theoretical perspective, two types of conflicts over maternal investment could unfold during this period: mother-offspring conflict and sibling rivalry. Yet, this developmental milestone has been rarely studied in primates. Here, we used behavioural data collected from the only natural population of habituated mandrills (*Mandrillus sphinx*) to investigate the changes in maternal care and mother-juvenile relationship throughout the transition to siblinghood, by comparing juveniles who recently experienced the birth of a younger sibling, to juveniles who did not. We found that the birth of a younger sibling was often associated to an abrupt cessation of the weaning process for the juvenile, and to a decrease in maternal affiliation. Juvenile's reactions were sex-specific, as young females groomed their mother more often, while young males ranged further away from their mother after the birth of their sibling. Juveniles' responsibility in maintaining proximity and initiating affiliations with the mother remained unaffected, and they did not show more signs of conflicts or anxiety compared to juveniles without a younger sibling. According to our results, the loss of maternal care faced by juveniles undergoing their transition to siblinghood does not induce signs of overt conflict in the family, but may affect the sexes differently. This study contributes to explain why short interbirth intervals often pose a risk to juvenile survival in monotocous primates; in addition, contrasts across studies highlight the importance of examining the transition to siblinghood in species with various life histories and ecologies.

INTRODUCTION

Sibling competition to access and monopolise parental care (Trivers, 1974) has been extensively studied across taxa (see for reviews: Mock and Parker, 1998; Roulin and Dreiss, 2012). Sibling competition can impact offspring's development, with long-term consequences on their morphology (e.g. insects: Schrader et al., 2018; birds: de Kogel and Prijs, 1996; mammals: Fisher et al., 2018; Hofer and East, 2008), physiology (e.g. birds: Drummond and Rodríguez, 2013; Nettle et al., 2015; Verhulst et al., 2006; mammals: Fey and Trillmich, 2008; Guenther and Trillmich, 2015; Stauffer et al., 2018) and behavior (e.g. birds: Bebbington et al., 2017; Ekman et al., 2002; mammals: Guenther and Trillmich, 2015; Hudson et al., 2011), and can ultimately impact their fitness, for instance in species where siblicide is common (e.g. birds: Braun and Hunt, 1983; Fujioka, 1985; Lougheed and Anderson, 1999; mammals: Andersen et al., 2011; Hofer and East, 2008). Most empirical studies to date have, however, focused on brood- or litter-rearing species (especially in mammals, see for reviews: Drummond, 2006; Hudson and Trillmich, 2008; Roulin and Dreiss, 2012), where same-age siblings compete over the same maternal resources at the same time. Most of the theoretical models and evolutionary hypotheses have thus been developed for intra-brood competition (Hudson and Trillmich, 2008). Inter-brood competition, where siblings are not at the same developmental stage (Roulin and Dreiss, 2012), has been largely neglected so far, which is surprising given that Trivers' original model was developed for species producing singletons (Trivers, 1974).

Monotocous mammals, which produce one offspring at a time, offer unique opportunities to study inter-brood competition without the confounding effect of intra-brood competition (Hudson and Trillmich, 2008). These species generally have long developmental periods, often with a juvenile phase, during which offspring develop strong and enduring bonds with their mother that can extend way beyond infancy (e.g. yellow baboons, *Papio cynocephalus*: Silk et al., 2006b, 2006a; asian elephants, *Elephas maximus*: Lynch et al., 2019; red deer, *Cervus elaphus*: Clutton-Brock et al., 1982). Weaned offspring can also keep benefiting from post-weaning forms of maternal care, such as protection against predators, facilitated access to food or social support (Clutton-Brock, 1991). Several empirical studies have recently suggested that these maternal resources could improve offspring's growth (e.g. chimpanzees, *Pan troglodytes*: Samuni et al., 2020), and future reproductive success and

longevity (chimpanzees: Crockford et al., 2020; Stanton et al., 2020; red deer: Andres et al., 2013). Such forms of maternal care could therefore be the stake of sibling competition as monopolising these resources might be advantageous for offspring.

In line with this, recent empirical studies showed that diluting maternal resources between several, different-age siblings could be costly. In Galapagos fur seals (*Arctocephalus galapagoensis*) and sea lions (*Zalophus wollebaeki*) for instance, mothers can still be nursing their previous offspring by the time they give birth to the next one, and the older sibling may attempt to prevent the newborn from nursing or directly attack it, reducing its survival probability by 50% (Trillmich and Wolf, 2008). Similarly in false vampire bats (*Megaderma lyra*), Leippert and colleagues (2000) reported a case of a newborn being killed by its older, weaned sibling. In several primate species, including in humans, short interbirth-intervals (IBI) can reduce survival for both the older (in rhesus macaques, *Macaca mulatta*: Lee et al., 2019; in yellow baboons: Tung et al., 2016; in humans, *Homo sapiens*: Conde-Agudelo et al., 2006; Rutstein, 2005; Wendt et al., 2012) and the younger sibling (Lee et al., 2019), and can even have intergenerational effects (Zipple et al., 2019). Despite such evidence, studies on monotocous mammals thus far have mostly focused on mother-offspring conflicts during developmental milestones, such as weaning (see for review: Maestripieri, 2002), rather than on sibling competition – maybe because of the overriding importance of lactation in mammals (Hudson and Trillmich, 2008). Siblings, however, likely compete for other resources than milk but the behavioural mechanisms at play remain largely unknown.

The birth of a younger sibling is the last step in a mother's shift from her current reproductive event to the next one, thus represents an ideal developmental milestone to study the interplay between sibling competition and mother-offspring conflict. In primates, previous studies reported contrasting changes in mother-juvenile relationships throughout the transition to siblinghood. In captive and free-ranging cercopithecines, the birth of a younger sibling induces an abrupt decrease in time spent in close spatial proximity and in the interaction rate between the mother and the juvenile, often driven by the juvenile itself (Devinney et al., 2001; DiGregorio et al., 1987; Holman and Goy, 1988; Schino and Troisi, 2001). Maternal aggression and rejection increases, often accompanied by signs of stress and "depression" in the offspring (Bolwig, 1980; Devinney et al., 2001; DiGregorio et al., 1987; Holman and Goy, 1988). In wild chacma baboons, however, maternal behaviour does not

change following the birth of a new infant but juveniles solicit their mother more often and show more signs of distress (especially those that experience this transition at an older age) than juveniles without a sibling (Delaunay et al., 2023). In wild bonobos, juveniles face an abrupt five-fold increase in cortisol level and a decrease in neopterin level after the birth of their sibling which endures for more than six months, but show little behavioural changes (Behringer et al., 2022). In industrialised modern human societies, the arrival of a younger sibling is often characterized by a decrease in maternal care and in the rate of mother-child interactions, with a switch in who initiates interactions – from mother to children becoming the primary initiator (Dunn et al., 1981; Dunn and Kendrick, 1980; Stewart et al., 1987; Volling, 2012). Confrontational behaviours with the mother increase, as well as signs of distress and clinging/demanding behaviours (Dunn et al., 1981; Volling, 2012). Children's behavioural adjustment show high inter-individual variability in humans (Dunn et al., 1981; Volling, 2012), however, and its quality (i.e. relatively positive *vs.* negative reactions to the birth of the younger sibling) is associated, potentially causally, with the quality of siblings' relationship later in life (Brody, 1998; Pike et al., 2005).

Importantly, species life history traits might influence juveniles' adjustment to the birth of a younger sibling. For instance, the birth of a younger sibling, when it triggers weaning or co-occurs with it, might induce a harsher transition than in species where inter-birth intervals are longer. In line with this, in juvenile rhesus macaques, steeper decreases in nursing and maternal care are associated with more signs of distress in the first month after the birth of their sibling (Devinney et al., 2003, 2001). On the contrary, in chacma baboons, juveniles have already been weaned several months before their mother give birth, and the birth is not associated with any major change in mother-offspring relationship (Delaunay et al. 2023). These two developmental milestones, weaning and TTS, do not always occur simultaneously across species or individuals. For instance, in some populations, including mandrills, high-ranking females can conceive when they are lactating, while subordinate females display a slower reproductive pace (Dezeure et al., 2022), which could translate into a harsher transition for offspring born to higher-ranking females.

In this study, we investigated changes affecting the mother-juvenile relationships following the birth of a younger sibling in a natural population of a long-lived social primate, the mandrill (*Mandrillus sphinx*). Mandrills live in huge multimale-multifemale

groups, sometimes up to several hundred individuals, mainly composed of females and their offspring (Abernethy et al., 2002). Mandrills form matrilineal societies (Charpentier et al., 2007), where females are philopatric and inherit their rank from their mother, while males disperse upon sexual maturity. Mandrills are seasonal breeders, with most births occurring during the rainy season (Dezeure et al., 2022), meaning that interbirth intervals often present a bimodal distribution, and that most offspring experience the birth of their younger sibling either during the next birth season, or two seasons later. Females give birth to one offspring every 1-3 years (Setchell et al., 2002), which they breastfeed for 8 months on average in captivity (Setchell and Wickings, 2004). Importantly, female mandrills can be lactating and pregnant simultaneously (Dezeure et al., 2022), which means that the birth of a younger sibling may accelerate or terminate abruptly the weaning process, generating competition among siblings.

Here, we used behavioural data collected since 2015 on the only natural population of habituated mandrills (*Mandrillus sphinx*) to investigate the immediate changes in the mother-juvenile relationship during the transition to siblinghood (hereafter, TTS). Following Delaunay and colleagues (2023), we compared mother-juvenile interactions among juveniles with no younger sibling and those of similar age who recently experienced the birth of a younger sibling, and tested the following predictions: (P1) following the birth of a younger sibling, juveniles would no longer be nursed or carried by their mother, independently of their age, while juveniles without a younger sibling would show a more gradual age-related decline for these two behaviours. In addition, juveniles who underwent TTS at a young age would show a more abrupt decrease than juveniles who experienced the birth of a younger sibling at an older age; (P2) the amount of grooming interactions between the mother and the juvenile would decrease after the birth of a younger sibling, with a shift in patterns of initiations of such interactions, from mostly mother-initiated to mostly juvenile-initiated as found in humans; (P3) juveniles would associate less often with their mother and would become more responsible for initiating and maintaining spatial proximity with their mother following the birth of their younger sibling; (P4) juveniles who recently experienced the birth of a younger sibling, and especially the younger ones, would display more tantrum (a behaviour commonly considered as a behavioural manifestation of mother-offspring conflict; Barrett and Henzi, 2000; Maestripieri, 2002) and more self-directed behaviours (generally

indicating anxiety; Castles et al., 1999; Maestripieri et al., 1992; Palagi and Norscia, 2011) than those who did not.

METHODS

Study site and population

We studied a natural population of habituated mandrills who freely ranges in the Lékédi Park and its surroundings, located in southern Gabon, daily monitored since 2012 by the Mandrillus Project. This population originated from 65 individuals initially living in a semi-free ranging population housed at CIRMF (Centre International de Recherches Médicales de Franceville, Gabon), who were released in two waves in the Lékédi Park, in 2002 and 2006 (Peignot et al., 2008). Captive-born females started to breed with wild males in 2003, and in late 2022, only 4 females out of 250 individuals in the group were captive-born. All individuals, including infants and juveniles, are recognized thanks to facial and body features by trained observers. During daily monitoring, observers on foot record data on individual life-history, developmental trajectory and behaviour. In this study, we used data used collected on 191 juveniles between January 2015 and October 2022.

Individual data

Individual birth dates were assessed with certainty when observed in the field (*N*= 88 infants), or estimated within a time-window of 1 day to 2 months for the remaining 103 infants, based on patterns of mother's sexual swellings and infants' physical appearance. Individual birth order was inferred based on maternal reproductive history when known. We then divided birth order in three different classes: first- born, second- born, later-born (when birth rank ≥ 3).

Behavioural data

Since 2015, trained observers collected daily *ad libitum* and 5-min focal behavioural observations on all individually-recognized infants and juveniles (Altmann, 1974). During focal observations, we recorded the occurrence of suckling, ventral carrying and grooming bout with the mother. For grooming bouts, we recorded the direction of the interaction, and the

identity of the individual who initiated and ended the grooming event. We also collected the occurrence of tantrums and anxiety-related behaviours (e.g. self-scratch or yawning) displayed by the focal individuals. Maintenance of spatial proximity was assessed by recording every close approach or leave (to and from 1m) between focal individuals and their mother. Every two minutes, we also recorded the identity of all groupmates – including the mother – that were in body contact and within 5 meters around the focal individual.

In this study, we aimed to investigate the short-term behavioural response to the birth of a younger sibling. Following Delaunay and colleagues (2022), we compared juveniles who recently experienced the birth of a younger sibling – within the three months following the birth of the newborn – with juveniles who did not yet. In our sample of focal observations, juveniles who had experienced the birth of a younger sibling were 11- to 32-months old. Therefore, we restricted our dataset to this age-range. Juveniles who experienced the birth of a younger sibling more than three months ago were excluded from the study. When a newborn died before three months of age, we excluded all observations of the older sibling following this death. Individuals who were observed both before and after the birth of their younger sibling were included in each group respectively (*N* = 72). We used a total of 4866 focal observations (mean ± SD = 25.48 ± 28.66 per individual) and 6989 scan (mean ± SD = 36.40 ± 41.88 per individual) from 191 individuals (*N* = 79 with a younger sibling, mean age ± SD = 21.1 ± 4.6 months; *N* = 184 without a younger sibling, mean age ± SD = 16.3 ± 3.6 months) born from 76 mothers.

Mothers' social rank was established using the outcomes of approach-avoidance interactions during *ad libitum* and focal samplings performed on adult females. We computed yearly linear hierarchies using normalized David's score. Individuals' social ranks were highly correlated between years (Dezeure et al., 2022), therefore, we assigned each female a unique relative rank from 2012 to 2022. We then divided adult females into three classes of rank of similar size (high-ranking, medium-ranking, and low-ranking; Charpentier et al., 2020).

Statistical analyses

TTS effects on maternal care

To characterize the impact of TTS on maternal care, we used two measures: suckling frequency and ventral carrying frequency. For each focal observation, we recorded whether the juvenile i) suckled or ii) was carried ventrally by its mother at least once (yes = 1, no = 0). Preliminary inspection of the data revealed that juveniles with a younger sibling were no longer suckling or being carried by their mother, so we provided below a descriptive analysis.

TTS effects on maternal grooming

First, for each focal observation, we recorded whether the focal juvenile received grooming from its mother at least once (binary, yes/no – model 1), and whether it groomed its mother (binary, yes/no – model 2). We modelled the probability to receive or give grooming to the mother with two Generalized Linear Mixed Models (GLMM) with a binomial error structure.

Second, we considered every grooming event, and recorded whether it was initiated by the juvenile (1) or by its mother (0). We restricted this dataset to the first grooming event recorded during a focal observation, and discarded any other grooming event that occurred after this first event, regardless of the direction, because we considered these events as potentially non-independent. We modelled the probability that a grooming bout was initiated by the juvenile (*vs.* the mother) with a GLMM with a binomial error structure (model 3) using 396 grooming bouts with a known initiator.

TTS effects on mother-juvenile spatial proximity

To investigate mother-juvenile proximity, we first used scan data to estimate how often a juvenile was found in close proximity to the mother. For each scan observation, we recorded whether the juvenile focal was found in proximity (1) or not (0) to its mother. We considered two distinct ranges of proximity: body contact (model 4), and within 5m from the mother (model 5). We ran two GLMMs with a binomial error structure.

Second, we used focal data to characterize juveniles' responsibility in the maintenance of spatial proximity. We considered every approach and leave between the mother and the focal juvenile, and recorded whether it was initiated by the juvenile (1) or by the mother (0). Using 1199 approaches and 1350 leaves between the mother and the focal juvenile, we ran two GLMMs with a binomial error structure to investigate the probability that an approach and a leave are initiated by the juvenile (models 6 and 7, respectively).

TTS effects on mother-juvenile conflict

To investigate the effect of TTS on mother-juvenile conflict, we considered two measures: juvenile tantrums and juvenile anxiety-related behaviours (yawning and self-scratches). For each focal observation, we recorded whether i) a tantrum occurred (binary, 1/0 – model 8), and ii) the juvenile displayed at least one anxiety-related behaviour (binary, 1/0 – model 9). We ran two GLMMs with a binomial error structure.

Fixed and random effects

For each model, we tested the effect of having recently experienced the birth of a younger sibling (yes/no), and included the following fixed effects: focal juvenile's age (in months), sex and birth order, and maternal rank. We tested the interaction terms between the recent birth of a younger sibling and the focal juvenile age and sex (except for model 8 because tantrums were rarely recorded). We also included three additional fixed effects: (1) in model 3, grooming direction and its interaction term with the birth of a younger sibling; (2) in most models, duration of the focal observation (in seconds) (except in models 3, 6 and 7 because the probability that a behaviour is initiated by the juvenile did not depend on the duration of the observation, and models 4 and 5 because based on scan data). In all models, we included the year of observation as a random effect, and the focal juvenile identity nested in the mother identity to account for repeated observations.

Statistical methods

All statistical analyses were performed using the R Studio software (version 4.0.2). We ran mixed models using the "*glmmTMB*" function from the glmmTMB package (Brooks et al., 2017), and the "*bglmer*" function from the blme package (Dorie et al., 2021) to confirm the results with a Bayesian approach whenever we obtained a singular fit. We assessed fit singularity using the function "*check_singularity*" from the performance package (Lüdecke et al., 2021). To control for the age of focal juveniles, we first visually checked the relationship between age and our response variables. Whenever this relationship was not linear, we fitted univariate models with a linear, a second- or third-degree polynomial function to model the effect of age (random effects were also included), and compared model fits, selecting the model with the lowest AIC (Zuur et al., 2009). All quantitative variables were z-transformed

(mean = 0, SD = 1) using the "*scale*" function from the car package (Fox and Weisberg, 2019) to facilitate model convergence and to compare effect sizes across estimates (Harrison et al., 2018). To diagnose the presence of multicollinearities, we computed the variance inflation factor (VIF) for each predictor of each model using the function "*check_collinearity*" from the performance package. VIFs were inferior to 2 in all cases, indicating that multicollinearities did not impact coefficients' estimation in our models. To test the significance of our fixed factors, we calculated the likelihood ratio test (LRT) and its associated p-values for each model using the "*drop1*" function, and computed the 95% Wald confidence intervals. Non-significant interactions were removed from the full model to limit the risk of over-parameterization and facilitate the interpretation of simple effects. Finally, we checked the distribution of the residuals using "simulateResiduals" from the DHARMa package (Hartig and Lohse, 2021).

RESULTS

TTS effects on maternal care

We first investigated the impact of the birth of a younger sibling on maternal care. Juveniles with a younger sibling were no longer nursed or carried by their mother, independently from the age at which they entered TTS (Fig. 1a, 1b). In contrast, suckling and carrying probabilities gradually decreased with age for juveniles without a younger sibling, and definitely ceased around 25 months-old for suckling (Fig. 1a) and 21 months-old for carrying (Fig. 1b). Juveniles without a younger sibling were still suckling in ~15% of the observations at 11-12 months-old (mean probability ± SD = 0.151 ± 0.360, i.e. once every 30min), in ~7% at 17-18 months-old (mean ± SD = 0.066 ± 0.248, i.e. once every 75min), and in ~3% at 21-22 months-old (mean ± SD= 0.034 ± 0.181, i.e. once every 145min). Similarly, they were still being carried in ~3% of the observations at 11-12 months-old (mean ± SD = 0.029 ± 0.169, i.e. once every 170min), and in 0.4% at 17-18 months-old (mean ± SD = 0.004 ± 0.064, i.e. once every 1250min).

TTS effects on maternal grooming

We then investigated if the grooming relationship with the mother changed following the birth of a younger sibling. Juveniles in TTS were significantly less likely to be groomed by their mother than juveniles without a younger sibling (Odds Ratio (OR) = 0.58, mean probability ±

SD = 0.08 ± 0.27 for juveniles with a younger sibling; 0.09 ± 0.29 for those without, Table 1, Fig. 2a), although the difference in raw grooming probability was small between the two categories on study juveniles. The probability to groom the mother tended to be influenced by the interaction between the sex of the focal juvenile and its sibling status (p = 0.091): female juveniles with a younger sibling tended to be more likely to groom their mother than females without a younger sibling (mean probability ± SD = 0.06 ± 0.24 for females with a younger sibling; 0.01 ± 0.11 for females without), while male juveniles were equally likely to groom their mother independently of their sibling status (males with a younger sibling: 0.01 ± 0.10; without: 0.01 ± 0.08, Table 1, Fig. 2b). Juveniles born from medium- or low-ranking females were also significantly less likely to be groomed by their mother than those born from high-ranking females (OR = 0.53 and 0.49 respectively, Table 1), but maternal rank did not influence the probability to groom the mother. Juvenile's age and birth order did not influence the probability to receive or give grooming to the mother, and both sexes were equally likely to be groomed by the mother (Table 1).

Juveniles with and without a younger sibling were as likely to initiate a grooming with their mother (Table 2). The probability to initiate a grooming was significantly predicted by its direction: when grooming their mother, juveniles initiated most of the interactions (0.83 ± 0.38), while grooming received were mostly initiated by the mother (OR = 0.03, 0.17 ± 0.38). Juveniles initiated significantly more grooming bouts with their mother as they grew older (OR = 1.47, Table 2). Juvenile's sex, birth rank or maternal rank did not influence the probability to initiate a grooming (Table 2).

TTS effects on mother-juvenile spatial proximity

Mother-juvenile proximity was partially influenced by the birth of a younger sibling: although the probability to be in body contact with the mother was similar in both groups (Table 3, Fig. 3a), the probability to be within 5m around the mother was significantly influenced by the interaction between juvenile's sex and sibling status (Table 3, 3b). Male juveniles with a younger sibling were less likely to range within 5m of their mother than males without a younger sibling (mean probability ± se = 0.23 ± .042 and 0.46 ± 0.50 respectively), while female juveniles were as likely to range within 5m as those without (0.40 ± 0.49 for those with a sibling, 0.41 ± 0.49 for those without). Juveniles were less likely to be in body contact and

within 5m around their mother as they grew older (OR = 0.80 and 0.77 respectively), and first-born juveniles were more likely to be in body contact than later-born juveniles (OR = 1.67, Table 3). Maternal rank did not predict the probability to be in body contact or within 5m around the mother (Table 3).

Juveniles with and without a younger sibling were equally responsible of initiating an approach with their mother (Table 4). The probability to leave one another was similar for juveniles and their mother in general, and independent from the birth of a younger sibling (Table 4). Juveniles born to higher-ranking females were more likely to initiate an approach to their mother (OR = 2.10, Table 4). Juvenile's age, sex and birth order did not influence the probability to approach or leave their mother, and the probability to leave the mother was independent from maternal rank (Table 4).

TTS effects on mother-offspring conflicts

Tantrums were uncommon, and juveniles' probability to throw a tantrum was independent from their sibling status, decreased as they grew older, and was lower for juveniles born to low-ranking females than those born to high- and medium-ranking females (OR = 0.39 and 0.53, respectively, Table 5). Juveniles' sex and birth rank did not influence the probability to display a tantrum (Table 5).

Finally, juveniles with a younger sibling were as likely to display anxiety-related behaviours as juveniles without a younger sibling (Table 5). Juveniles born to low-ranking females significantly displayed more anxiety-related behaviours than juveniles born to high- or medium-ranking females (OR = 1.28 and 1.32 respectively, Table 5). The probability to display anxiety-related behaviours was independent from juveniles' sex, age and birth rank (Table 5).

DISCUSSION

In this study, we investigated the changes in maternal care and mother-juvenile relationship during the transition to siblinghood (TTS) in wild mandrills. First, following our prediction (P1), we found that nursing and maternal carrying abruptly stopped after the birth of a younger sibling, thus juveniles who entered TTS at a younger age experienced a greater loss of maternal care. Second, we showed that juveniles with a younger sibling received less

maternal grooming (P2), although the magnitude of this loss was small (they lost on average a tenth of time of maternal grooming compared to their counterparts). Contrary to our prediction (P2), female juveniles with a younger sibling tended to groom their mother more often than females without a sibling (6 times more), while males tended to groom their mother independently of their sibling status, and TTS did not impact the probability to initiate a grooming in both sexes. Third, contrary to our prediction (P3), juvenile males spent less time close to their mother following the birth of their sibling, while spatial proximity remained stable for juvenile females. However, juveniles from both sexes were mostly responsible for maintaining spatial proximity with their mother, independently from the birth of their sibling. Finally, we showed that juveniles with a younger sibling neither displayed more tantrums nor signs of anxiety than those without (P4). We discuss below the implications of our findings for the understanding of parent-offspring conflict and sibling rivalry in primates.

First, mandrill mothers dramatically decreased their level of maternal investment toward their juvenile when giving birth, as they stopped nursing and carrying them, and groomed them less often. Thus, in mandrills, the birth of the younger sibling terminates the weaning process for the older sibling, as mothers are unable to nurse two offspring at the same time. In free-ranging, provisioned rhesus macaques, juveniles also stopped suckling their mother after the birth of their sibling (Devinney et al., 2001), although mothers in this population can sometimes nurse two consecutive offspring at the same time (Lee et al., 2019). By contrast, in chacma baboons and bonobos, juveniles were already weaned several months before their mother gave birth (Behringer et al., 2022, Delaunay et al., 2023). Mothers' ability to nurse while being pregnant might largely depends on their ecology and life-history. For instance, mandrills live in a rich environment where food is unlikely to be limiting which, like provisioned macaques, might enable them to face the cumulated costs of late lactation and early pregnancy at the same time (Dezeure et al., 2022). In contrast, chacma baboons live in an arid environment where food is drastically limited, which might force females to space out births by weaning their previous offspring before starting a new reproductive cycle. In bonobos and orang-utans, where the older juvenile is also weaned before the birth of the younger sibling, mothers may start a new reproductive cycle only when the older juvenile has reached nutritional independence and learnt most skills needed to extract food (Behringer et al., 2022; van Noordwijk and van Schaik, 2005).

In addition to these two obvious forms of maternal care, mandrill mothers also groomed their juvenile less often, and this decrease did not seem to be driven by the mother or the juvenile in particular, as juvenile's and mother's probability to initiate grooming or close proximity did not change with the TTS. These results partially resemble previous findings in macaques and industrialized human societies, where maternal grooming or maternal attention and responsiveness (in macaques and humans, respectively) decreased (Devinney et al., 2001; Dunn and Kendrick, 1980; Kendrick and Dunn, 1980). However, juvenile's reaction to these changes seems highly variable across studies and species: in macaques, juveniles seemed to be responsible for the decrease in maternal grooming (Devinney et al., 2001), while in humans, children initiated more interactions with their mother following the birth of a sibling, as a likely attempt to compensate for the loss of maternal attention (Dunn et al., 1981; Dunn and Kendrick, 1980; Stewart et al., 1987; Volling, 2012). In chacma baboons, although maternal behaviour did not change with TTS, juveniles nevertheless solicited their mother more often (Delaunay et al., 2023).

Surprisingly, age did not mediate the effect of TTS on mother-juvenile relationships. As the birth of the younger sibling terminated the weaning process for the juvenile and the loss incurred in terms of suckling was larger for young juveniles, we were expecting juveniles who entered TTS at a younger age to show stronger reactions. Indeed, in rhesus macaques, juveniles who experienced a greater decrease in nursing after their sibling's birth showed more signs of distress (Devinney et al., 2003). In humans, as well, the increase in anxiety, clinginess, and confrontational behaviours toward the mother after the birth of the newborn was more marked in younger children (Dunn et al., 1981; Kendrick and Dunn, 1980; Volling et al., 2014). Recent studies in macaques and baboons also showed that having a too close in age younger sibling increased mortality risks at all ages for the older sibling (Lee et al., 2019; Tung et al., 2016), most likely because it induced a decrease in maternal investment. In mandrills, however, the birth of a younger sibling was perceived similarly and independently of age (and thus, of weaning). A potential explanation could be that juvenile mandrills adjust to their mother's reproductive pace, and juveniles experiencing TTS at younger age could already be independent enough from their mother that the birth of their younger sibling is not more stressful for them than for juveniles experiencing TTS later in life.

In contrast to two recent studies in wild baboons and bonobos, (Behringer et al., 2022, Delaunay et al., 2023), juvenile mandrills' reactions were sex-specific. Indeed, juvenile females tended to increase their grooming rate toward their mother, while juvenile males associated less often with them. These differences may be triggered by several, non-mutually exclusive factors. First, females' increased grooming could result from an attraction to the newborn, which is a common behaviour in primates, where juvenile and adult females often try to touch or handle infants of others (Dunayer and Berman, 2018; Hrdy, 1976; Meredith, 2015). A common way to gain access to the infant is to initiate a grooming with the mother, resulting in new mothers receiving increased levels of grooming and attention (Caselli et al., 2021; Frank and Silk, 2009; Henzi and Barrett, 2002). In wild chacma baboons, although juvenile females reacted in a similar way than their male counterparts to the birth of their sibling, they nevertheless interacted more often with their newborn sibling than males did (Delaunay et al., 2023). Second, mandrills' sex-specific reactions might reflect life history differences between sexes. Indeed, in such matrilineal society, maintaining and/or reinforcing close social bonds with the mother could be more advantageous for juvenile females than for males, as strong social bonds with close maternal kin in adulthood, and particularly with the mother, translate into fitness advantages in female cercopithecines (Silk et al., 2010, 2003 and see Charpentier et al., 2012 for semi-free ranging mandrills). In addition, as younger sisters typically outrank older ones (Pereira, 1989), the birth of a younger sibling could be costlier for females. Hence, juvenile females could groom their mother more often in an attempt to strengthen their bond with their mother and retain maternal support against their younger sister, but testing this hypothesis would require to investigate whether juveniles' reaction to TTS differ with the newborn's sex, which we were unable to do. On the contrary, the birth of a younger sibling for juvenile males might result in greater independence from their mother and the development of relationships with other individuals, such as male peers, with whom they could interact later in life (Amici et al., 2019).

Despite facing a drastic decrease in maternal care, juvenile mandrills showed little indications that this transition was a source of conflict with their mother or of anxiety. Indeed, they did not throw more tantrums or displayed more signs of anxiety, nor did they take greater responsibility to initiate interactions with their mother. Tantrums have often been considered as a conspicuous form of behavioural conflict over parental investment in

primates, expressed during developmental milestones where mother and juvenile's evolutionary interests diverge, such as weaning (Maestripieri, 2002). In mandrills, tantrums are often less conspicuous than in baboons (*pers. obs*.), and are already rare by the age juveniles enter TTS. Although the youngest juveniles were still able to throw tantrums, conflicts with the mother could be expressed through more subtle behaviours. In chacma baboons for instance, juveniles solicited their mother more often after the birth of their younger sibling, which suggests a conflict over the amount of maternal investment received (Delaunay et al., 2023). Surprisingly, juvenile mandrills did not seem more anxious after the birth of their sibling. Studies in several cercopithecine species reported increased signs of distress or "depression" during TTS (Delaunay et al., 2023, Devinney et al., 2003, 2001; Schino and Troisi, 2001). In bonobos, a recent study reported a strong increase in cortisol level following the birth a younger sibling, but they did not investigate whether this physiological changes were also manifested through distress behaviours (Behringer et al., 2022). In mandrills, the birth of a younger sibling could also induce physiological changes that could be undetectable behaviourally. Alternatively, the lack of conflict and anxiety behaviours in mandrills could also reflect the fact that the birth of a younger sibling does not induce conflict with the mother, which could be the case if juveniles are already independent enough by the time their mother give birth, or if the fitness benefits of having a younger sibling outweigh the costs linked with the loss of maternal care and attention.

Finally, the decrease in maternal care induced by the birth of the younger sibling could translate into sibling rivalry (Trivers, 1974). As mothers can nurse and be pregnant at the same time in mandrills, pregnancy could represent a perfect case study of interbrood sibling competition, where the monopolisation of maternal care through suckling by the older sibling could directly reduce the viability of the foetus. After the birth of the younger sibling, competition for milk could also occur, as in Galapagos fur seals and sea lions (Trillmich and Wolf, 2008), if the older sibling disagrees with the abrupt end of weaning that it experiences. In mandrills, juvenile's aggressive behaviours toward the infant have never been observed, but older siblings sometimes attempt – and even more rarely succeed – to suckle their mother at the same time as their younger sibling (*B.R.T. and M.J.E.C. pers. obs.*). Similar observations were reported from the free-ranging rhesus macaques population in Cayo Santiago, with mothers occasionally nursing two consecutive offspring at the same time (Lee et al., 2019). In

this population, despite living in a relatively rich environment, short interbirth intervals between two siblings reduced survival chances for both the older and younger sibling, most likely due to the dilution of maternal resources (Lee et al., 2019). Recent findings from the same mandrill population showed that the duration of interbirth intervals was highly correlated to female's rank, with higher-ranking females giving birth to a new offspring every year on average, while lower-ranking females do so once every two years (Dezeure et al., 2022), a difference that was not observed in provisioned captive mandrills (Setchell et al., 2002). Therefore, juveniles who entered TTS at the youngest ages might be born to females who can afford the combined energetic costs of gestation and lactation, with little costs for the older sibling, explaining the absence of overt mother-offspring conflict during TTS. Whether mandrill juveniles could pay other costs, similar to those of rhesus macaques, such as decreased survival or slower development for instance, when having a close-in-age younger sibling, remains to be tested.

Our study investigated changes in maternal care and mother-juvenile relationship following the birth of a new sibling in a natural population of mandrills. The birth of a younger sibling induced an abrupt decrease in maternal care, terminating the weaning process for those who enter TTS at a young age. Juveniles' reactions to TTS were sex-specific, with females increasing affiliation with their mother while males decreased their association with the mother, but did not seem to induce conflicts with the mother or to trigger anxiety for the juveniles. Our results suggest that, although TTS could induce mother-offspring conflict and sibling competition over maternal investment, young mandrills adjust to their mother's reproductive pace. Overall, our study adds up to recent studies in primates investigating this intriguing developmental milestone, and highlights an intriguing variety of reactions across species, likely mirroring contrasts in life histories and ecologies.

AUTHORS' CONTRIBUTION

A.D., E.H. and M.J.E.C. conceived the ideas and designed the methodology, B.R.T. and L.S. collected the data, A.D., O.C.D. and M.J.E.C. formatted the data, A.D. and O.C.D. performed the analyses, A.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY

Datasets and scripts used in this study are available in the following public repository: XXX

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TABLES

Fixed factor	*Level*	*Estimate*	*2.5 %*	*97.5 %*	*LRT*	*P-value*
Model 1: Probability to receive grooming from the mother						
Intercept		-1.511	-2.278	-0.745	-	-
Presence of a younger sibling (No)	Yes	**-0.546**	**-1.006**	**-0.086**	**5.641**	**0.018**
Juvenile's age		0.096	-0.045	0.237	1.777	0.182
Juvenile's sex (Female)	Male	-0.249	-0.549	0.051	2.695	0.101
Juvenile's birth rank (First-born)	Second-born	-0.410	-0.894	0.073	3.632	0.163
	Later-born	-0.019	-0.381	0.343		
Maternal rank (High-ranking)	Medium-ranking	**-0.627**	**-1.021**	**-0.233**	**15.292**	**< 0.001**
	Low-ranking	**-0.720**	**-1.088**	**-0.353**		

Focal duration		**0.708**	**0.555**	**0.861**	**105.755**	**< 0.001**
Model 2: Probability to groom the mother						
Intercept		-4.595	-5.778	-3.411	-	-
Presence of a younger sibling (No)	Yes	1.379	0.337	2.421	-	-
Juvenile's age		0.157	-0.183	0.497	0.710	0.400
Juvenile's sex (Female)	Male	-0.904	-1.744	-0.064	-	-
Juvenile's birth rank (First-born)	Second-born	-0.774	-1.923	0.376	3.014	0.222
	Later-born	-0.669	-1.561	0.223		
Maternal rank (High-ranking)	Medium-ranking	0.133	-0.844	1.110	0.763	0.683
	Low-ranking	-0.266	-1.249	0.717		
Focal duration		**1.317**	**0.691**	**1.942**	**33.206**	**< 0.001**

Presence of a younger sibling (No)*Juvenile's sex (Female)	(Yes, male)	-1.337	-3.015	0.340	2.849	0.091

Table 7: Results of the mixed models analysing the probability to receive (model 1) and give (model 2) grooming to the mother during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 4866 focal observations on 191 juveniles (N=79 with a younger sibling, N=184 without). Juvenile identity nested in mother identity, and year of observation were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold.

Fixed factor	*Level*	*Estimate*	*2.5 %*	*97.5 %*	*LRT*	*P-value*
Intercept		1.3403	-0.2139	2.8944	-	-
Presence of a younger sibling (No)	Yes	0.7690	-0.2700	1.8080	2.3707	0.1236
Juvenile's age		**0.3859**	**0.0576**	**0.7142**	**5.3712**	**0.0205**
Juvenile's sex (Female)	Male	-0.4557	-1.2240	0.3125	1.6259	0.2023
Grooming direction (Juvenile-Mother)	Mother-Juvenile	**-3.662**	**-4.980**	**-2.344**	**47.152**	**< 0.001**
Juvenile's birth rank (First-born)	Second-born	0.0922	-1.2365	1.4209	1.3879	0.500
	Later-born	0.4942	-0.4724	1.4609		
Maternal rank (High-ranking)	Medium-ranking	0.5332	-0.4869	1.5533	1.2710	0.5297

	Low-ranking	0.1574	-0.7766	1.0915	

Table 8: Results of the mixed model testing the probability that a grooming event is initiated by the juvenile (vs. the mother, model 3). Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 396 grooming events on 128 juveniles (N=23 with a younger sibling, N=120 without). Juvenile identity nested in mother identity, and year of observation were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold.

Fixed factor	*Level*	*Estimate*	*2.5 %*	*97.5 %*	*LRT*	*P-value*
Model 4: Probability to be in body contact with the mother during a scan observation						
Intercept		-1.024	-1.732	-0.316	-	-
Presence of a younger sibling (No)	Yes	-0.287	-0.689	0.115	1.991	0.158
Juvenile's age		**-0.228**	**-0.340**	**-0.116**	**16.237**	**< 0.001**
Juvenile's sex (Female)	Male	-0.147	-0.464	0.169	0.831	0.362
Juvenile's birth rank (First-born)	Second-born	**-0.619**	**-1.114**	**-0.124**	**6.123**	**0.047**
	Later-born	**-0.328**	**-0.736**	**0.080**		
Maternal rank (High-ranking)	Medium-ranking	-0.196	-0.673	0.281	4.528	0.104

	Low-ranking	-0.510	-0.974	-0.046		
Model 5: Probability to be within 5m around the mother during a scan observation						
Intercept		0.561	-0.214	1.337	-	-
Presence of a younger sibling (No)	Yes	0.107	-0.303	0.517	-	-
Juvenile's age		**-0.258**	**-0.339**	**-0.177**	**39.442**	**< 0.001**
Juvenile's sex (Female)	Male	0.053	-0.293	0.400	-	-
Juvenile's birth rank (First-born)	Second-born	-0.061	-0.586	0.464	2.710	0.258
	Later-born	-0.329	-0.767	0.109		
Maternal rank (High-ranking)	Medium-ranking	-0.015	-0.483	0.453	0.005	0.998

	Low-ranking	-0.003	-0.461	0.456		
Presence of a younger sibling (No)*Juvenile's sex (Female)	(Yes. male)	**-1.011**	**-1.543**	**-0.479**	**13.931**	**< 0.001**

Table 9: Results of the mixed models analysing juveniles' probability to be in body contact (model 4) or within 5m around their mother (model 5) during a scan observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 6989 focal observations on 192 juveniles (N=78 with a younger sibling, N=184 without). Juvenile identity nested in mother identity, and year of observation were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold.

Fixed factor	*Level*	*Estimate*	*2.5 %*	*97.5 %*	*LRT*	*P-value*
Model 6: Probability that an approach is initiated by the juvenile						
Intercept		2.645	1.764	3.526	-	-
Presence of a younger sibling (No)	Yes	-0.351	-1.206	0.503	0.758	0.384
Juvenile's age		-0.116	-0.278	0.045	1.900	0.168
Juvenile's sex (Female)	Male	-0.084	-0.400	0.231	0.144	0.705
Juvenile's birth rank (First-born)	Second-born	-0.263	-0.730	0.204	1.372	0.504
	Later-born	-0.108	-0.505	0.289		
Maternal rank (High-ranking)	Medium-ranking	**-0.375**	**-0.874**	**0.125**	**12.111**	**0.002**

	Low-ranking	**-0.742**	**-1.213**	**-0.270**		
Model 7: Probability that an leave is initiated by the juvenile						
Intercept		-0.326	-0.910	0.257	-	-
Presence of a younger sibling (No)	Yes	0.201	-0.500	0.901	0.373	0.542
Juvenile's age		0.052	-0.086	0.189	0.400	0.527
Juvenile's sex (Female)	Male	-0.193	-0.471	0.085	1.920	0.166
Juvenile's birth rank (First-born)	Second-born	0.047	-0.379	0.473	2.640	0.267
	Later-born	0.256	-0.101	0.614		
Maternal rank (High-ranking)	Medium-ranking	-0.212	-0.625	0.201	3.220	0.200

	Low-ranking	0.094	-0.298	0.486	

Table 10: Results of the mixed models analysing the probability that an approach (model 6) or a leave (model 7) are initiated by the juvenile (vs. its mother). Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using respectively, 1199 approaches between the mother and the juvenile on 134 juveniles (N=21 with a younger sibling, N=128 without), and 1350 leaves on 141 juveniles (N=33 with a younger sibling, N=132 without). Juvenile identity nested in mother identity, and year of observation were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold.

Fixed factor	*Level*	*Estimate*	*2.5 %*	*97.5 %*	*LRT*	*P-value*
		Model 8: Probability of tantrum				
Intercept		-4.109	-5.098	-3.119	-	-
Presence of a younger sibling (No)	Yes	-0.373	-1.531	0.784	0.500	0.480
Juvenile's age		**-0.325**	**-0.609**	**-0.041**	**5.384**	**0.020**
Juvenile's sex (Female)	Male	0.489	-0.082	1.060	2.680	0.102
Juvenile's birth rank (First-born)	Second-born	-0.197	-1.049	0.655	0.749	0.688
	Later-born	-0.299	-0.995	0.397		
Maternal rank (High-ranking)	Medium-ranking	-0.383	-1.089	0.322	**8.330**	**0.016**

	Low-ranking	-1.024	-1.754	-0.293		
Focal duration		**0.445**	**0.199**	**0.692**	**13.946**	**< 0.001**
Model 9: Probability of anxiety-related behaviours						
Intercept		0.202	-0.281	0.684	-	-
Presence of a younger sibling (No)	Yes	0.112	-0.161	0.385	0.700	0.403
Juvenile's age		-0.073	-0.154	0.008	3.280	0.070
Juvenile's sex (Female)	Male	0.061	-0.124	0.246	0.450	0.502
Juvenile's birth rank (First-born)	Second-born	-0.095	-0.384	0.194	2.006	0.367
	Later-born	-0.164	-0.398	0.071		

Maternal rank (High-ranking)	Medium-ranking	**-0.027**	**-0.277**	**0.222**	**7.097**	**0.029**
	Low-ranking	**0.247**	**0.009**	**0.484**		
Focal Duration		**0.669**	**0.603**	**0.734**	**440.446**	**< 0.001**

Table 11: Results of the mixed models analysing the probability to display a tantrum (model 8) and anxiety-related behaviours (model 9) during a focal observation. Estimates, 95% confidence intervals (CI), LRT statistics and p-values of the predictors were estimated using 4866 focal observations on 191 juveniles (N=79 with a younger sibling, N=184 without). Juvenile identity nested in mother identity, and year of observation were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold.

FIGURES

Figure 3: Probability to (a) suckle and (b) be carried by the mother during a focal observation according to juvenile's age and sibling status, using raw data from 4866 focal observations on 191 juveniles. In all panels, "TTS" refers to juveniles who recently experienced the birth of a younger sibling and "Control" those who did not. For graphical purposes, we pooled values per age class so that "11" represent the mean probability to suckle/be carried for all juveniles aged 11-12 months old, "13", juveniles 13 and 14 months old etc. In (a), "25" represents the pooled values for all juveniles older than 25 months old as suckling was no longer observed after this age, and in (b), "21" represents the pooled values for all juveniles older than 21 months-old as carrying was no longer observed after this age. Dots represent the average value for a given age class and vertical bars represent the standard errors.

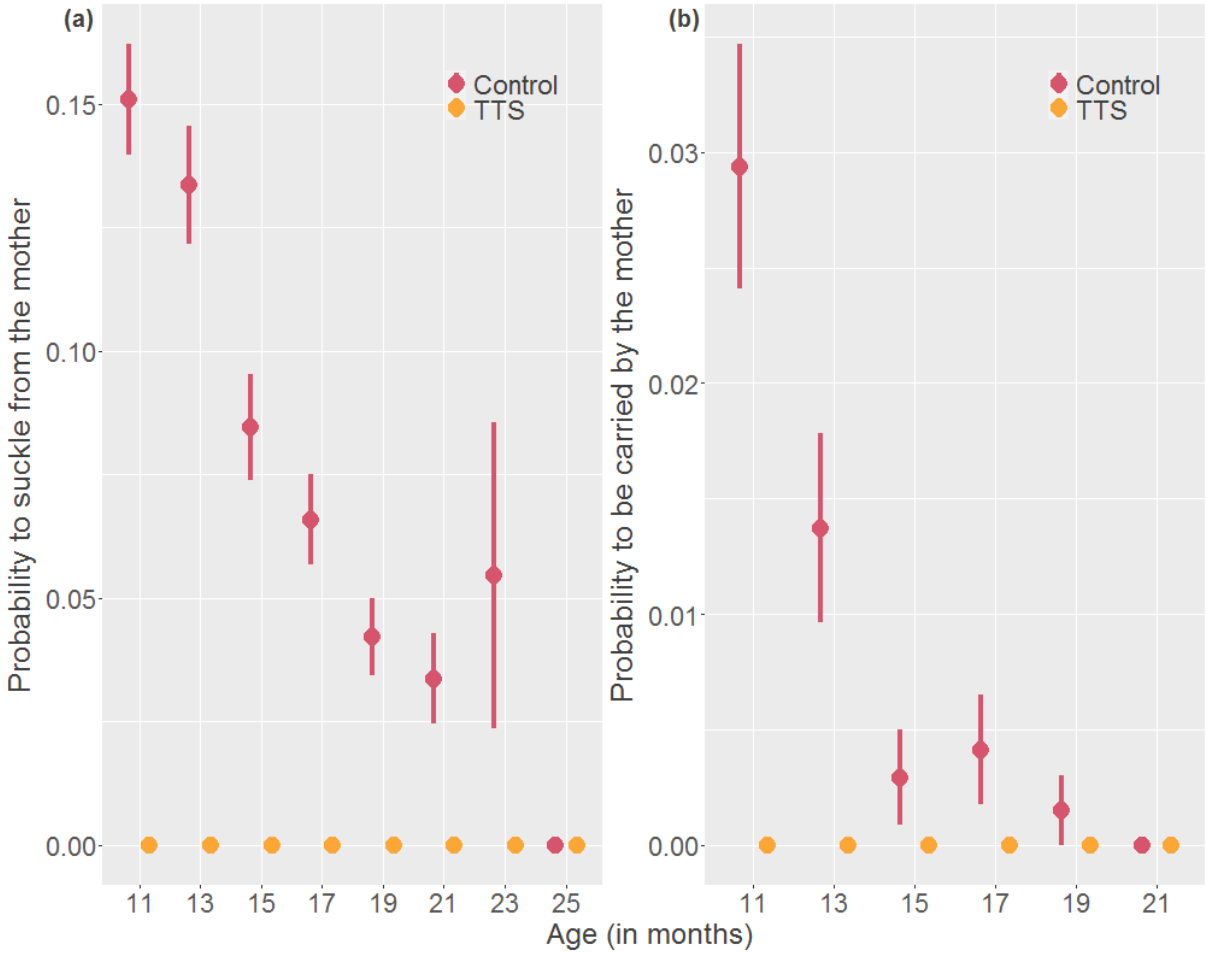


*Figure 4: Influence of the birth of the younger sibling on mother-juvenile grooming interactions. In all panels, "TTS" refers to juveniles who recently experienced the birth of a younger sibling and "Control" those who did not. (a) Predicted probability to be groomed by the mother depending on the sibling status during a focal observation. (b) Predicted probability to groom the mother depending on the sibling status and focal juvenile's sex (females on the left side of the graph, males on the right). Dots are fitted values from the models, and boxplots show the median of the distribution of the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively) and the whiskers include a maximum of 1.5 times the interquartile range. The effect of the predictor "Sibling status" and the associated p-values are shown. "ns": not significant (p>0.05), *: p<0.05, **: p<0.01, ***: p<0.001.*

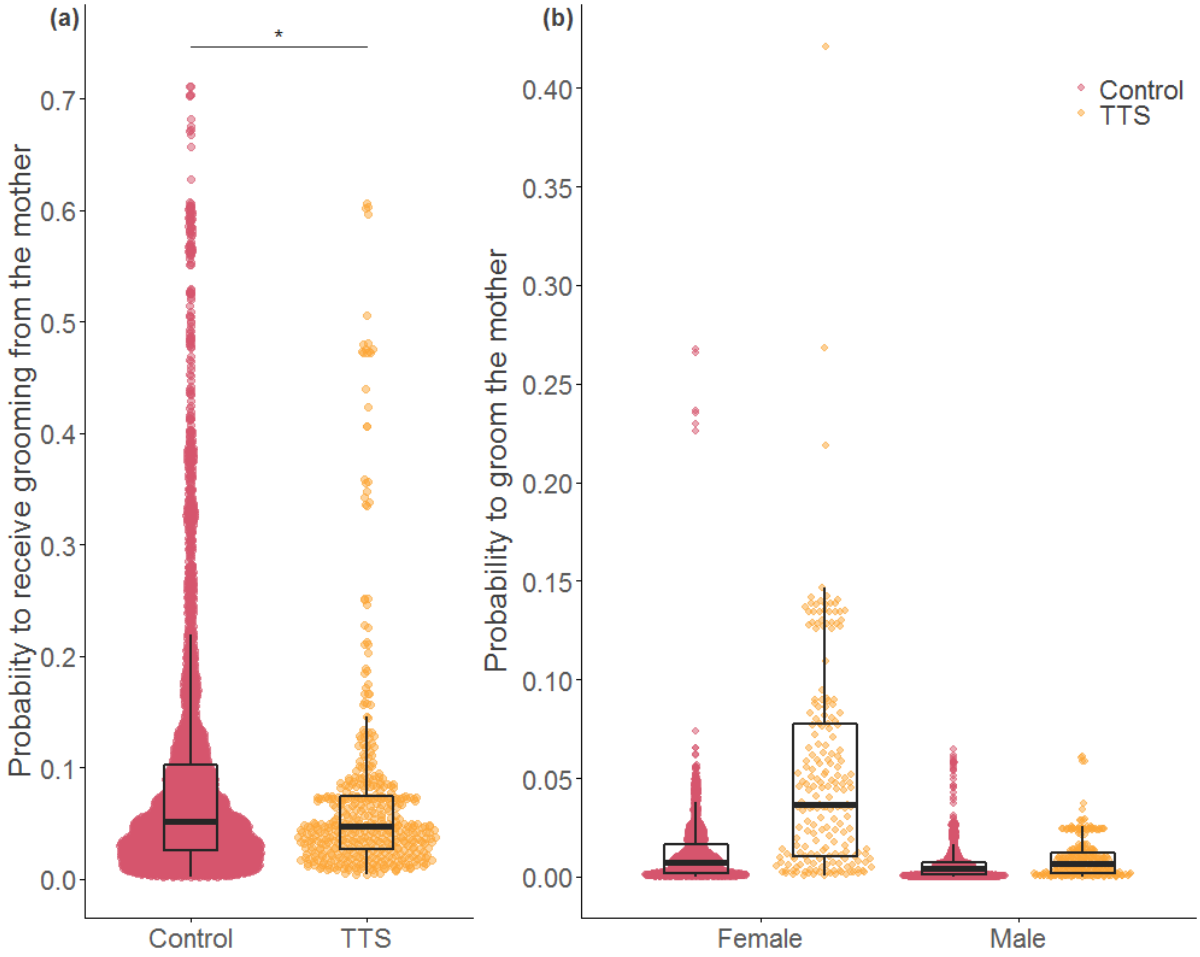
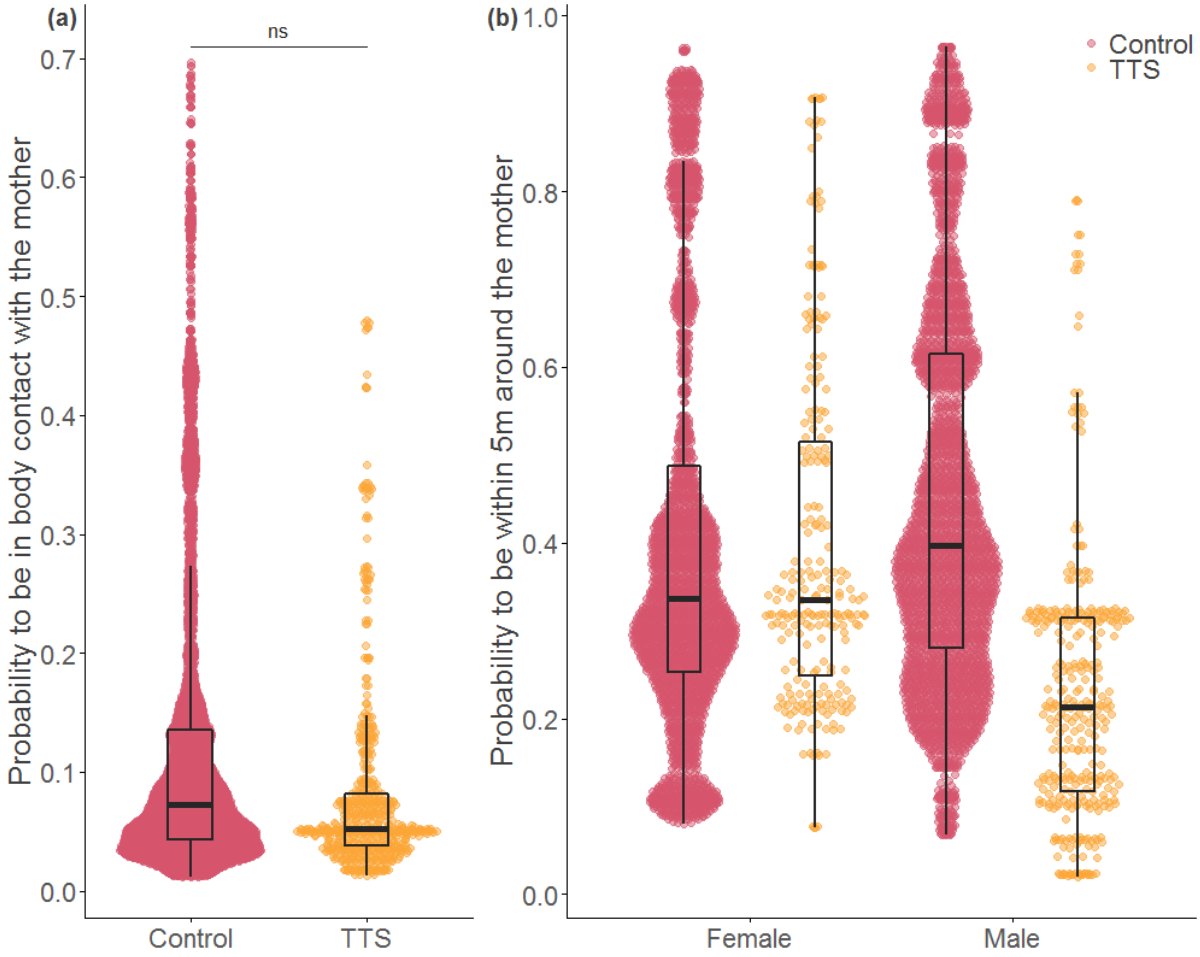


*Figure 5: Influence of the birth of the younger sibling on mother-juvenile proximity. In all panels, "TTS" refers to juveniles who recently experienced the birth of a younger sibling and "Control" those who did not. (a) Predicted probability to be in body contact with the mother depending on the sibling status during a scan observation. (b) Predicted probability to be within 5m around the mother depending on the sibling status and focal juvenile's sex (females on the left side of the graph, males on the right). Dots are fitted values from the models, and boxplots show the median of the distribution of the fitted values (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively) and the whiskers include a maximum of 1.5 times the interquartile range. The effect of the predictor "Sibling status" and the associated p-values are shown. "ns": not significant (p>0.05), *: p<0.05, **: p<0.01, ***: p<0.001.*



Chapter 4: Sibling competition over maternal attention in wild baboons

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SUMMARY

The behavioural manifestations of sibling rivalry in children, as well as their psychological and emotional underpinnings, have attracted much interest (Brody, 1998; Pollet and Hoben, 2011; Salmon and Hehman, 2014; Schlomer et al., 2011; Volling et al., 2010). Children often try to disrupt affiliative interactions between their parents and siblings, a behaviour which is typically interpreted as the expression of jealousy, and intensifies between same-sex and close-in-age siblings, as well as among those who receive differential maternal treatment. In non-humans, studies of sibling competition have mostly focused on conflicts over provisioning in broods or litters (Hudson and Trillmich, 2008; Roulin and Dreiss, 2012), and little is known on sibling interactions in long-lived species where, as in humans, mothers produce one young at a time but maintain long-lasting bonds with grown-up offspring (but see Grebe et al., 2022). Here we examine the context, targets, and function of sibling interferences in mother-offspring affiliative interactions in wild chacma baboons (*Papio ursinus*). First, we found that such interventions typically occur in contexts expected to elicit sibling competition, being 10 times more likely within than outside the family, and most frequent when the mother is grooming a sibling, instead of resting. Second, offspring preferentially target same-sex and younger siblings, as well as those receiving more maternal grooming within the sibship, thus largely echoing patterns observed in children. Finally, interferences are largely unsuccessful at granting access to maternal grooming for the interferers, and those offspring who interfere most are the least successful at obtaining maternal grooming. Instead of strategic attempts to secure more maternal grooming, such interferences may thus reflect spontaneous emotional reactions to an affiliative interaction witnessed between the mother and a sibling. Our study shows that baboon siblings can compete far beyond dependency and over other maternal resources than food, thus filling a critical gap to understand sibling rivalry through an evolutionary lens. It further sets an original and relevant context to study the development of complex emotions like jealousy in non-humans.

RESULTS

Sibling competition is widespread in both humans and non-human animals, and can impact individual development and fitness (Hudson and Trillmich, 2008; Nitsch et al., 2013; Pollet

and Hoben, 2011; Roulin and Dreiss, 2012; Stockley and Parker, 2002). Behavioural ecologists have mainly focused on brood- or litter-rearing species where several same-age, dependent siblings share parental provisioning (Drummond, 2006; Roulin and Dreiss, 2012). In these species, sibling competition can lead to death (O'Connor, 1978), but generally ceases when offspring reach nutritional independence (Mock and Parker, 1998). In contrast, in humans, mothers rarely breastfeed more than one offspring at a time, but typically care for several siblings of different ages (Schlomer et al., 2011; Sear, 2011). Sibling conflicts can start at the birth of a new sibling, continue during childhood and extend into adulthood (Pollet and Hoben, 2011; Volling et al., 2010). On top of parental provisioning, children may also compete over parental attention and affiliation (Schlomer et al., 2011) by disrupting interactions between their parents and siblings (Hart et al., 2004; Miller et al., 2000; Teti and Ablard, 1989; Volling et al., 2002). The success of such interventions at re-directing attention and affiliation is rarely evaluated, and such interferences are typically interpreted as emotional reactions of jealousy towards the bond linking their parents and siblings. In human families, the intensity of sibling competition peaks when genetic relatedness is low, when sibships are large, among same-sex and close-in-age siblings, and when they feel that their parents treat them differently (Brody, 1998; Hart, 2010a; Lawson and Mace, 2009; Salmon and Hehman, 2015, 2021; Volling et al., 2010). Similar patterns have never been explored in non-humans.

Here, we investigated the form and function of competitive interactions between siblings in wild chacma baboons (*Papio ursinus*) – a monotocous, social primate. In particular, we examined siblings' interferences in mother-offspring affiliative interactions in order to test whether these interferences represent sibling competition, and if they prove successful at attracting maternal affiliation. We further explored variation in sibling traits that may modulate the frequency of such interferences. Chacma baboons live in matrilineal societies, where females are philopatric and males disperse around puberty (Cheney et al., 2004; Engh et al., 2006). Females produce one offspring every two years on average, and weaning occurs during the second year of life (Dezeure et al., 2021a). Like humans, offspring have a long developmental period, and form strong, long-lasting bonds with their mother (Silk et al., 2010), often characterized by preferential grooming relationships. We collected data on siblings' interferences in mother-offspring grooming sessions on 16 families and 49 siblings aged 0 to 9 years (median = 3.89 years-old, range = 0.09-8.75) still co-residing with their

mother (median family size = 3 offspring, range = 2-5). We considered an interference any behaviour that could potentially impact the grooming interaction, including aggression, affiliation and close proximity (Mielke et al., 2021) (see STAR Methods). In primates, grooming is a primary affiliative behaviour, through which individuals develop and maintain social bonds (Silk et al., 2006b), which can further translate into fitness benefits (Campos et al., 2020; Silk et al., 2003). Here, we first examined the contexts of sibling interferences in maternal grooming, to test whether they are compatible with sibling rivalry. Second, we examined the traits of the siblings that are most targeted by interferences within sibships, rooting our predictions in psychological observations made on children. Finally, we tested two hypotheses regarding the function of sibling interferences in maternal grooming proposing that interferences aim at gaining access to maternal grooming, or alternatively that they aim at disrupting affiliation witnessed between parents and siblings, as expected if they are emotionally driven by jealousy.

(1) In which contexts do offspring interfere most in maternal grooming sessions?

If interferences in maternal grooming reflect sibling rivalry, we expect them to occur within, rather than between families. We first investigated whether individuals interfere more frequently in grooming bouts involving maternal relatives than in those involving unrelated individuals. We found that offspring interfere in 12.35% of grooming within their family (mean probability to interfere ± SD = 0.12 ± 0.15) while they interfered in 1.43% grooming in other families (mean probability to interfere ± SD = 0.01 ± 0.01), suggesting that interferences in mother-offspring grooming interactions are a family phenomenon.

If interferences in maternal grooming are a manifestation of sibling competition, we further expect them to be more frequent when the mother affiliates with a sibling rather than when she rests on her own. Using 1330 observations on maternal grooming (*N* = 698 observations) and resting mothers (*N* = 632) and a binomial Generalized Linear Mixed Model (GLMM, model 1; STAR Methods), we first tested whether offspring preferentially interfere when their mother is resting compared to when she is already engaged in a grooming session with a sibling. We found that offspring interfered more often when the mother was engaged

in a grooming session with one of their sibling than when she was resting (Table 1, Fig. 1), although this difference progressively faded away as offspring grew older.

(2) Which siblings are the main targets of interferences?

Next, if interferences reflect sibling competition, we expect them to specifically peak in sibling dyads experiencing more intense competition, namely, between same-sex, closer-in-age siblings, and when parents treat them differentially, in line with patterns observed in children. To measure maternal differential treatment in chacma baboons, we computed a "*Favouritism Index*" (*FI*) using maternal grooming allocation among offspring (see STAR Methods). Offspring individual *FI* value represents how much maternal grooming it receives compared to what it could expect based on its sibship size. Differential treatment within a sibling dyad thus represents the difference between the sibling grooming and the sibling interfering *FI* values. Using 698 observations on maternal grooming (binomial GLMM, model 2; see STAR Methods), we found that offspring interfered preferentially against same-sex siblings, especially among dyads of male siblings (rate of interference per observation (mean ± se): male (interferer)-male (sibling) dyads = 0.08 ± 0.39, female-female = 0.04 ± 0.32, female-male = 0.02 ± 0.41, male-female = 0.01 ± 0.41, Table 2, Fig. 2.a), and younger siblings (0.04 ± 0.31, i.e. 0.5 interference *per* hour) compared to older siblings (0.02 ± 0.44, i.e. 0.24 interference *per* hour, Table 2, Fig 2.b). Offspring also interfered preferentially against siblings which receive more maternal grooming than themselves (mean ± se = 0.02 ± 0.31 against a sibling equally favoured and 0.04 ± 0.34 against a sibling groomed 1.5 times more than the interferer; Table 2, Fig. 2.c). Age difference did not influence the probability to interfere (Table 2).

(3) Do offspring interfere to gain access to maternal grooming?

If offspring interrupt grooming sessions between their mother and their sibling in order to re-direct grooming towards themselves, we expect them to interfere more often in contexts where they are more likely to succeed in such re-direction. Nevertheless, interferers' chances to gain access to maternal grooming were not higher when their mother was grooming with a sibling than when she was resting (*N* = 877 interferences, model 3, Table 3, mean success probability ± se = 0.13 ± 0.31 during a resting, 0.10 ± 0.35 during a grooming).

Second, we expect more interferences from those juveniles who are regularly successful at gaining access to maternal grooming following an interference than from those who are rarely successful. Using a binomial GLMM (model 4, *N* = 501 interferences), we found that offspring were more successful at disrupting maternal grooming when they grew older (Table 4.a, Fig. 3.a). However, offspring's probability to interfere in their siblings' maternal grooming was highest for younger offspring, drastically decreasing with age between 0 and 4 years old, and stabilizing around 5% after 4 years old (binomial GLMM, model 5, Table 4.b, Fig 3.b), meaning that offspring which interfered the most, the youngest ones, were the least successful to disrupt a maternal grooming. Offspring sex or *FI* value did not influence their chances of success or their probability to interfere (Table 4.a, 4.b).

DISCUSSION

We showed that offspring interferences occur preferentially in contexts expected to trigger sibling competition, being most frequent within the family, and when the mother is grooming with a sibling, rather than when she is on her own. Interferences in mother-offspring grooming interactions were most frequent when the grooming involved a same-sex, younger sibling, and one more favoured by maternal grooming. Finally, offspring were generally unlikely to gain access to maternal grooming by interfering. Our results extend our understanding of sibling competition in primates in several ways.

First, our results showed that different-age siblings compete over access to their mother in chacma baboons, and keep doing so as long as they live in the same group as their mother. In such species, offspring typically keep benefitting from post-weaning maternal care – such as protection against predators and other risks, facilitated access to food, or social benefits such as grooming, support in conflicts or information transfer (Clutton-Brock, 1991; Crockford et al., 2020; van Noordwijk, 2012; Zipple et al., 2019) – which potentially improve their fitness (Andres et al., 2013; Crockford et al., 2020; Foster et al., 2012; Holand et al., 2012; Samuni et al., 2020; Stanton et al., 2020), but whether such resources may be the stake of sibling competition has never been studied. In our study, competing to access the mother may allow siblings to maintain a strong bond with their mother, which is likely associated with a range of health and social benefits (Silk, 2007; van Noordwijk, 2012). Specifically, in baboon societies, mothers transmit their social rank to their daughters (Cheney et al., 2004), as well

as social capital to both immature daughters and sons, mostly by supporting them during conflicts with groupmates (Silk, 2009). Mother-offspring bonds may vary in intensity among grown-up individuals, explaining why siblings could compete to maintain the strongest possible bond with their mother, a behaviour which is likely prevalent in species that share long-lasting maternal bonds.

Second, our finding that maternal differential treatment influences offspring interferences mirrors studies on humans that showed that children perceiving themselves as disfavoured by their parents reported higher levels of conflicts and more distant relationships with their siblings (Jensen et al., 2013; Kowal and Kramer, 1997; Loeser et al., 2016; Thompson and Halberstadt, 2008). Although our measure of maternal favouritism only captured one component of differential treatment (i.e. differential grooming) compared to human studies (which also consider differential negative and controlling behaviours, for instance, see e.g. Brody et al., 1992), our results suggest that offspring perceive and react to differential maternal grooming allocation. Previous studies in several species already reported that primates pay specific attention to patterns of affiliations from their close social partners and kin (Schino and Sciarretta, 2016; Schülke et al., 2020), and assess third-parties relationship strength (e.g. Webb et al., 2020), but our findings suggest that chacma baboons may be able to compare their own affiliative relationship with a social partner to a third-party's relationship with this same partner, and react accordingly. Whether maternal differential treatment can impact other aspects of siblings' relationships in chacma baboons, as in humans (e.g. Brody, 1998; Volling et al., 2010), remains to be tested.

Third, the fact that offspring interferences are generally unsuccessful at granting access to maternal grooming, and that those offspring interfering the most are the least successful, suggests that interferences may reflect spontaneous emotional reactions to affiliations witnessed between the mother and a sibling, rather than strategic attempts to secure maternal grooming. Similarly, in humans, children display jealous reactions when they lose maternal attention exclusivity to a rival sibling, characterized by attempts to distract their mother and/or their sibling from their activity, and to reclaim maternal attention (Hart et al., 2004; Miller et al., 2000; Mize and Jones, 2012; Teti and Ablard, 1989; Volling et al., 2002). Moreover, siblings' interferences in chacma baboons strikingly mirror patterns of sibling rivalry reported in humans. Interferences were more common between same-sex siblings,

and especially between males, which is consistent with findings in humans (Salmon and Hehman, 2015, 2014), and suggests that same-sex siblings seem to be perceived as larger competitive threats in both humans and non-human primates. Siblings were also twice as likely to interfere against a younger than an older sibling, which likely reflects the fact that younger siblings usually monopolise more maternal care and attention (Clutton-Brock, 1991). It may also reflect their lower competitive abilities, as it may be more risky to interfere against older siblings that are physically stronger and may retaliate against the interferer. Surprisingly, we could not detect any effect of sibling age difference on competitive interferences, which contradicts theoretical expectations (Trivers, 1974) as well as findings on humans (Salmon and Hehman, 2021).

Lastly, the commonalities observed between patterns of sibling rivalry described in baboons and children suggest that they may similarly be driven by jealousy at a proximate level. Jealousy is a complex social emotion that arises when a valuable bond is threatened by a third-party (Panksepp, 2010; Parrott and Smith, 1993; Volling et al., 2002), and can prompt attempts to disrupt the interaction and regain the attention of the valued social partner (Hart, 2010b). Ultimately, jealousy is an emotional response aiming to protect a social relationship against potential intruders (Nesse, 1990), and is therefore expected in species were social bonds influence fitness – such as the mother-offspring bond in primates (Silk et al., 2006b, 2006a). In humans, jealousy is an intrinsic part of sibling relationships (Parrott, 1991; Volling et al., 2010), and in non-human primates, several studies investigating grooming interferences reported more frequent interferences when the grooming involved a kin or a close social partner, however only alluded to the potential role of jealousy in mediating these behaviours (Mielke et al., 2021, 2017, but see Webb et al., 2020). The occurrence of jealousy in non-human animals is still highly debated (e.g. Bekoff, 2010, 2000; De Waal, 2019), but has mostly been investigated in human-pet interactions, which yielded contrasted results (Abdai et al., 2018; Cook et al., 2018; Harris and Prouvost, 2014; Prato-Previde et al., 2018a, 2018b). Studying jealousy in relevant social contexts and relationships that could have driven its evolution in non-human animals, such as mother-offspring relationships, would provide a better framework to uncover the existence of complex social emotions such as jealousy in non-human animals (van Kleef, 2018; Webb and de Waal, 2018). Given how poorly our results support the maternal grooming hypothesis compared to the

emotional reaction one, and the similarities in the form and context of sibling competition in baboon and human sibships, it thus seems parsimonious to propose that competitive interferences may represent the expression of jealous behavior in chacma baboons (de Waal, 1999, 2011).

To conclude, our results show that sibling competition occurs far beyond maternal dependency, and most likely over maternal attention, in wild chacma baboons, which extends our understanding of the determinants and dynamics of family conflicts in non-human animals. The striking similarity of the context and forms of sibling interactions in young baboons and humans point out to the expression of jealous behaviours, adding to the growing debate on the expression of complex emotions in other animals, and offering a novel, relevant context to study emotional development in young animals.

STAR METHODS

Resource availability

Lead contact

Further information and requests for resources and protocols should be directed to and will be fulfilled by the lead contact, Axelle Delaunay (axelle.delaunay@proton.me).

Material availability

This study did not generate new unique reagents.

Data and code availability

All data and codes necessary to analyse them are available on the following repository: XXX. Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

Experimental model and subject details

We studied wild chacma baboons living in Tsaobis Nature Park, on the edge of the Namib Desert (22°23’ S, 15°44’ E). We collected data on two well-habituated troops (J and L,

habituated since 2005 and 2000, respectively) between August and December 2021. The groups were followed on foot every day from dawn to dusk by trained observers. All individuals, including infants, are individually recognizable thanks to small ear-notches performed during captures and/or other distinctive features (Huchard et al., 2013). We included every maternal family (i.e. a mother and all her offspring) with at least 2 offspring living in the group during the study (N = 8 families in L troop, N = 8 families in J troop). Family size ranged from 2 to 5 offspring (N = 5 families with 2 offspring, N = 7 with 3 offspring, N = 2 with 4 offspring and N = 2 families with 5 offspring). In total, we included 49 offspring in this study, aged from 6 days old to 8.9 year-old (median = 4.10 year-old). Although adult daughters were included, adult and sub adult sons (8 year-old and older) still living in their natal group were excluded from this study because, unlike adult daughters, it is unclear how much they still contribute to family dynamics in this matrilineal society (Cheney et al., 2004).

Method details

Individual data

Female dominance rank was established separately for each group using *ad libitum* observations of approach-avoidance and agonistic interactions: displacements, supplants, attacks, chases and threats (Huchard et al., 2010). We computed a linear hierarchy using corrected David Scores (David, 1987; Gammell et al., 2003), using the 'DS' function from the EloRating package (Neumann and Kulik, 2020), and then transformed it into a proportional hierarchy with relative ranks to control for group size. Each female was thus assigned one rank ranging from 0 (low-ranking) to 1 (high-ranking).

Individual birth dates were assessed with certainty when observers were present in the field during the birth, or estimated using a combination of two methods (Dezeure et al., 2021b), respectively based on infant developmental transitions in body coloration using a standardised protocol, and on mother's reproductive history, and especially information on her conception date.

Age difference was defined as the number of days between the births of two consecutive offspring in the current family. If an offspring died before the start of the study,

we therefore considered its two adjacent siblings to be consecutive and calculated their age difference accordingly.

Behavioural observations

We conducted 5-minutes focal observations on i) mother-offspring dyads when mothers were engaged in a grooming session with one of their offspring (hereafter 'grooming' observation) or ii) resting mothers (hereafter 'resting' observation). We recorded all behaviours (hereafter, 'interferences') from any third-party individual (hereafter, 'interferer') that could affect the grooming dyad or the mother (in the case of a resting observation), including aggressive behaviours (attack, chase, bite, push, slap, threat, displacement, supplant), affiliative behaviours (body contact, come-here faces, grunt, jumping on one groomer, lipsmacks, play, presenting, touch), tantrum behaviours (gecks, complaint grunt, other screams), maternal care solicitations (soliciting access to the nipple, soliciting grooming, suckling, starting a triadic grooming session with the groomers), and proximity behaviours (approaching or passing by within 1m from the dyad). Interferers' identity was systematically recorded and, if assignable, we also reported toward which groomer the interference was directed. In grooming observations, we considered 3 potential outcomes for interferences: i) the grooming continues, ii) the grooming is interrupted but the interferer does not get access to one of the groomers, and iii) the grooming is interrupted and the interferer starts grooming with one of the previous groomers. In the last case, we recorded the identity of the new grooming partners. In addition, we monitored any changes in the direction of the grooming between the groomers, and reported who initiates the end of the grooming. Finally, in both observations, we monitored continuously the presence of all offspring within a perimeter of 10m around the grooming dyad or the mother. If the mother engaged in another activity before the end of the five minutes, observers stopped the observation. Mother-offspring dyads or mothers were sampled no more than once every half hour. In total, we collected 89.29 hours of observations across 1330 observations in 16 families, including 45.84 hours across 698 'grooming' observations (mean ± SD = 2.87 ± 1.16 hours and 43.63 ± 18.80 observations per family), and 43.46 hours across 632 'resting' observations (mean ± SD = 2.72 ± 0.68 hours and 39.50 ± 9.19 observations per family).

In addition, we recorded all occurrence of grooming sessions *ad libitum* between mothers and offspring throughout the day. Grooming bouts involving the same mother-offspring dyad were discarded if they occurred within 30 minutes from a previous bout to ensure independence between observations. A total of 1995 maternal grooming sessions of known direction were collected.

Quantification and statistical analysis

Calculation of the Favouritism Index

In order to calculate the level of maternal favouritism for each offspring, we computed a 'Favouritism Index' using *ad libitum* grooming data to increase our sample size of grooming interactions. For each mother, we calculated the total number of grooming events allocated to each of her offspring. We then computed her pattern of grooming allocation among offspring, i.e. which percentage of these maternal grooming each offspring received. We then computed a Favouritism Index (FI) for each offspring as follow:

$$FI = \frac{\%Grec - \%Gexp}{\%Gexp}$$

Where *%Grec* represents the observed percentage of maternal grooming received by one offspring, and *%Gexp* represents the expected percentage of maternal grooming one offspring should receive if the mother was allocating her grooming equally between all her offspring, independently of offspring age (*%Gexp* = 1/number of offspring in the family). *FI* therefore represents the extent to which each offspring is more or less favoured by its mother compared to what it should receive given its family size. *FI* ranged from -1 (when offspring were never groomed by their mother) to +1.76 (meaning that these offspring experienced an increase of maternal grooming of 176% compared to what they would be expected to receive). Note that FI does not account for offspring age: our aim here is to measure the absolute maternal grooming allocation as offspring experience it, as we cannot know whether offspring control for their own age (and their sibling age) in the way they perceive maternal grooming allocation.

(1) In which context do offspring interfere most in maternal grooming sessions?

To test if offspring interfere more frequently when their mother is engaged in a grooming session with one of their sibling than when she is resting on her own, we considered each maternal grooming and resting observations (*N* = 1330) and checked whether each offspring interfered at least once (yes: 1; no: 0). For grooming observations (*N* = 698), we considered the occurrence of interference from any offspring except the one engaged in grooming, and for resting observations (*N* = 632), we considered the occurrence of interference from any offspring. We then modelled the probability of interference with a binomial Generalized Linear Mixed Model (GLMM, model 1) and tested the influence of maternal activity (grooming *vs.* resting). We included interferer's age (in years) and sex, and the corresponding interaction term with maternal activity as grooming relationship with the mother typically differs between sexes and changes with age, which could induce differential motivation in gaining access to maternal grooming. We further included maternal dominance rank, troop identity and observation duration (in seconds) in order to account for a lower probability of observing an interference when an observation was shortened as controls. Finally, we fitted a nested random effect of the interferer identity within its mother identity, and a random effect of the observation identity.

(2) Which siblings are the main targets of interferences?

To investigate against which siblings offspring interfere the most, we considered each maternal grooming observation (*N* = 698) and modelled the probability to interfere by a given offspring (yes: 1; no: 0) with a binomial GLMM (model 2). We tested the influence of four sibling dyad's traits: sex combination (interferer's sex – sex of the sibling involved in the grooming), age difference (in days), birth order of the sibling engaged in the grooming (older/younger than the interferer), and the difference between sibling's and interferer's *FI*s (if positive, the interferer is less favoured by maternal grooming allocation). We further included the interferer's age with a quadratic function (in years), the mother's dominance rank, troop identity and observation duration (in seconds) as controls. Finally, we included a nested random effect of offspring identity within mother identity, and a random effect of observation identity. Our analysis, which investigated variations in the probability to interfere *per time unit* in a given bout, controlled for the fact that differential maternal treatment, by allocating more grooming to a particular siblings generates more opportunities to interfere against the 'favourite' sibling.

(3) Do offspring interfere to gain access to maternal grooming?

To test if offspring interfere more frequently in contexts when they are more likely to succeed in re-directing maternal grooming towards themselves, we considered each interference performed by any offspring when its mother was resting or grooming a sibling (*N* = 877), and checked whether this interference was successful (yes: 1; no: 0). We considered an interference to be successful if it allows the offspring to groom with its mother, independently of the grooming direction, and of the exclusivity of the grooming (i.e. if an offspring interfere in a grooming between its mother and a sibling and it results in a triadic grooming interaction where the interferer grooms with its mother and not its sibling, we considered the interference to be successful). We modelled interference's success with a binomial GLMM (model 3) and tested the influence of maternal activity (grooming *vs.* resting), interferer's age (with a third degree polynomial function) and sex. We included the two interaction terms between maternal activity and interferer's age and sex, and controlled for maternal rank and troop identity. We fitted a nested random effect of the interferer identity within its mother identity, and a random effect of the observation identity.

Second, to test if offspring who interfere more frequently in grooming sessions between their mother and their sibling are those who are regularly successful at gaining access to maternal grooming, we ran two different models. We first examined the probability of success of a given interference depending on individual's traits. Out of 501 interferences between siblings, 65 successfully stopped the grooming without the interferer gaining access to one of the previous groomers (i.e. the mother or the sibling) and 30 successfully stopped the grooming and gave the interferer access to one of the previous groomers. Due to this small sample size, we pooled the two types of outcomes, and considered an interference successful if it stops the grooming, regardless of giving access to one of the groomers. For each interference, we modelled the probability of success with a binomial GLMM (model 4) and tested the influence of three traits: interferer's age (in years), sex and *FI* value. We further controlled for maternal rank and troop identity, and fitted a nested random effect of the interferer identity within its mother identity, and a random effect of the observation identity. Then, we modelled the probability for each offspring to interfere in a grooming between their mother and any of their sibling with a binomial GLMM (model 5). Fixed effects comprised

offspring's age (in years) with a quadratic function, sex, and *FI* value. We further controlled by maternal rank and troop identity. Mother identity was included as a random effect.

All models used in this study, along with sample size, are summarized in Table S1.

Statistical methods

All statistical analyses were conducted in R Studio version 4.0.2. GLMMs were run using the 'glmer' function from the lme4 package (Bates et al., 2015). When we obtained a singular fit, we confirmed the results by running the same models with a Bayesian approach, using the function 'bglmer' from the blme package (Chung et al., 2013). All quantitative variables were z-transformed (mean = 0, SD = 1) using the 'scale' function from the car package (Fox and Weisberg, 2019) in order to facilitate model convergence and to compare effect sizes across estimates (Harrison et al., 2018). To diagnose the presence of multicollinearities, we computed the Variance Inflation Factor (VIF) for each predictor in each model using the 'vif' function from the car package (Fox and Weisberg, 2019). These were lower than 2 in all cases. The significance of fixed factors was tested using the Likelihood Ratio Test (LRT) and the associated p-values computed by the 'drop1' function. We further calculated the 95% Wald confidence intervals. To test for pairwise differences between multiple levels of a categorical variable (e.g. "sex combination"), we changed the reference category sequentially (Pinheiro and Bates, 2006). To validate models, we checked the distribution of the residuals using the function 'simulateResiduals' from the DHARMa package (Hartig and Lohse, 2021).

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AUTHOR CONTRIBUTIONS

Conceptualization, A.D., E.H. and M.J.E.C; Methodology, A.D. and E.H.; Investigation, A.D., V.R., R.E. and P.K.; Formal Analysis, A.D.; Writing – Original Draft, A.D., E.H. and M.J.E.C; Writing – Review & Editing, all authors; Project Administration, A.H., A.C. and G.C.; Funding Acquisition, E.H. and A.D.

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TABLES

Table 12: Younger offspring interfere more frequently when the mother is grooming.one of their sibling. Results of the mixed model analysing the probability for an offspring to interfere in its mother's activity during a focal observation depending on the nature of the activity (grooming with a sibling vs. resting, model 1). Estimates, confidence intervals, LRT statistics and p-values were estimated using 1330 focal observations (N = 698 observations on grooming mothers, N = 632 on resting mothers) across 16 families and 49 offspring. Offspring identity nested in mother identity, and focal observation identity were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values for the simple predictors are not shown.

Response variable: Probability to interfere in maternal activities (0/1)					
Fixed effect	Level	Estimate	CI 95%	LRT	P-value
Maternal activity	Resting (Ref : Grooming)	-0.288	[-0.592;0.016]	-	-
Interferer's age	Age	-53.883	[-68.069;-39.698]	**-**	**-**
	Age^2	27.145	[-13.888;40.402]		
Interferer's sex	Male (Ref: female)	-0.064	[-0.448;0.319]	0.111	0.739
Maternal rank		0.164	[-0.084;0.411]	1.458	0.227
Troop	L (Ref: J)	-0.020	[-0.555;0.515]	0.005	0.941
Observation duration		-0.009	[-0.142;0.125]	0.016	0.900
Maternal activity * Interferer's age	Resting (Ref : Grooming); Age	**23.291**	**[7.144;39.438]**	**19.260**	**<0.001**

Maternal activity * Interferer's age	Resting (Ref : Grooming); Age²	**-19.599**	**[-35.681;-3.516]**		

Table 13: Offspring interfere more against younger, same-sex and more favoured siblings. Results of the mixed model analysing offspring's probability to interfere in a grooming between its mother and one sibling, according to the traits of the sibling dyad (model 2). Estimates, confidence intervals, LRT and p-values were estimated using 698 focal observations on mother-offspring grooming across 16 families and 49 offspring. Offspring identity nested in mother identity, and focal observation identity were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values for the simple predictors are not shown.

Response variable: Probability to interfere in a grooming between the mother and a sibling (0/1)					
Fixed effect	Level	Estimate	CI 95%	LRT	P-value
Sex combination (Interferer's sex - sex of the sibling involved in the grooming	FM (Ref: FF)	-0.598	[-1.227;0.0.30]	**17.883**	**<0.001**
	MF (Ref : FF)	**-0.998**	**[-1.696;-0.299]**		
	MM (Ref : FF)	0.751	[-0.056;1.557]		
	MF (Ref: FM)	-0.399	[-1.128;0.330]		
	MM (Ref: FM)	**1.349**	**[0.475;2.223]**		
	MM (Ref: MF)	**1.748**	**[0.809;2.687]**		
Age difference		-0.056	[-0.296;0.184	-0.018	1.00
Interferer's birth order	Younger (Ref: older)	**0.884**	**[0.040;1.728]**	**4.407**	**0.036**
Favouritism Index difference		**0.301**	**[0.002;0.599]**	**4.701**	**0.030**

Interferer's age	Age	**-67.155**	**[-86.584;-47.729]**	**64.927**	**<0.001**
	Age^2	**28.341**	**[16.182;40.501]**		
Maternal rank		**0.361**	**[0.008;0.713]**	**4.672**	**0.031**
Troop	L (Ref: J)	**0.921**	**[0.122;1.721]**	**5.741**	**0.017**
Observation duration		**0.233**	**[0.045;0.422]**	**5.975**	**0.015**

Table 14: Interference's success in giving access to maternal grooming is similar in resting and grooming context. Results of the mixed model analysing the probability that an interference successfully allows an offspring to groom with its mother (model 3) depending on maternal activity (resting vs. grooming). Estimates, confidence intervals, LRT statistics and p-values were estimated using 877 interferences across 306 focal observations (N = 494 interferences on maternal grooming, N = 383 on maternal resting) across 16 families and 49 offspring. Offspring identity nested in mother identity, and focal observation identity were included as random effects. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values for the simple predictors are not shown.

Response variable: Interferer's success probability to gain access to the mother (0/1)					
Fixed effect	Level	Estimate	CI 95%	LRT	P-value
Maternal activity	Resting (Ref : Grooming)	0.374	[-0.252;0.999]	0.965	0.326
Interferer's age	Age	**39.815**	**[30.469;49.161]**	**51.284**	**<0.001**
	Age^2	**-14.753**	**[-22.040;-7.466]**		
	Age^3	**12.652**	**[4.927;20.377]**		
Interferer's sex	Male (Ref: female)	-0.185	[-0.829;0.458]	0.493	0.482
Maternal rank		-0.126	[-0.517;0.265]	0.397	0.529
Troop	L (Ref: J)	-0.055	[-0.879;0.770]	0.011	0.916

Table 15: Younger offspring are less successful in disrupting maternal grooming but interfere more frequently. Results of the mixed models analysing (a) offspring's probability to successfully disrupt a maternal grooming (model 4), and (b) offspring's probability to interfere in a grooming between their mother and any of their sibling (model 5). Estimates, confidence intervals, LRT statistics and p-values were estimated using 501 interferences across 180 maternal grooming observations in model 4, and using 49 individuals across 16 families in model 5. Offspring identity nested in mother identity and observation identity were included as random effects in model 4, and mother identity in model 5. For categorical predictors, the reference category is indicated between parentheses. Significant effects are indicated in bold. Whenever an interaction is significant, LRT and p-values for the simple predictors are not shown. Favouritism Index (FI) represents the extent to which each offspring is more or less favoured in terms of grooming by its mother compared to what it should receive given its family size. FI is positive if the offspring receives more maternal grooming than what it could expect.

		(a) Individual's probability to successfully disrupt a maternal grooming				(b) Individual's propensity to interfere in maternal grooming			
Fixed effect	Level	Estimate	CI 95%	LRT	P-value	Estimate	CI 95%	LRT	P-value
Interferer's age	Age	**0.540**	**[0.191;0.889]**	**11.296**	**0.001**	**-7.688**	**[-9.475;-5.901]**	**101.301**	**<0.001**
	Age²	-	-	-	-	**2.662**	**[1.377;3.948]**		
Interferer's sex	Male (Ref: female)	-0.077	[-0.926;0.771]	-0.070	1.000	-0.198	[-0.582;0.186]	0.998	0.318
Interferer's *FI*		-0.060	[-0.475;0.355]	0.171	0.679	-0.232	[-0.502;0.038]	2.675	0.102
Maternal rank		0.072	[-0.384;0.528]	0.244	0.621	0.279	[0.014;0.543]	3.123	0.077
Troop	L (Ref: J)	-0.252	[-1.290;0.786]	0.335	0.563	0.496	[-0.198;1.189]	1.707	0.191

FIGURES

Figure 6: Young offspring interfere more often when the mother is grooming a sibling than when she is resting. Predicted probability to interfere depending on maternal activity (grooming: the mother is grooming with a sibling; resting: the mother is resting on her own) and interferer's age (in years). Dots are fitted values, curves show the predicted linear fit, and shaded areas show 95% confidence intervals from the corresponding mixed model (model 1).

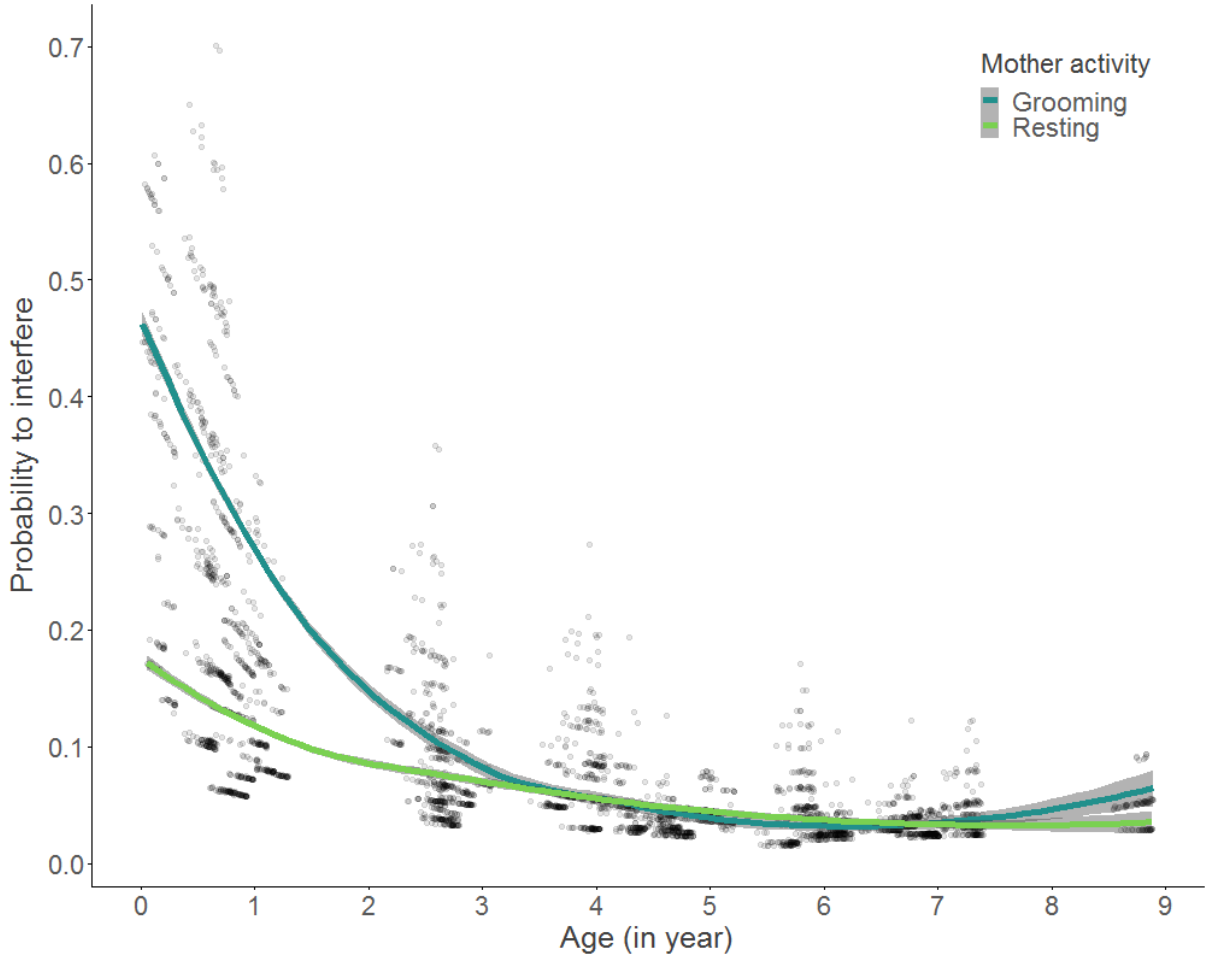


Figure 7: Offspring target specific siblings. Probability to interfere in a grooming between the mother and a sibling according to (a) siblings sex combination (interferer sex-sex of the sibling grooming: FF = female-female, FM = female-male, MF = male-female, MM = male-male); (b) sibling's birth order (older = older than the interferer, younger = younger than the interferer); and (c) difference in Favouritism Index (FI) between the interferer and the sibling grooming with the mother. Positive values indicate that the sibling grooming is more favoured by maternal grooming than the interferer. All panels show the partial residuals of model 2, based on 698 grooming observations. In (a) and (b), boxplots represent the median of the distribution of partial residuals (black horizontal bar), the 25th and 75th quartiles (bottom and top of the boxes, respectively), the lower and upper whiskers include a maximum of 1.5 times the interquartile range, and dots represent outlier points. In (c), dots represents partial residuals, and for graphical purposes, the regression line in blue is the simple linear fit, shaded areas represent the 95% confidence intervals. In (a) and (b), asterisks represent significant differences between the levels of the two categorical fixed effects, sex combination, and sibling birth order, respectively.

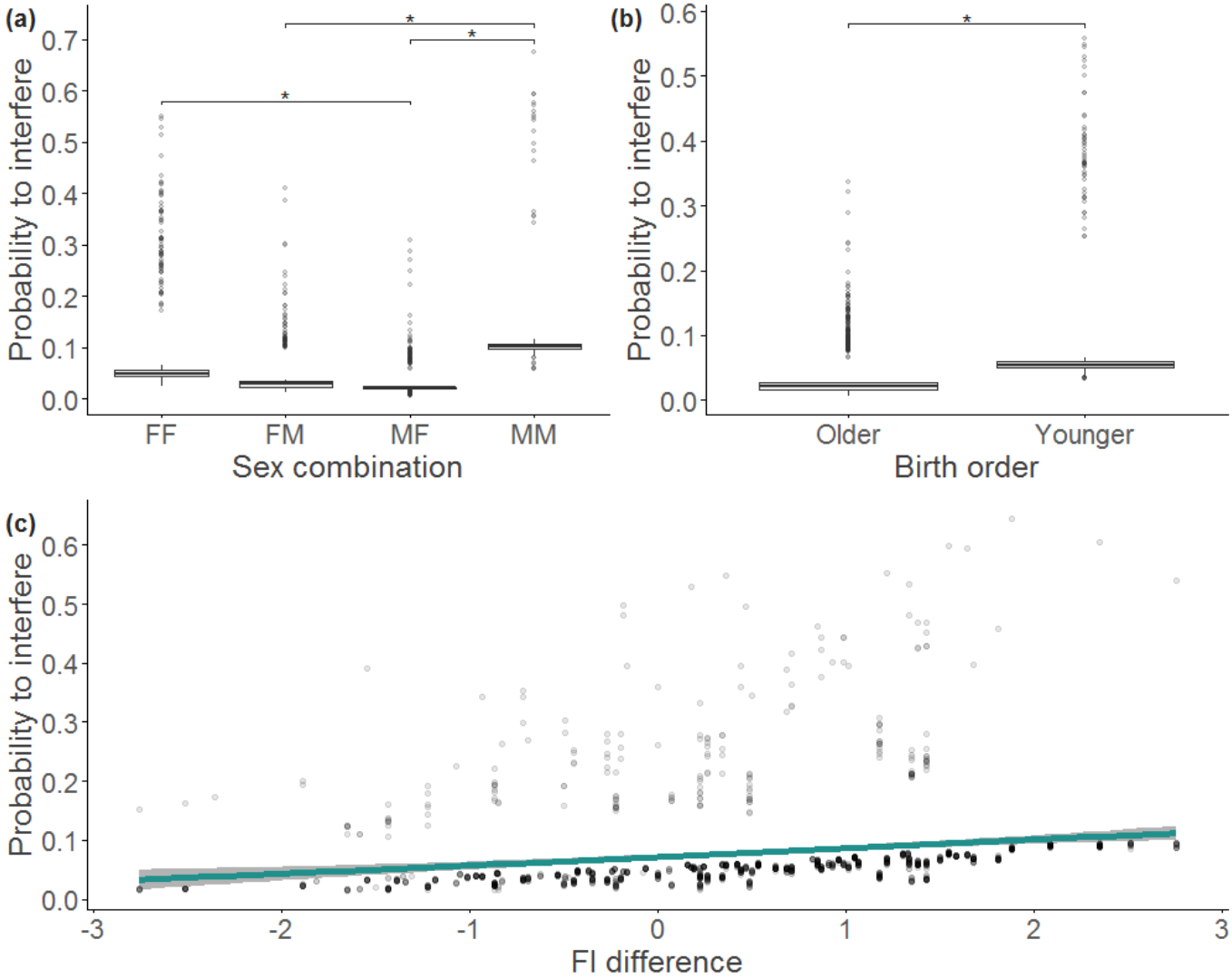
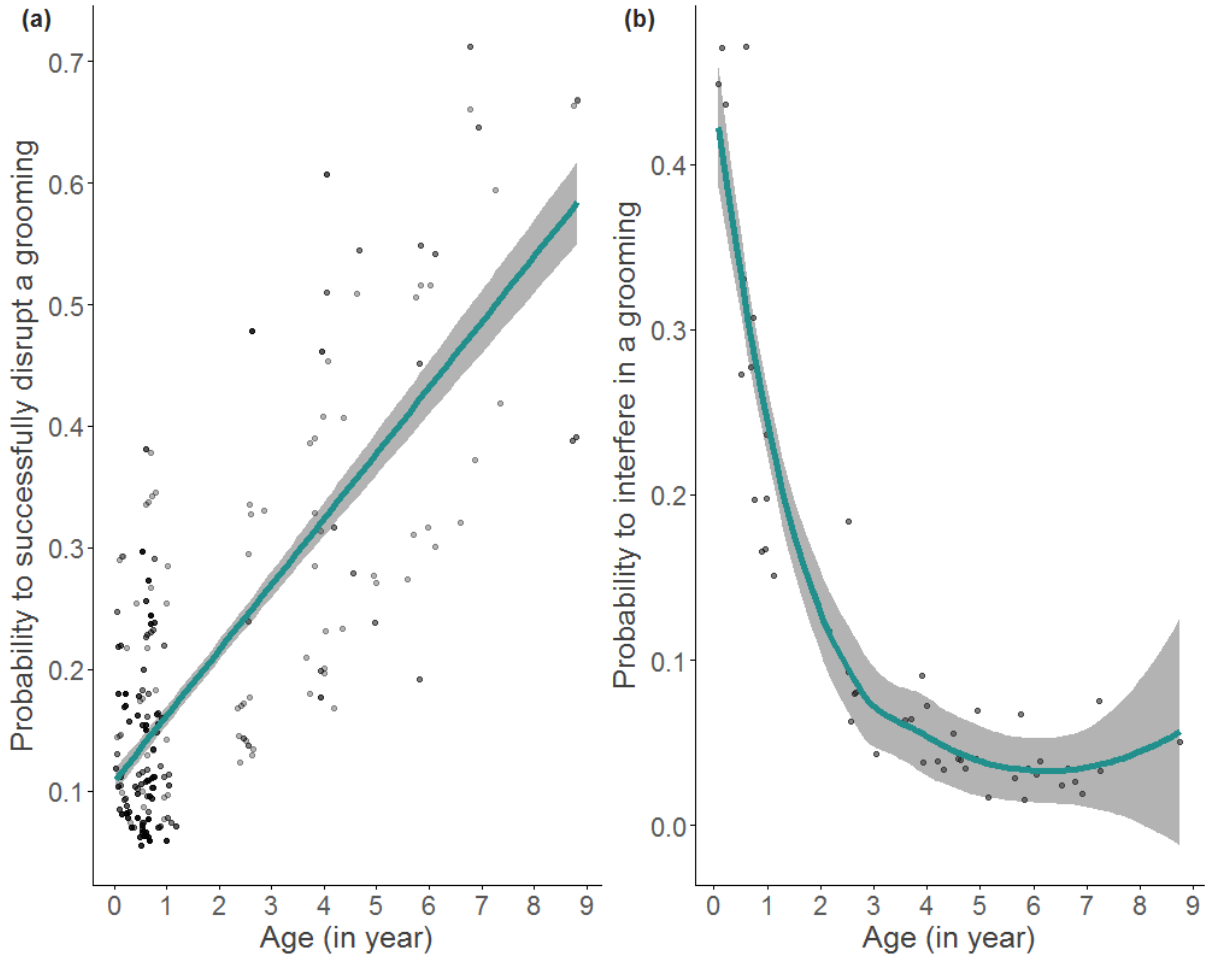


Figure 8: Younger offspring are less successful to again access to maternal grooming but interfere more frequently. Predicted probabilities to (a) successfully disrupt a grooming between the mother and a sibling, and (b) interfere in a grooming between the mother and a sibling as a function of interferer's age (in years). Dots are fitted values, curves show the predicted linear fit, and shaded areas show 95% confidence intervals from the corresponding mixed model (model 4 and 5, respectively).



SUPPLEMENTARY MATERIALS

Table S1: Summary of all the models used in the study, with the corresponding sample sizes.

Model	Response variable	Fixed effect	Random effect	Model type (Sample size)
Model 1	Probability to interfere	Maternal activity; interferer's age^2; interferer's age^2*maternal activity; interferer's sex; interferer's sex*maternal activity; maternal rank; troop; observation duration	Interferer identity nested in mother identity; observation identity	Binomial GLMM (N = 1330)
Model 2	Probability to interfere in a grooming between the mother and a sibling	Sex combination; age difference; birth order; favouritism index difference; interferer's age^2; maternal rank; troop; observation duration	Interferer identity nested in mother identity; observation identity	Binomial GLMM (N = 698)
Model 3	Interference success probability	Maternal activity; interferer's age^3; interferer's age^3*maternal activity; interferer's sex*maternal activity; maternal rank; troop	Interferer identity nested in mother identity; observation identity	Binomial GLMM (N = 877)
Model 4	Interference success probability	Interferer's age; interferer's sex; interferer's *FI*; maternal rank; troop	Interferer identity nested in mother identity; observation identity	Binomial GLMM (N = 501)

Model 5	Individual's propensity to interfere in maternal grooming	Interferer's age ^{2}; interferer's sex; interferer's *FI*; maternal rank; troop	Mother identity	Binomial GLMM (N = 49)

General Discussion

Sibling relationships in long lived mammals have been studied mainly through the lens of kin cooperation. This is puzzling because, although kin should cooperate together more than non-kin, they also often share more resources and, as such, may have more incentives to compete than non-kin. In this thesis, I investigated sibling relationships at various developmental stages and the extent to which siblings compete in two primate species, chacma baboons and mandrills. I further examined different factors that may modulate sibling competition, and tried to identify the different maternal resources at stake. In manuscripts 1 and 2, I focused on an intriguing developmental milestone, the birth of a younger sibling. This period is often considered as a stressful transition for the older sibling and has major theoretical implications regarding sibling competition and parent-offspring conflict. However, it has rarely been studied in wild primates. In manuscript 1, we showed that, although young chacma baboons have already been weaned for several months and don't seem to lose any maternal care when they transition to siblinghood, they solicit their mother more often and appear more distressed than age–matched juveniles with no younger sibling. In manuscript 2, we showed that the birth of a younger sibling in mandrills is generally coupled with weaning and induces an abrupt decrease in all forms of maternal care toward the older sibling. Juveniles show sex-specific reactions but do not show overt signs of conflict with their mother. In manuscript 3, we investigated whether siblings may compete over access to their mother, by competitively interfering in each other's maternal grooming. We showed that grooming interferences occur primarily in contexts expected to elicit sibling competition, and that offspring target preferentially same-sex, younger siblings, and those favoured by the mother. Grooming interferences are generally unsuccessful to gain access to maternal grooming, and offspring interfering the most are the least successful to obtain maternal grooming. These results suggest that grooming interferences may reflect a spontaneous emotional reaction rather than strategic attempts to gain maternal grooming.

In the following discussion, we integrate these results in a broader context to evaluate how they may improve our understanding of intrafamilial conflicts over maternal investment and complex emotions in non-humans. First, we discuss the causes and consequences of sibling rivalry in monotocous mammals in the light of our results. Based on this, we then examine how sibling rivalry may differ in monotocous species from polytocous ones, and the extent to which our findings, overall, may help us to understand the evolutionary origins of

sibling rivalry in humans. Finally, we examine the emotional dimension of sibling competition in primates in the light of jealousy in humans, and discuss how this work may contribute to our understanding of complex emotions in non-human animals.

1. *Causes and consequences of sibling competition in monotocous primates*

1.1.Intrafamilial conflict over maternal investment

Mother-offspring conflict in primates has been mostly studied during early ontogeny, such as the weaning period or around mother's cycle resumption (e.g. Altmann, 1980; Gore, 1986; Maestripieri, 2002; Mandalaywala et al., 2014), with the underlying assumption that conflict would cease once individuals are nutritionally independent and/or the mother starts to care for another offspring. The birth of a younger sibling has thus rarely been studied, especially in wild populations, and has revealed contrasting patterns regarding mother-offspring conflict during this developmental milestone. In free-ranging rhesus macaques, mother-offspring relationship weakens during TTS but this decrease is primarily driven by juveniles themselves, which show little signs of distress (Devinney et al., 2001). In wild bonobos, although juveniles do not experience a decrease in maternal care, TTS induces a five-fold increase in cortisol level immediately after the birth (Behringer et al., 2022). Thus, if the birth of a younger sibling induces a conflict between the mother and the older sibling, it does not translate into behavioural conflict in these two species. In contrast, in humans, children undergoing TTS experience a decrease in maternal care and display more distress and confrontational behaviours with their mother (Dunn et al., 1981; Dunn & Kendrick, 1980; Stewart et al., 1987; Volling, 2012). In chacma baboons, juveniles who recently experienced the birth of a younger sibling solicit their mother more often and show more signs of anxiety than juveniles who did not have a younger sibling yet (*manuscript 1*). Although these reactions are not associated with any quantitative or qualitative changes in maternal behaviour, they suggest a discrepancy between the amount of care and attention provided by the mother, and the amount requested by the juvenile. In particular, juveniles need to solicit their mother more frequently to obtain a level of care similar to the pre-sibling arrival's period. In mandrills, however, the birth of a younger sibling does not induce any detectable signs of conflict with the mother (*manuscript 2*). Our findings, taken together with previous studies, indicate that

mother-offspring conflict may extend after the end of maternal provisioning. However, offspring's reaction to TTS is highly variable across species, which suggest that mother-offspring conflict after nutritional independence may be mediated by species life history and/or ecology. Typically, conflict could be more intense in species showing shorter interbirth intervals relatively to their developmental period (e.g. humans, Jones, 2011), and in harsher environments (e.g. chacma baboons in Tsaobis).

Our understanding of sibling competition between different-age offspring in primates mainly comes from the well-documented negative fitness consequences of short maternal interbirth intervals, a proxy of sibling competition intensity (e.g. Emery Thompson et al., 2016; Lee et al., 2019; Tung et al., 2016). However, the proximate mechanisms (e.g. behavioural, physiological) driving such effects remain unexplored. Evidence of overt behavioural conflict between different-age siblings over maternal care in monotocous mammals is scarce: in Galapagos fur seals and sea lions, unweaned yearlings compete for maternal milk by aggressing their newborn younger sibling (Trillmich & Wolf, 2008). In false vampire bats, weaned juveniles sometimes also attempt to kill their younger sibling, perhaps as a way to extend the period of post-weaning dependency, when they acquire hunting skills from their mother (Leippert et al., 2000). In primates, sibling relationships have been poorly studied during the developmental period (Lonsdorf & Ross, 2012), except in the context of competition over rank acquisition in matrilineal societies (e.g. Datta, 1988). To the best of my knowledge, only Lee (1987) investigated sibling competition across various contexts in vervet monkeys, highlighting grooming as the first focus of competition. Our results point out that siblings may be in competition over maternal investment at various developmental stages (*manuscript 1 and 3*). In manuscript 1, we suggest that chacma baboon juveniles' reactions to TTS could reflect competition with the infant over maternal attention. In mandrills, however, we did not detect any signs of conflict between siblings, despite the fact that the infant diverts a significant amount of maternal care from the older sibling (*manuscript 2*). The absence of overt conflict does not necessarily reflects the absence of evolutionary conflict though (G. A. Parker et al., 2002). We did not study behavioural conflict between juvenile and infant siblings – because juveniles rarely interact aggressively with their infant siblings – but such competition could be expressed through decreased interest in the infant and lower rates of interaction, as observed in humans (Kendrick & Dunn, 1980, 1982; Volling et al., 2014).

Furthermore, in chacma baboons, different-age siblings keep competing over access to maternal grooming and attention as long as they co-reside with their mother, from infancy to adulthood for females. Hence, this work highlights the fact that different-age sibling can compete over maternal resources, and that this competition most likely does not translate into agonistic interactions as observed in other taxa (e.g. the example mentioned above).

To sum up, maternal investment appears to induce conflicts within the family in monotocous primates, although these conflicts seem to be mediated at the proximate level by more subtle behaviours than in other taxa. In addition, the extent to which competition does occur and its intensity seems highly variable across species. In the following section, we discuss the different factors that may modulate sibling competition both between and within-species.

1.2. What shapes sibling competition in monotocous primates?

Factors modulating between-species variations in sibling competition

Juvenile chacma baboons and mandrills strikingly show contrasted reactions to the birth of a younger sibling (*manuscript 1 and 2*) that also differ from other primate studies, highlighting the potential mediating role of life-history. For instance, in birds, between species differences in developmental pace and brood size drives the variability in aggressiveness in sibling conflicts (Gonzalez-Voyer et al., 2007). Similarly in monotocous primates, species generation time and developmental pace could modulate sibling competition. In particular, the length of maternal interbirth intervals proportionally to offspring's developmental pace may be of critical importance for mother-offspring conflict at TTS. Juveniles who are nutritionally, physically or socially more dependent on their mother by the time she gives birth may experience a harsher transition and show more negative reactions. In line with this, in orang-utans, offspring still associate with their mother after she has given birth to their younger sibling, but are already fully weaned and have learnt most skills needed to extract food (the most critical skills to acquire in this solitary species). Older offspring in orang-utans thus show little reaction to TTS (van Noordwijk & van Schaik, 2005). In bonobos and chimpanzees, which exhibit shorter IBI than orang-utans, offspring are nutritionally weaned at their sibling's birth, but still rely critically on post-weaning maternal care (Behringer et al., 2022; Crockford et al., 2020; Samuni et al., 2020). TTS induces an increase in cortisol levels in wild bonobos but not

chimpanzees (Behringer et al., 2022; Tkaczynski et al., 2020), as well as more frequent attempts to initiate body contact with the mother in both species (Behringer et al., 2022; Clark, 1977). In rhesus macaques, offspring are sometimes still suckling in the days preceding the birth of their younger sibling, and steeper decreases in nursing time and the amount of maternal care received are associated with more signs of distress during the first month following the birth of the sibling (Devinney et al., 2003, 2001). Finally, in humans, which exhibit much shorter IBI than other great apes given their slow developmental period (Jones, 2011), and where mothers care for several different-age dependent children at the same time (Sear, 2011), mother-offspring conflict can be particularly intense during TTS, characterized by strong decrease in maternal care and increase in children's confrontational and distress behaviours (Dunn et al., 1981; Dunn & Kendrick, 1980; Stewart et al., 1987; Volling, 2012). Based on this framework, given that weaning ceases when the mother gives birth to the younger sibling in mandrills, while chacma baboons are weaned earlier, juvenile mandrills would be expected to either show more conflicts, or similar levels than chacma baboons.

However, our results are at odds: why do chacma baboon juveniles, who are weaned when they experience TTS, show some signs of conflicts with the mother (*manuscript 1*), while mandrills, who experience both weaning and TTS at the same time, do not (*manuscript 2*)? This counter-intuitive pattern could be driven by differences in their socio-ecology. Mandrills are seasonal breeders, and despite living in a relatively rich environment where food seems rarely limiting, the birth season occurs during the annual food peak (Dezeure et al., 2022). Hence, juveniles experience TTS and the end of weaning, which is the most critical period for offspring survival (Janson, 2005; Van Schaik & van Noordwijk, 1985), during the most favourable season. This timing may buffer the energetic challenge that juvenile likely face, and may mitigate mother-offspring conflict. In line with this, juvenile chacma baboons whose weaning ends during the annual food peak display less tantrum (generally considered indicative of mother-offspring conflict, e.g. Barrett & Henzi, 2000) than those who experience it when food is scarce (Dezeure et al., 2021). In contrast, the chacma baboon study population lives in a challenging semi-desertic environment, where food is highly limited. Although juvenile baboons are all weaned at TTS and we did not measure any decrease in maternal investment in terms of grooming and spatial proximity, our results suggested that juveniles may experience a decrease in maternal attention. This decrease may reflect a decrease in

other forms of post-weaning maternal care, for instance maternal support against conspecifics, which might bear substantial costs if it reduces e.g. their foraging success (Lynch et al., 2020). Breeding seasonality also induces socio-ecological differences: in mandrills, indeed, most births occur between November and February. Offspring are thus born in large cohorts of same-aged groupmates, sometimes up to 60 or more individuals (including many paternal half-siblings with whom they form differentiated social relationships: Charpentier et al., 2020). Yearlings also often form "crèche" (*pers. obs.*), an association between several infants and juveniles, and an adult male. Although the paternity relationships between the adult male and the immatures is still unknown, belonging to a "crèche" with many same-age individuals may provide opportunities to socialize and increase autonomy from the mother in mandrills, which may also reduce mother-offspring conflict. By contrast, in chacma baboons, juveniles are no longer closely associated to an adult male around TTS (*A.D. unpublished data*) and have less same-age individuals to interact with, which may lead juveniles to rely more on their maternal bond than mandrills do.

Factors modulating within-species variations in sibling competition

- *Maternal rank*

Several factors may modulate intrafamilial conflicts within species, such as maternal or offspring traits. First, throughout this work, maternal rank seems to have pervasive effects on maternal care, mother-offspring and sibling relationships (*manuscript 1, 2 and 3*). Female rank modulates access to food in many species, and higher-ranking females are generally in better body condition than lower-ranking ones, allowing them to invest more in their reproduction (Shivani et al., 2022). As such, female rank has been linked to shorter IBIs and faster reproductive paces across many primate species, including chacma baboons and mandrills (chacma baboon: Dezeure et al., 2023; mandrill: Dezeure et al., 2022; rhesus macaque: Gomendio, 1990; yellow baboon: Gesquiere et al., 2018; mountain gorilla: Wright et al., 2020; chimpanzee: Pusey et al., 1997). In addition, offspring born to higher-ranking females also have increased survival, and accelerated growth rate and behavioural maturation (Altmann & Alberts, 2005; Dezeure et al., 2023; Schneider-Crease et al., 2022). This accelerated reproductive pace has sometimes been linked to lower quality maternal care, with high-ranking mothers exhibiting more rejecting behaviours and less affiliations toward

their infants than lower-ranking ones, which may allow them to shorten weaning (e.g. in vervet monkey: Fairbanks & McGuire, 1995; P. C. Lee, 1984). Yet, we did not observe such patterns in both study systems. High-ranking female baboons and mandrills invest more than lower-ranking ones to maintain an affiliative relationship with their offspring (i.e. increased proximity maintenance in chacma baboons, increased grooming in mandrills), who unexpectedly show more signs of conflicts (i.e. increased solicitation in chacma baboons, increased tantrum in mandrills). Offspring reactions may reflect the fact that the fast reproductive pace of high-ranking females may favour maternal reproductive interests over offspring's developmental ones, swaying the resolution of the evolutionary mother-offspring conflict at the mother's advantage. This could trigger behavioural conflict in offspring born to high-ranking females, which would still have benefitted from an extended period of maternal investment, even if shorter IBIs do not increase mortality risks. We did not yet test whether maternal rank modulates juveniles' response to TTS but we are planning to add such analysis to manuscript 2 before submission. This analysis will be particularly interesting to implement because, in mandrills, females can be lactating and pregnant at the same time, but juveniles born to high-ranking females experience TTS nearly 6 months earlier than juveniles born to lower-ranking mothers (*A.D. unpublished data*, Dezeure et al., 2022). Hence, offspring born to higher-ranking females may need to adjust more to their mother's reproductive pace than lower-ranking offspring do. Furthermore, high-ranking females' faster reproductive rates and lower offspring mortality may lead to larger sibship (i.e. family) size in higher-ranking matrilines (*A.D. unpublished data*) – i.e. more different-age siblings co-residing with their mother at the same time – which may increase sibling competition over maternal grooming and attention. In line with this, offspring interfere more frequently in their siblings' maternal grooming in high-ranking families than in low-ranking ones (*manuscript 3*). Larger sibships, broods or litters are associated with increased sibling competition in many species (e.g. domestic rabbit: Drummond et al., 2000; pig: Andersen et al., 2011; great tit: Neuenschwander et al., 2003), including in humans (Lawson & Mace, 2009).

- *Siblings' age difference*

Second, our work highlights the mediating effect of individual characteristics on sibling competition, including juveniles' age and sex. Short interbirth intervals, and thus, small age difference between siblings, should theoretically trigger more intense sibling rivalry from the

older sibling because of a reduced period of exclusive maternal investment (Trivers, 1974). In line with this, short interbirth intervals increase mortality risks for both the older and younger siblings in several primate species, including humans (Conde-Agudelo et al., 2006; Frye et al., 2022; D. S. Lee et al., 2019; Tung et al., 2016; Zipple et al., 2019). In primates, these effects on survival have been generally attributed to an earlier weaning for the older sibling, as observed in mandrills (*manuscript 2*). The absence of any mediating effect of offspring's age on TTS (*manuscripts 1 and 2*) or on grooming interferences (*manuscript 3*) is therefore puzzling. In humans, increases in anxiety, clinginess, and confrontational behaviours toward the mother after the birth of the younger sibling is more pronounced in younger children (Dunn et al., 1981; Kendrick & Dunn, 1980; Volling et al., 2014). Age difference further mediates sibling relationships later in life in humans, with siblings exhibiting more frequent and more intense conflicts when they are closer in age during childhood (e.g. Salmon & Hehman, 2021; Tanskanen et al., 2017). In contrast in primates, close-in-age siblings generally show lower rates of aggression and higher rates of affiliation than siblings further apart (Amici et al., 2019; Grebe et al., 2022; P. C. Lee, 1987), suggesting that the high fitness costs associated with short interbirth intervals may not translates into behavioural conflicts in these species. In humans, the mediating effect of age proximity on sibling competition may be exacerbated as humans exhibit very short interbirth intervals compared to their slow developmental pace, and may not be representative of the patterns observed in other primate species. Our findings in manuscript 3 further suggest that monopolization of maternal grooming and attention may occurs from any siblings, regardless of their age. In this case, the costs associated to competition would not change with the targeted sibling's age and competitive interactions would be expected between siblings of any ages.

- *Siblings' sexes*

In mandrills, juveniles' reaction to TTS is sex-specific, inducing increased independence in males and increased affiliations toward the mother in females (*manuscript 2*). In contrast, in other species, including chacma baboons (*manuscript 1*), both sexes showed similar reactions to the birth of their younger sibling (Behringer et al., 2022; Devinney et al., 2001). In humans, the effects of child's sex, or of the combination of sexes between the older and the younger siblings, on TTS are inconsistent (e.g. Dunn et al., 1981; Stewart et al., 1987; Volling, 2012). In baboons and mandrills, as well as in other primate studies, the effect of the combination of

sexes during TTS has never been studied yet, but we would expect more negative reactions from the older sibling to the birth of a younger sibling with whom competition is more intense. In line with this prediction, young baboons interfere more frequently when mothers are grooming same-sex siblings, with male-male dyads interfering the most against each other (*manuscript 3*). In primates, few studies have investigated the impact of siblings' sexes on their relationships during the developmental period. In mountain gorillas, aggressive behaviours between siblings were equivalent in all sex combinations (Grebe et al., 2022) but this study did not investigate aggressions in relation to maternal care. In humans, males are generally more violent toward their siblings than girls and conflicts are more frequent and more intense between brothers and in mixed-sex dyads than in sisters dyads (reviewed in Salmon & Hehman, 2014).

More broadly, the influence of siblings' sexes on sibling competition likely varies with a species' social organization. For instance, in species with sex-biased dispersal, sibling competition is expected be more intense between siblings from the philopatric sex. In matrilineal societies, such as chacma baboon and mandrill, females are the philopatric sex, and younger sisters typically outrank the older ones (Pereira, 1989). During ontogeny, mothers generally bias their investment toward daughters, grooming and spending more time in close proximity than with sons (Kulik et al., 2016). Hence, sisters may be costlier than brothers because they monopolise more maternal care and attention, and may also induce lifelong rank-related costs. Sibling competition may thus be most intense between females in such societies. In line with this, in spotted hyenas, where females are philopatric and socially dominant over males, female cubs are stronger competitors than males (Benhaiem et al., 2012), and appear better able to survive intense sibling rivalry compared to males (Hofer & East, 1997). On the contrary, in species where males are philopatric, such as chimpanzees and bonobos, sibling competition could be more intense between brothers. To my knowledge, no studies to date have investigated patterns of sibling competition during development in these species, although in chimpanzees, male siblings affiliate and play less with their infant younger sibling than females when the age difference is small, but this pattern reverses when the age difference is large (Lonsdorf et al., 2018) – which may reflect higher competition for maternal care at younger ages in males. In bonobos, males incur an abrupt decrease in maternal riding around their sibling's birth (Behringer et al., 2022), which could also trigger

more competition than in females. Finally, in mountain gorillas, where both males and females can disperse (Robbins et al., 2009; Stoinski et al., 2009), siblings' aggression rates were similar for all sex combinations (Grebe et al., 2022). However, the interplay between competition and cooperation between siblings from the philopatric sex may be complex to disentangle because they affiliate and cooperate preferentially throughout their life (e.g. Mitani, 2009; Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006).

1.3.The long arm of early life environment

This work examines some proximate mechanisms that could drive the important fitness effects of early life social environment and social adversities (e.g. reviewed in Snyder-Mackler et al., 2020). In several long-lived social mammal species, the sources of early-life social adversity with the strongest negative fitness consequences are linked to disruptions of maternal support and care such as maternal loss and the birth of a close-in-age sibling (e.g. primates: Crockford et al., 2020; D. S. Lee et al., 2019; Tung et al., 2016; Zipple et al., 2019, 2021; killer whales: Foster et al., 2012; spotted hyenas: Gicquel et al., 2022; Strauss et al., 2020; elephants: Berger et al., 2021; Lahdenperä et al., 2016; J. M. Parker et al., 2021; red deers: Andres et al., 2013). In yellow baboons for instance, females who lost their mother before 4 years-old or have a close-in-age younger sibling face a respectively three- and two-fold increase in mortality risks at all ages, and their offspring further have increased chances of dying of respectively 50% and 40% before reaching 4 years-old themselves (Tung et al., 2016; Zipple et al., 2019). However, while maternal loss has a strong and consistent effect across all species where it has been investigated, the birth of a close-in-age younger sibling has been less systematically considered (among all the studies cited above, only Berger et al., 2021; Gicquel et al., 2022; D. S. Lee et al., 2019; Tung et al., 2016; Zipple et al., 2019 examined the effect of a competing sibling), and the proximate mechanisms driving such effects remain speculative at best. With this work, we provide valuable insights into the deleterious effects of having a too close-in-age younger sibling, by confirming that it could be linked to an earlier weaning. Indeed, in mandrills, the birth of the younger sibling induces an abrupt weaning, but the pathways linking the loss of maternal care to an increase in mortality risks at all ages (including weaned offspring) remain to be examined. At least two main mechanisms could explain these effects. First, it may stems directly from an energetic loss, with younger juveniles being less skilled at finding and processing food and relying more on maternal

provisioning than older ones. Second, it could be due to a broader effect of decreased access to the mother and to the other non-nutritional resources she may provide. For instance, in African elephants, orphan juveniles have lower survival than non-orphan ones (J. M. Parker et al., 2021), potentially mediated by differential access to key social partners such as adult females, who generally provide fitness advantages to their close affiliates via ecological and social knowledge (Goldenberg & Wittemyer, 2017; McComb et al., 2001, 2011).

Furthermore, little is known on how mother-offspring and sibling conflict during the developmental period both impact relationships between the different family members later in life. In humans for instance, inter-individual variability in children's reaction to the birth of a younger sibling is high, with some children coping well while others struggle to adjust (reviewed in Volling, 2012; Volling et al., 2017). Children's adjustment may have long-lasting effects on siblings' relationships. Indeed, those individuals who showed more difficulties to adjust to the birth of a younger sibling during their developmental period (e.g. displaying more negative behaviours toward their mother or toward the infant) experience poorer sibling relationships several months/years later (Dunn et al., 1994; Kendrick & Dunn, 1982; Stillwell & Dunn, 1985). During my PhD, I conducted preliminary analyses on chacma baboons to investigate inter-individual variability in juveniles' reactions to TTS. Our sample included only 8 individuals that were followed continuously both before and after the birth of their younger sibling. This limited sample size prevented us to draw any strong conclusions. However, descriptive data suggested that chacma baboon juveniles may show some inter-individual differences in their reactions to TTS. Future research should investigate these differences and test whether the intensity of mother-offspring conflict around TTS is associated with the strength of sibling relationships later in life. Such analysis would require, however, a few more years of data, especially in long-living species such as primates. For instance, juveniles reacting more negatively to TTS may exhibit lower affiliation rates with their infant younger sibling, which may in turn decrease the strength of their sibling relationship on the longer term (Maestripieri, 2018).

Lastly, siblings are important socialization agents in both humans and non-human primates (Brent et al., 1997; Brody, 1998; Lonsdorf et al., 2018; Pollet & Hoben, 2011; Stanton et al., 2017). Children experiencing less competitive sibling relationships, notably because of more egalitarian parental treatment, show greater prosociality, less problematic social

behaviours and better mental health in humans (Brody, 1998, 2004; Brody et al., 1987, 1992; Lawson & Mace, 2010; Peng et al., 2018). Similar associations could exist in non-human primates. For instance, if sibling competition induces weaker social bonds between siblings during ontogeny, it may later impact their social skills and integration. Sibling competition could also influence offspring's personality, maybe *via* birth order effects as in humans (Sulloway, 1996, 2001). In line with this, in olive baboons (*Papio anubis*), early-life adversity – in particular, maternal loss – influences females' interaction style (i.e. how they initiate interactions with other individuals). Females who experienced more adversities during ontogeny exhibit less benign interaction styles, which are associated with decreased social integrations (Patterson et al., 2022). Finally, little is known on how sibling relationships may change throughout life. In humans, some evidence suggests that closer-in-age siblings show more conflicts during childhood but also closer relationships in adulthood (Pollet, 2007; Pollet & Hoben, 2011), suggesting that sibling competition and relationships are dynamic over time. Whether sibling relationships exhibit similar patterns in primates remain to be investigated but could be of critical importance in nepotistic species such as mandrills and chacma baboons, where social support between maternal kin largely impacts fitness (Silk, 2009).

2. *How does sibling competition in monotocous mammals differ from polytocous species?*

2.1. Resources at stakes

One of the key question throughout this thesis was to identify the maternal resources at stake in sibling conflicts. Results in manuscripts 1 and 2 confirm the fact that different-age siblings likely do not compete for maternal milk, in contrast to Galapagos fur seals and sea lions (Trillmich & Wolf, 2008). Indeed, in our study population, juveniles chacma baboon are already weaned for several months by the time their mother gives birth (Carboni et al., 2022; Dezeure et al., 2021). In mandrills, the arrival of the younger sibling ends the weaning process (*manuscript 2*). In the latter, anecdotal field observations of juveniles requesting maternal nipple after their sibling's birth nonetheless suggest that they may disagree with the abrupt cessation of nursing they experience (*B.R.T. and M.J.E.C. pers. obs.*), even though these juveniles did not seem to belong to any particular group (e.g. juveniles which experience the birth of their younger sibling at a very young age, or born to very low-ranking mothers, …). In

rhesus macaques, the birth of a younger sibling may not always induce weaning, as mothers are sometimes seen nursing the older sibling at the same time as their infant (D. S. Lee et al., 2019). In this case, the older sibling's nursing bout would necessarily allow it to get some milk (as opposed to comfort suckling), which would induce sibling competition as the milk ingested by the older sibling will not be available for the younger one. Mothers most likely play a critical role to prevent this competition, for instance by preventing the older sibling to access her nipple before the infant has suckled enough. Similar behaviours have been observed in Galapagos fur seals, sea lions (Trillmich & Wolf, 2008) and spotted hyenas (White, 2008). Overall, our findings suggest that, even if competition for maternal milk may be possible in mandrills, it would be restricted to a very short period of time in juveniles' life, and is unlikely to be the primary resource at play in sibling competition in primates more broadly.

Our results in manuscript 1 and 3 point out the importance of maternal attention in sibling competition. Although maternal attention has been sometimes pointed out as a maternal resource over which siblings may compete in primates (e.g. Achenbach & Snowdon, 1998; Nicolson, 1987; Small & Smith, 1981), it has never been thoroughly investigated. Similarly, in humans, maternal attention is considered a maternal resource *per se*, and an issue of conflict between siblings (e.g. Salmon & Hehman, 2014; Schlomer et al., 2011; Thomas et al., 2015; Volling et al., 2010), but is never clearly defined. Maternal attention is considered to be a limited resource (Salmon & Hehman, 2014) as mothers may not be able to give attention to all of their offspring at the same time. As such, it can be monopolised by an offspring. In humans, experimental manipulation of maternal attention triggers competitive reactions between siblings in early/middle childhood: in an experimental design where the mother was told to give exclusive attention to one of her children while ignoring the other one, the sibling she ignored displayed negative emotions, such as sadness or anger, and attempted to disrupt the interaction between its mother and sibling and to divert its mother's attention toward itself (Miller et al., 2000; Teti & Ablard, 1989; Volling et al., 2002). However, from middle childhood to early adolescence, maternal attention was the least commonly cited source of conflict among siblings (Dunn & Munn, 1987; McGuire et al., 2000). Maternal attention may thus be more or less critical, depending on children's age, being more valuable to young children. Alternatively, older children may better regulate their reactions to the loss of maternal attention (Kopp, 1989). More broadly, defining, and thus, measuring maternal

attention in both humans and non-human primates is challenging. Moreover, from an evolutionary perspective, the potential benefits associated with the monopolisation of maternal attention remain unclear, which questions its role in sibling competition. Monopolising maternal attention may be a way to secure other forms of maternal care, such as social support against conspecifics or protection against predators (Clutton-Brock, 1991), or maintain the social bond with the mother if it increases the probability of future maternal grooming. In addition, mothers may be repositories of various forms of wealth, such as material (e.g. territories), social (e.g. social connections) or embodied capital (e.g. knowledge), that are often transmitted to offspring (Smith et al., 2022; Strauss & Shizuka, 2022). Monopolising maternal attention may thus grant privileged access to such wealth, which could then trigger inequalities between siblings if some inherit more than others. The study of maternal attention could benefit from studies on social attention in primates. Social attention is typically measured through head orientation, gaze direction or glance rate (Renevey et al., 2013; Schino & Sciarretta, 2016; Schülke et al., 2020) from an individual to others, typically in response to a stimuli (e.g. agonistic or affiliative interaction in the group), and allows individuals to keep track of dominance and social alliance networks in the group (Schülke et al., 2020). Previous studies in rhesus macaques and mandrills showed that adult females pay more attention to their adult kin and close affiliates in general (Schino & Sciarretta, 2016; Schülke et al., 2020). Similarly, mothers may also pay selective attention to their offspring, and this attention may vary from one offspring to another depending on the strength of their bond, or on offspring's solicitation rate.

Finally, there is a need to study post-weaning maternal care more in depth. Such forms of care may include protection against predators, social support against conspecifics, facilitated access to food, social learning opportunities, and information transfer (Clutton-Brock, 1991; Crockford et al., 2020; van Noordwijk, 2012), and are generally nonexclusive and non monopolisable (van Noordwijk, 2012). Several lines of research could be explored. First, the relative importance of these different resources may vary across species. In orang-utans, for example, learning from the mother to use tools to extract and process food may be particularly critical, while baboons should benefit more from learning social skills from their mother, required to maintain long-term relationships with others. A potential way to identify key post-weaning maternal resources would be to focus on orphan immature individuals of

different ages, and test whether they experience e.g. decreased foraging success or decreased social interactions or integration, compared to non-orphan individuals (see in African elephants: Goldenberg & Wittemyer, 2017). Second, it is unclear whether these resources are limited and can be diluted between siblings, which is a prerequisite for sibling competition to occur over these resources. Future studies could investigate whether the amount of maternal resources "received" per offspring (e.g. rates of maternal grooming or maternal support during conflict, or ability to cofeed with the mother) decreases with an increasing number of siblings. Third, it is still unknown whether such forms of maternal care entail any costs for the mother, as predicted by Trivers' definition of parental investment (1972). Potential costs to the mother could include changes in time-budget, with mothers having more different-age offspring allocating more time to social interactions, instead of e.g. foraging or resting activities compared to mothers with less offspring for instance. Alternatively, mothers may also allocate more of their social time to their offspring instead of non-offspring social partners, such as their own maternal sisters, which may impact their social integration at the group level. In chimpanzees, a few studies investigated the costs associated with caring for a dependent juvenile, but results are inconsistent: while some studies reported that mothers with a dependent juvenile have reduced daily range and spend less time interacting with other mothers (Halperin, 1979; Pontzer & Wrangham, 2006), others did not find any change in mothers' time allocated to feeding, resting, and interacting with other community members (Stanton et al., 2017). Overall, post-weaning maternal care has remained largely unstudied, and may offer exciting future research avenues.

2.2.Mechanisms

As demonstrated with this thesis, sibling competition may take more subtle forms in primates. Indeed, juvenile aggression toward their newborn siblings has never been observed in our study populations, in contrast to patterns observed in the Galapagos fur seals and sea lions for instance (Trillmich & Wolf, 2008). In manuscript 3, we show that siblings may compete by interfering in their siblings' affiliation with the mother. These interferences are subtle because they rarely involve aggressive behaviours (*personal observation*) and, as they are rarely successful, would have gone unnoticed if focusing only on aggression or dominance relationships and their outcomes (such as supplant behaviours traditionally used to investigate dominance interactions). Focusing on specific contexts that may elicit competition

from a proximate perspective, such as maternal grooming, may help to spot competitive interactions between siblings. Future investigations should focus on identifying other contexts that may elicit sibling competition, and compare sibling relationships in these contexts to control situations. For instance, sibling competition could be less intense between orphan siblings than between non-orphan ones who still benefit from maternal care (e.g. Reddy & Mitani, 2019), or when the mother is far away compared to when she is in close proximity to her offspring. For example, in humans, maternal presence *vs.* absence in the home largely influences sibling conflicts, with more agonistic interactions unfolding when she is around than when she is absent (Corter et al., 1983). In addition, focusing on triadic interactions and third-party relationships may be more relevant in species with complex social life (J. J. Massen et al., 2020). Third-party interactions, i.e. when a third individual influences the course, the outcome or the aftermath of an interaction between two other individuals (J. J. Massen et al., 2020), have been best described in the context of coalitionary support, policing, or reconciliation in primates (reviewed in Massen et al., 2020). Several recent studies investigated third-party interventions in affiliative interactions and revealed that individuals may use such behaviours to prevent the formation of bonds between a third-party and their close social partners, or of alliances that could shift power balances (J. J. M. Massen et al., 2014; Mielke et al., 2017, 2021; Mondragón-Ceballos, 2001; Schino & Lasio, 2018; C. E. Webb et al., 2020). Our findings in manuscript 3 thus suggest that siblings may use third party interactions to influence their siblings' relationships with their mother, thus providing new insights on how individuals may shape their social environment by using flexible and strategic behaviours (J. J. Massen et al., 2020).

3. The emotional aspect of sibling competition in primates

Several aspects of this thesis, by their similarities to patterns of sibling rivalry in humans, underline the potential emotional underpinning of sibling competition in primates. First, our results in manuscript 1 and 3 emphasize the potential role of maternal attention in sibling competition in chacma baboons. Second, siblings react negatively to differential maternal treatment, interfering more often against those siblings that receive more maternal grooming than themselves (*manuscript 3*). In humans, the loss of maternal attention to a rival sibling is associated to negative reactions, such as attention-seeking behaviours, attempts to divert the mother's attention toward oneself, or negative emotions such as anger or sadness (Hart et

al., 2004; Miller et al., 2000; Mize & Jones, 2012; Teti & Ablard, 1989). Children also react to parental differential treatment, i.e. when parents direct different levels of positivity (e.g. affectionate behaviours), negativity (e.g. quarrels), responsiveness (e.g. answering a question), verbalisation (e.g. initiate communication), and control (e.g. requesting the child to behave a certain way) between their children (e.g. Brody et al., 1992). Siblings report more conflicts and poorer relationships with each other when experiencing greater level of parental differential treatment within the family (e.g. Brody et al., 1987; Jensen et al., 2013; Kowal & Kramer, 1997; Richmond et al., 2005; Volling & Elins, 1998). Importantly, in humans, these emotional and behavioural reactions have been regularly linked to jealousy (e.g. Hart et al., 2004; Loeser et al., 2016; Miller et al., 2000; Volling et al., 2002), and sibling jealousy is often considered as an important aspect of sibling relationships (Kowal et al., 2006; Volling et al., 2002, 2010), and some authors argue that sibling competition over parental attention is by definition sibling jealousy (Volling et al., 2010).

Jealousy is a complex social emotion that arises when an individual perceives its relationship with a valuable social partner as threatened by a third-party (Parrott, 1991; Parrott & Smith, 1993). This emotion can only arise within a social triangle composed of three different individuals, the jealous one, its social partner, and a rival, and in reaction to the perceived (or real) loss of the valuable relationship to the rival (Volling et al., 2002, 2010). In contrast, *envy*, an emotion often confused with jealousy, arises in a social context involving only two individuals, when a person lacks someone else's success, possessions, or qualities, and desire it or wishes that the other person lacked it (Parrott & Smith, 1993). As a social emotion, jealousy is intrinsically linked to the interpersonal complex in which it arises, and rather than a single emotional expression, may be expressed through a complex of blended emotions, behaviours and thoughts (Izard, 1991; Panksepp, 2010; Parrott, 1991). In humans, jealousy is often expressed through overt behaviours aiming to regain the attention of the valuable social partner, or to interrupt the interaction between the valuable social partner and the rival (Hart, 2010). Jealousy may thus facilitate the retention of valuable social relationship against potential intruders, in line with emotion's ultimate function to increase an animal's ability to cope with situational stress or opportunities (Nesse, 1990). As such, jealousy may have emerged in a wide range of species where social relationships provide fitness benefits and could arise in the context of any fitness-enhancing social relationship

(Abdai et al., 2018; Morris et al., 2008). However, jealousy has been mainly investigated in humans so far, and mostly in the context of sexual/romantic relationships (Buss, 2000; Volling et al., 2010) despite the prevalence and intensity of sibling jealousy (Parrott, 1991). Jealousy is a "secondary" emotion – i.e. emotions that are experienced, evaluated and reflected on, involving higher brain centres in the cerebral cortex, as opposed to "primary" emotions (i.e. basic emotions triggering rapid reactions to stimuli, such as fear) (Bekoff, 2000, 2010). As such, there is still much debate whether non-human animals even have the capacity to experience non-basic emotions (e.g. Bekoff, 2000, 2010; De Waal, 2019; de Waal, 2011; or see comments on Cook et al., 2018, that gives a rapid overview of the main current controversies on animal jealousy). The initial assumption that non-human animals did not have the complex socio-cognitive skills and neural pathways necessary to experience such secondary emotions is increasingly challenged, as evidence that non-human animals show behavioural, neurophysiological, hormonal and cognitive responses similar to humans in the same situations accumulates (Bekoff, 2000; De Waal, 2019; Kret et al., 2022; Panksepp, 2010). Another argument frequently cited as a hindrance to the study of jealousy, and more generally of complex emotions in animals, is the fact that emotions are private experiences that cannot be directly measured in others (de Waal, 2011; C. E. Webb et al., 2020). In this respect, many researchers in affective sciences suggested to separate the study of feelings, which are private states that cannot be known to others, from the study of emotions, which are expressed through measurable behavioural and physiological manifestations (Adolphs & Anderson, 2018; de Waal, 2011; Prinz, 2005). As a side note, this argument is true for non-human animals as much as for humans because our knowledge of other's private experiences rely on their own reports (which are associated with inevitable biases), and thus should not prevent researchers to investigate complex emotions in animals (Abdai & Miklósi, 2018; de Waal, 2011). Other authors further suggested to focus on 'jealous behaviours' rather than 'jealousy' so as to be clear that they refer to the emotion from a functional perspective, rather than to its felt component (Abdai et al., 2018; Abdai & Miklósi, 2018; C. E. Webb et al., 2020).

In non-human animals, empirical investigations of jealousy remain limited to a handful of studies, most of which focused on human-dog interactions (Abdai et al., 2018; Cook et al., 2018; Harris & Prouvost, 2014; Prato-Previde, Nicotra, et al., 2018; Prato-Previde, Nicotra, Velia, et al., 2018). While some of them found that dogs exhibit jealous behaviours when their

owner attend to a social rival (Abdai et al., 2018; Harris & Prouvost, 2014), others did not find any evidence for jealous reactions (Cook et al., 2018; Prato-Previde, Nicotra, et al., 2018; Prato-Previde, Nicotra, Velia, et al., 2018). However, most of these studies failed to recreate the appropriate social context in which jealousy could arise, as they used fake dogs as rivals (Cook et al., 2018; Harris & Prouvost, 2014; Prato-Previde, Nicotra, Pelosi, et al., 2018, but see Abdai et al., 2018; Prato-Previde, Nicotra, Fusar Poli, et al., 2018 that used real dogs as rivals), despite evidence that dogs do not mistake fake dogs with real ones[2] (Prato-Previde, Nicotra, et al., 2018). Studying a social emotion such as jealousy should start by identifying the appropriate social relationships (e.g. sexual bonds, friendships or parent-offspring bonds) and the particular contexts (i.e. with individuals that can be perceived as rivals) that could elicit this emotion (van Kleef, 2018; C. Webb & de Waal, 2018; C. E. Webb et al., 2020), and that could have selected for this emotional response in evolutionary times. In primates, two experimental studies investigated the neural substrates of jealousy. Both reported neural and endocrine changes in males in response to social closeness between their associated female and an adult male rival, similarly to the neurophysiological responses observed in humans (Coppery titi monkeys, *Callicebus cupreus*: Maninger et al., 2017; rhesus macaques: Rilling et al., 2004). Only one study used a behaviour-centred approach to study jealousy in captive chimpanzees (C. E. Webb et al., 2020). They showed that chimpanzees display jealous behaviours in response to social closeness between their close affiliates and social intruders newly introduced in the colony. Previous studies in primates and horses focused on interferences in sexual or affiliative interactions, with findings consistent with a jealousy-based explanation (e.g. Baniel et al., 2018; Mielke et al., 2017, 2021; Mondragón-Ceballos, 2001; Schneider & Krueger, 2012), but at best only mentioned jealousy as a potential proximate mechanism (Baniel et al., 2018; Mielke et al., 2017, 2021). Our results in manuscript 3 (and, to some extent, in manuscript 1) therefore adds up to this small set of studies, and extend it in several ways. Our findings are the first reports of jealous reactions (i) within a parent-offspring relationship context in non-human animals, (ii) in natural conditions, and (iii) in chacma baboons, a species much less closely related to humans than chimpanzees. Overall, this work emphasizes the need to investigate jealousy as a proximate mechanism promoting competitive or negative interactions across various social contexts, such as

[2] Which should come as a surprise for most of us

threatened sexual (e.g. Baniel et al., 2018; Smuts, 1985) or social bonds (e.g. C. E. Webb et al., 2020). If similar situations trigger similar behavioural, physiological and neural responses in non-human and human animals, the most parsimonious explanation would be similar mechanisms (de Waal, 1999, 2011). Such an interpretation would, undoubtedly, help us to unravel the evolutionary origins of human jealousy which may be deeply rooted in our (non-human) evolutionary history. In addition, deciphering the diversity of contexts in which such emotional reactions can be detected will also deliver precious insights about the situations, partners and resources that non-humans value most, which is an important information to understand their minds and, ultimately, promote conditions that are compatible with their psychological welfare.

4. General conclusion and future directions

This thesis emphasizes that sibling relationships may not be as harmonious as previously thought in two long-lived, monotocous, social primates, chacma baboons and mandrills. We show that both mother-offspring conflict and sibling competition may arise around maternal subsequent reproduction, and that siblings keep competing for maternal grooming and attention throughout their developmental period, and even in adulthood in females. Moreover, sibling competition may take subtle forms, such as maternal solicitations or non-aggressive interferences that are only detectable when focusing on contexts and triadic relationships. Hence, sibling competition in primates may be very different in its forms from sibling competition in other species, such as polytocous siblicidal bird species or spotted hyenas, or monotocous Galapagos sea lions and fur seals, and more similar to the quarrels observed in human children. This thesis is an exploratory work on sibling relationships that I hope will bring attention and more in-depth investigations on sibling competition in primates. In particular, siblings are important social partners throughout life in many group-living species, and understanding how their relationships may derive from a complex interplay between cooperation and competition may be a necessary key step to fully appreciate the fitness effects of siblings' support and the evolution of nepotistic societies. My work also highlights the potential emotional aspect of sibling competition in primates, which may renew interests in studying secondary emotional states such as jealousy in non-human animals, as well as its development, by providing a relevant social context to investigate its occurrence, and that may have contributed to its evolution.

Importantly, this work focused mainly on the effect of a competitive younger sibling on the older sibling (*manuscript 1 and 2*) but it is worth noting that older sibling may also have a competitive impact on their younger sibling (as shown in *manuscript 3*). For instance, while many studies focused on the 'helper' role of older sibling on infant's development and socialization in primates (e.g. Brent et al., 1997; Lonsdorf et al., 2018), several studies reported that older sibling may also incur costs to them, *via* reducing maternal investment (e.g. Berman, 1992; D. S. Lee et al., 2019; Oelze et al., 2020). Hence, future work should investigate consequences of sibling competition for both parties, as well as of how sibling relationships are affected by the extent of sibling asymmetries in age, experience or ability to attract maternal care (i.e. favoritism) among them.

More broadly, this work could be extended in several ways. First, I would like to investigate more in depth the nature of post-weaning maternal resources in baboons, by investigating differences in foraging success and social integration of immature orphans compared to non-orphan individuals of the same age. Specific attention will be given to the quality of sibling relationships and the potential mediating effect of compensatory relationships, for instance, with older siblings. Second, we would like to investigate the potential drivers of variation in sibling relationships, investigating whether ecological (e.g. food availability) and social factors (e.g. maternal investment and maternal style) may impact sibling cooperation and competition. Finally, in these matrilineal societies, adult sisters may vary in their level of cooperation and social support, and it would be interesting to examine whether these variations are linked to the conditions experienced during development, such as age proximity and sex ratio of their sibship, but also sibling relationships in early-life.

French summary of the PhD

INTRODUCTION

L'investissement parental a évolué dans de nombreux taxons, et s'exprime sous la forme d'une grande diversité de soins parentaux : par exemple, protéger ou réchauffer des œufs ou des poussins, nourrir des jeunes (Clutton-Brock, 1991; Royle et al., 2012). D'un point de vue évolutif, l'investissement parental est défini comme « tout investissement par un parent dans sa progéniture qui augmente la survie et le futur succès reproducteur de cette progéniture, au détriment de la capacité du parent à élever de futurs descendants » (Trivers, 1972). Du fait de sa nature limitée et d'une asymétrie de l'apparentement entre les différents membres de la famille, l'investissement parental est à l'origine de conflits entre ceux-ci (Trivers, 1974). Les parents essaient d'investir le moins possible dans leurs enfants (conflit parent-enfant), et moins que leur partenaire (conflit sexuel entre parents). Enfin, chaque enfant essaie de monopoliser le plus d'investissement parental, au détriment de ses frères et sœurs (compétition dans la fratrie, Trivers, 1974). Cette dernière peut avoir lieu à la fois entre des frères et sœurs issus d'un même évènement reproductif (dans le cas de portée ou nichée par exemple), donc de même âge, ou entre des frères et sœurs issus de différents évènements reproductifs, et donc d'âge différent (Parker & Macnair, 1979; Roulin & Dreiss, 2012; Trivers, 1974).

La compétition dans la fratrie a été très étudiée chez les espèces animales, avec un fort biais sur les espèces produisant des portées/nichées, et notamment chez les oiseaux (Roulin & Dreiss, 2012). Notre compréhension des conflits dans la fratrie se trouvent donc limitée au seul cas de la compétition entre frères et sœurs de même âge, qui ont les mêmes besoins au même moment en terme de ressources parentales. Chez les humains, la rivalité entre frères et sœurs a fait l'objet d'investigations de la part de diverses disciplines, notamment en psychologie développementale ou en anthropologie.

Chez les animaux, la compétition dans la fratrie a principalement été étudiée chez des espèces produisant des portées/nichées, et à une période développementale précise, c.à.d. avant l'indépendance nutritionnelle, lorsque l'investissement parental consiste principalement en nourrissage ou thermorégulation (revu dans Mock & Parker, 1998; Roulin & Dreiss, 2012). La compétition peut s'exprimer de diverses manières, soit de manière non violente, par exemple en réclamant de la nourriture aux parents (Manser et al., 2008; Mock

& Parker, 1998; Smiseth & Moore, 2002), soit de manière violente. Les frères et sœurs peuvent s'agresser physiquement pour déterminer qui aura accès aux ressources parentales, ce qui peut parfois conduire à la mort de certains d'entre eux (fratricide) (Drummond, 2006; Frank et al., 1991; Hofer & East, 2008; O'Connor, 1978). Divers facteurs peuvent moduler l'intensité de cette compétition à l'échelle d'une espèce: environnementaux (c.à.d. la quantité de nourriture présente dans l'environnement) ou individuels (apparentement génétiques et sexes des frères et sœurs, taille de la fratrie). A l'échelle inter-espèces, divers facteurs tels que la durée d'élevage des jeunes, le mode d'approvisionnement des parents ou encore la présence d'armement comme des dents influence l'intensité et la violence de la compétition entre frères et sœurs (Drummond, 2006; Gonzalez-Voyer et al., 2007). Enfin, cette compétition peut avoir de nombreuses conséquences : outre une augmentation de la mortalité, elle peut également affecter le développement, la physiologie ou encore la personnalité des frères et sœurs. En revanche, peu d'études se sont intéressées aux effets de plus long-terme sur la valeur sélective des individus.

Chez les humains, la compétition dans la fratrie a le plus souvent été étudiée sous l'angle de la théorie de l'attachement en psychologie (Ainsworth, 1979; Bowlby, 1969), plutôt sous celui des conflits parents-enfants comme chez les animaux. Les conflits sont souvent caractérisés par des disputes et des querelles, où l'origine du conflit est souvent difficile à identifier et à relier à l'investissement parental. De plus, il revêt fréquemment une dimension émotionnelle (Volling et al., 2010), lorsque les frères et sœurs sont jaloux de l'attention parentale données à l'un de ses frères/sœurs. De manière similaire aux animaux, l'intensité de la compétition varie en fonction des ressources environnementales, et des caractéristiques individuelles (par ex., le sexe ou la différence d'âge) (Brody, 1998; Pollet & Hoben, 2011; Salmon & Hehman, 2014; Volling et al., 2010). Certaines caractéristiques familiales peuvent aussi jouer un rôle, comme le fait que les parents traitent leurs enfants différemment, ce qui induit bien souvent de la jalousie (Brody et al., 1992; Loeser et al., 2016; Volling et al., 2010). Enfin, cette compétition peut aussi avoir de fortes conséquences sur la survie, le développement et la santé.

Toutefois, la compétition dans la fratrie a été très peu étudiée chez les espèces animales longévives, ne produisant qu'un petit à la fois (monotoques), comme de nombreux cétacés, ongulés, primates ou encore les éléphants (Hudson & Trillmich, 2008). Cette lacune

est principalement due à la difficulté à identifier les ressources maternelles pour lesquelles des frères et sœurs d'âge différent pourraient être en compétition une fois sevrés. Chez ces espèces, les jeunes restent souvent avec leur mère après le sevrage, qui continue à s'occuper d'eux en les protégeant contre les prédateurs ou leurs congénères, ou en leur transmettant leurs connaissances (Clutton-Brock, 1991; Crockford et al., 2020). Ces ressources peuvent améliorer la valeur sélectives des enfants (Andres et al., 2013; Crockford et al., 2020; Foster et al., 2012; Holand et al., 2012; Samuni et al., 2020). Chez ces espèces, diluer les soins parentaux entre plusieurs frères et sœurs semblent coûteux : un écart d'âge trop petit entre deux frères et sœurs peut avoir de forts impacts sur le développement, la survie et le succès reproducteurs des individus (Lee et al., 2019; Thompson et al., 2016; Tung et al., 2016; Zipple et al., 2019). Cependant, très peu d'études à ce jour se sont intéressées aux relations de compétition entre les frères et sœurs chez ces espèces.

OBJECTIFS

Le principal but de cette thèse est d'examiner l'occurrence de conflits dans la fratrie autour des soins maternels, et d'identifier les potentiels ressources maternelles en jeu chez deux espèces de primates sociaux monotoques, les babouins chacma (*Papio ursinus*) en Namibie, et les mandrills (*Mandrillus sphinx*) au Gabon. Nous utilisons pour cela une combinaison de données de long-terme de traits d'histoire de vie et des comportementales afin de comprendre les variations intra- et inter-espèces dans la réaction des juvéniles à la naissance de leur petit frère, et les dynamiques de compétition entre frères et sœurs d'âge différent pour des ressources maternelles non nutritionnelles.

MODELE D'ETUDE

Nous nous intéressons à deux espèces de cercopithecidae, les babouins chacma (Tsaobis Baboon Project, Namibie), et les mandrills (Mandrillus Project, Gabon). Ces deux espèces sont proches phylogénétiquement (Zinner et al., 2009), et de tailles similaires, et monotoques. En outre, elles partagent de nombreuses similarités dans leur organisation sociale: ce sont deux espèces vivant dans de larges groupes multimâles multifemelles avec un système de reproduction polygynandre, où les femelles sont philopatriques et les mâles dispersent à l'âge adulte (Abernethy et al., 2002; Bulger, 1993; Seyfarth, 1976). Elles forment des sociétés

matrilinéaires, où les filles héritent leur rang hiérarchique de leur mère, les plus jeunes sœurs étant de plus haut rang que les plus âgées (Charpentier et al., 2007; Cheney, 1977), et où les individus maintiennent des relations différenciées avec leurs apparentés maternels et paternels (Charpentier et al., 2007; Silk et al., 2006). Cependant, ces deux espèces diffèrent par certains aspects pertinents pour nos questions : les mandrills ont une histoire de vie légèrement plus rapide que les babouins, et vivent dans la forêt tropicale, où la nourriture n'est pas limitante. Les babouins chacma vivent dans un environnement désertique, caractérisé par une forte saisonnalité dans l'abondance de la nourriture. De plus, les mandrills se reproduisent de manière saisonnière, alors que les babouins ont une reproduction non-saisonnière (Dezeure et al., 2021, 2022). Chez les mandrills, les intervalles entre naissance sont donc répartis de manière bimodale, puisque un individu pourra avoir un petit frère/sœur l'année suivante, ou bien deux ans plus tard, alors que chez les babouins, les intervalles entre naissances ont une répartition unimodale, avec un intervalle moyen plus long que chez les mandrills. De plus, cette saisonnalité entraîne une organisation sociale différente entre les deux espèces : chez les mandrills, les mâles immigrent massivement dans les groupes de femelles lors de la saison reproductive et émigrent à la fin, alors que chez les babouins, les mâles peuvent rester plusieurs années au sein du même groupe, leur permettant de prodiguer des soins paternels à leur progéniture (Charpentier et al., 2008; Huchard et al., 2013; Moscovice et al., 2010).

RESULTATS

Je présente ici les résumés de chaque manuscrit présenté dans cette thèse.

Chapitre 2 : Transition vers la fraternité chez une population de babouin chacma sauvage (publié à : Animal Behaviour)

Chez les mammifères monotoques (c.à.d. les espèces où les femelles ne produisent qu'un petit à la fois), la plupart des individus vivent la naissance d'un petit frère/sœur au cours de leur vie. La transition vers la fraternité (TTS ci-après) a été rarement étudiée chez les primates, alors qu'elle constitue la dernière étape du passage de l'investissement maternel d'un enfant au suivant, et pourrait donc représenter une étape critique, à la fois pour le conflit mère-enfant, et la compétition dans la fratrie.

Dans cette étude, nous utilisons des données comportementales sur des juvéniles primates qui ont récemment fait l'expérience de la naissance d'un frère ou d'une sœur plus jeune, ou non, afin d'étudier les changements dans la relation mère-juvénile pendant la TTS dans une population sauvage de babouin chacma.

Nos résultats montrent qu'à l'arrivée d'un petit frère/sœur, (1) l'association spatiale entre la mère et le juvénile reste stable, (2) les mères ne diminuent pas leur probabilité d'initier la proximité ou les affiliations avec le juvénile, et (3) les juvéniles initient plus fréquemment la proximité et les affiliations avec leur mère, et montrent plus de signes d'anxiété après la naissance de leur petit frère/sœur.

Ces résultats suggèrent que les juvéniles ayant un petit frère/sœur sollicitent plus souvent leur mère, et cherchent à attirer l'attention maternelle plus que les juvéniles n'ayant pas encore de petit frère/sœur. Ainsi, les conflits entre la mère et les enfants pourrait s'étendre à la période post-sevrage, au cours de laquelle des ressources plus subtiles, telle que l'attention maternelle, pourraient être l'enjeu de compétition entre frères et sœurs.

Chapitre 3 : Un voyage inattendu : devenir un grand frère ou une grande sœur chez les mandrills sauvages (manuscrit en préparation)

Chez les mammifères monotoques, la naissance d'un petit frère/sœur a toujours été considérée comme une période stressante, bien qu'il s'agisse d'un évènement que presque chaque individu connaîtra dans sa vie. D'un point de vue théorique, deux types de conflits relatifs à l'investissement maternel pourraient se dérouler dans cette période : le conflit mère-enfant, et la compétition dans la fratrie. Pourtant, cette étape du développement a été rarement étudiée chez les primates.

Ici, nous avons utilisé des données comportementales collectées sur la seule population de mandrills habitués (*Mandrillus sphinx*) pour étudier les changements dans les soins maternels et la relation mère-juvénile au cours de la transition vers la fraternité. Pour cela, nous comparons des juvéniles qui ont récemment vécu la naissance d'un petit frère/sœur avec des juvéniles qui n'ont pas encore vécu cette expérience.

Nos résultats montrent que la naissance d'un petit frère/sœur entraîne l'arrêt brutal du processus de sevrage pour le juvénile, et une diminution des affiliations maternelles. Les réactions des juvéniles étaient spécifiques au sexe, les jeunes femelles toilettant leurs mères plus souvent, tandis que les jeunes mâles s'éloignaient davantage de leur mère après la naissance de leur petit frère/sœur. La responsabilité des juvéniles dans le maintien de la proximité et l'initiation des affiliations avec la mère est restée inchangée, et ils ne montrent pas plus de signes de conflits ou d'anxiété que les juvéniles qui n'ont pas encore de petit frère/sœur.

Ainsi, selon nos résultats, la perte de soins maternels à laquelle sont confrontés les jeunes à l'arrivée d'un petit frère/sœur n'induit pas de signes de conflits manifestes dans la famille, mais pourrait affecter différemment les deux sexes. Cette étude contribue à mieux comprendre pour des intervalles entre naissance courts représentent souvent un risque pour la survie des juvéniles chez les primates monotoques. En outre, les contrastes entre les études soulignent l'importance d'examiner la transition vers la fraternité chez des espèces ayant des histoires de vie et des écologies différentes.

Chapitre 4 : Compétition dans la fratrie pour l'attention maternelle chez des babouins sauvages (manuscrit en préparation)

Les manifestations comportementales de la rivalité fraternelle chez les enfants, ainsi que leurs fondements psychologiques et émotionnels, ont suscité un grand intérêt. Les enfants essaient souvent d'interrompre les interactions affiliatives entre leurs parents et leurs frères et sœurs, un comportement qui est souvent interprété comme l'expression de la jalousie, et qui s'intensifie entre les frères et sœurs de même sexe et d'âge proche, ainsi que parmi ceux qui sont reçoivent un traitement parental différentiel. Chez les non-humais, les études sur la compétition entre frères et sœurs se sont principalement concentrées sur les conflits liés à l'approvisionnement chez des espèces produisant des couvées ou des portées. On sait peu de choses sur les interactions entre frères et sœurs chez les espèces à longue durée de vie, où, comme chez les humains, les mères produisent un seul petit à la fois mais entretiennent des liens durables avec leur progéniture adulte.

Dans cette étude, nous nous intéressons au contexte, aux cibles, et à la fonctions des interférences entre frères et sœurs dans les interactions affiliatives entre la mère et ses enfants chez des babouins chacma sauvages.

Nos résultats montrent que de telles interventions se produisent généralement dans des contextes censés susciter la compétition entre frères et sœurs, étant 10 fois plus fréquentes à l'intérieur qu'à l'extérieur de la famille, et plus fréquentes lorsque la mère toilette un frère ou une sœur, au lieu de se reposer. Deuxièmement, les enfants ciblent de préférence les frères et sœurs de même sexe, et plus jeunes, ainsi que ceux qui reçoivent le plus de soins maternels au sein de la fratrie, reflétant ainsi largement les patrons observés chez les enfants. Enfin, les interférences ne permettent généralement d'accéder au toilettage maternel aux interférents, et les enfants qui interfèrent le plus réussissent le moins à obtenir du toilettage maternel.

Au lieu d'être des tentatives stratégiques pour obtenir plus de toilettage maternel, ces interférences peuvent donc refléter des réactions émotionnelles spontanées à une interaction affiliative observée entre la mère et un frère ou une sœur. Notre étude montre que les frères et sœurs babouin peuvent être en compétition bien au-delà de la période de dépendance nutritionnelle, et pour d'autres ressources maternelles que la nourriture, comblant ainsi une lacune importante pour comprendre la rivalité entre frère et sœurs avec une perspective évolutive. En outre, notre étude établit un contexte original et pertinent pour étudier le développement des émotions complexes comme la jalousie chez les animaux non-humains.

DISCUSSION GENERALE

Causes et conséquences de la compétition dans la fratrie chez les primates monotoques

Conflits intrafamiliaux autour de l'investissement maternel

Au cours de cette thèse, nous avons montré que les différents membres de la famille peuvent être en conflit pour l'investissement maternel. D'un côté, nos résultats montrent que le conflit mère-enfant peut s'étendre après la reproduction suivante de la mère (*manuscrit 1*),

bien que la plupart des études précédentes se soient concentrées sur le conflit mère-enfant pendant des périodes développementales antérieures, telles que le sevrage ou le moment où la mère recommence à cycler. Ensuite, nous montrons que les frères et sœurs peuvent également être en conflits pour des ressources maternelles, notamment le toilettage ou l'attention (*manuscrit 1 et 3*). Ce travail apporte un éclairage nouveau sur les relations intrafamiliales chez les primates non-humains, notamment sur le conflit entre frères et sœurs, dont les causes et les mécanismes ont été très peu étudiés. De plus, les études chez d'autres espèces de primates, y compris les humains, montrent que ce conflit peut être très variable entre espèces (*manuscrit 2*).

Facteurs de variations de la compétition dans la fratrie chez les primates monotoques

L'intensité de la compétition dans la fratrie semble très variables, à la fois entre espèces, et au sein d'une même espèce.

La variabilité inter-espèce est probablement liée aux différences d'histoire de vie entre espèces, comme c'est le cas chez les oiseaux (Gonzalez-Voyer et al., 2007). Notamment, la durée des différents évènements reproductifs des femelles par rapport à la durée du développement des enfants a probablement un fort effet sur les conflits mère-enfants au moment de la naissance d'un petit frère/sœur. Les enfants plus dépendants de leur mère nutritionnellement, socialement ou physiquement au moment de cette transition pourraient exprimer plus de conflits que ceux qui sont plus avancés dans leur développement lors de cette étape. Cependant, les différences que nous observons dans la réaction des juvéniles à la naissance d'un petit frère/sœur ne s'explique pas forcément par des différences d'histoire de vie. En effet, les juvéniles babouins sont sevrés depuis longtemps lorsque leur mère donne naissance mais montrent des signes de conflits (*manuscrit 1*), alors que les juvéniles mandrills, pour qui la naissance de leur petit frère marque la fin du sevrage, n'en montrent pas (*manuscrit 2*)? Les différences socio-écologiques pourraient expliquer de telles différences : les mandrills ont une reproduction saisonnière, et la période des naissances et donc de fin du sevrage a lieu au moment du pic d'abondance de nourriture dans l'environnement, ce qui pourrait mitiger les conflits mère-enfants (Dezeure et al., 2021, 2022).

Au sein des espèces, le rang hiérarchique maternel est généralement associé au succès reproducteur des femelles, les femelles de haut-rangs ayant généralement un rythme de reproduction plus rapide et un meilleur succès reproducteur (Altmann & Alberts, 2005; Cheney et al., 2004; Dezeure et al., 2022). Nos résultats montrent que les femelles de haut-rangs s'investissent plus dans le maintien des relations affiliatives avec leur juvénile, mais que ceux-ci expriment plus de comportement conflictuels (sollicitations plus fréquentes, colères, *manuscrit 1* et *2*). De plus, les frères et sœurs interfèrent plus souvent dans les interactions affiliatives avec leur mère dans les familles de haut-rangs (*manuscrit 3*). Ces résultats pourraient s'expliquer par le rythme de reproduction plus rapide et la taille de fratrie plus importante dans les familles de haut rang, ce qui induirait une compétition plus intense.

L'intensité de la compétition peut également dépendre de caractéristiques individuels, tels que la différence d'âge entre deux frères/sœurs, ou les sexes des individus. Étonnamment, la différence d'âge ne semble pas moduler l'intensité de la compétition dans la fratrie (manuscrits 1, 2 et 3). Ce résultat est surprenant car il est attendu théoriquement (Trivers, 1974), et il a été montré que la différence d'âge a des conséquences négatives importantes sur la valeur sélective des individus chez les primates (Conde-Agudelo et al., 2006; Frye et al., 2022; Lee et al., 2019) et influence les relations fraternelles chez les humains. Le sexe des frères et sœurs peut aussi influencer l'intensité de la compétition (*manuscrits 2* et *3*), mais les différentes études rapportent en générales des résultats incohérents. Plus largement, l'effet du sexe pourrait dépendre des traits d'historie de vie de chaque espèces, et notamment de la phylopatrie basée sur le sexe.

<u>Le long bras de l'environnement du début de la vie</u>

Ce travail contribue à notre compréhension des mécanismes proximaux qui pourraient sous-tendre les importantes conséquences de l'environnement et des adversités sociales du début de la vie (Snyder-Mackler et al., 2020). Chez de nombreuses espèces, la perte de la mère pendant l'enfance ou la naissance d'un frère/sœur trop proche en âge a des effets délétères sur le développement et la survie des individus. Nos résultats suggèrent que cela pourrait en partie être dû à un sevrage précoce (*manuscrit 2*). Plus largement, l'influence des conflits mère-enfant et dans la fratrie pendant la période développementale sur les relations sociales intrafamiliales plus tard dans la vie restent peu connue. Par exemple, chez les humains, la

réaction du grand frère/sœur à la naissance de son petit frère/sœur est associée à la qualité de leurs relations plus tard pendant l'enfance (Dunn et al., 1994). De même, la qualité des relations dans la fratrie a d'importantes conséquences développementales chez les humains, et peut influencer les compétences sociales et la personnalité des individus (Brody, 1998; Sulloway, 2001). L'existence de telles relations chez les primates non-humains n'a pour le moment jamais été explorée.

En quoi la compétition dans la fratrie chez les espèces monotoques diffère-t-elle de la compétition chez les espèces polytoques ?

Ressources

Tout d'abord, nos résultats renforcent l'idée que les frères et sœurs d'âge différents chez les primates monotoques ne sont vraisemblablement pas en compétition pour le lait maternel (*manuscrits 1* et *2*). En effet, les juvéniles babouins sont déjà sevrés depuis plusieurs mois à la naissance de leur petit frère/sœur. Chez les mandrills, la naissance d'un petit frère marque la fin de la période d'allaitement, mais ne semble pas induire de conflits avec le grand frère.

Nos résultats soulignent l'importance de l'attention maternelle comme enjeu potentiel de la compétition dans la fratrie. L'attention maternelle est parfois mentionnée chez les primates non-humains (Achenbach & Snowdon, 1998) mais n'est pas considérée comme une ressource maternelle en soi. Au contraire, chez les humains, l'attention maternelle est considérée comme une ressource que peuvent se disputer les frères et sœurs (Volling et al., 2010). Cependant, l'attention maternelle est rarement définie, est difficile à mesure empiriquement, et les bénéfices associés à la monopolisation de l'attention maternelle restent flous.

Plus généralement, les ressources maternelles post-sevrage ont été très peu étudiées. On considère généralement que de telles ressources incluent la protection contre des prédateurs, le support social contre des congénères, un accès facilités à la nourriture ou encore des opportunités d'apprentissage social (Clutton-Brock, 1991; van Noordwijk, 2012). Cependant, très peu d'études ont essayé (i) d'identifier ces ressources formellement, (ii) de tester si ces ressources sont limitées et peuvent être diluées entre les différents enfants, ce

qui impliquerait qu'elles peuvent être l'enjeu de la compétition dans la fratrie, et (iii) de tester si la fourniture de ces ressources aux enfants entraîne des coûts pour la mère.

Mécanismes

Nos résultats soulignent que la compétition dans la fratrie chez les primates non-humains pourrait se manifester par des comportements plus subtils que de simples agressions, comme chez les oiseaux par exemple. Nous montrons que le contexte des interactions est un aspect important pour pouvoir détecter une potentielle compétition (*manuscrit 3*). De plus, chez les espèces avec une organisation sociale complexe, les interactions triadiques pourraient être riches d'enseignements quant aux stratégies comportementales permettant de façonner l'environnement social, notamment dans le cadre de la compétition entre frère et sœur (Massen et al., 2020).

L'aspect émotionnel de la compétition dans la fratrie chez les primates

La similarité de certains de nos résultats avec les patrons de la compétition dans la fratrie chez les humains soulignent les potentiels fondements émotionnels de la compétition dans la fratrie chez les primates non-humains. En effet, les enfants réagissent souvent à la perte de l'attention maternelle ou à un traitement parental différentiel par des réactions jalouses (Miller et al., 2000; Volling et al., 2010), qui ressemblent fortement aux patrons comportementaux observés chez les babouins chacma (*manuscrit 1* et *3*). La jalousie est une émotion sociale complexe, qui se manifeste lorsqu'un individu perçoit sa relation avec un partenaire social comme menacée par un parti-tiers rival (Parrott, 1991). En tant qu'émotion sociale dont la fonction ultime serait de protéger les relations sociales contre des intrusions, cette émotion pourrait avoir évolué dans de nombreux taxons où les relations sociales apportent des bénéfices pour la valeur sélective des individus (Nesse, 1990). Cependant, la présence d'émotions complexes comme la jalousie chez les animaux non-humains est largement débattue (Bekoff, 2000; De Waal, 2019). Peu d'études à ce jour se sont intéressées à la jalousie chez les non-humains, sauf dans le cadre des relations humains-animaux de compagnies (Abdai et al., 2018; Harris & Prouvost, 2014). Notre étude apporte donc une première indication que les primates non-humains pourraient avoir des comportements jaloux dans le cadre des relations entre frère et sœur.

CONCLUSION GENERALE

Cette thèse souligne que les relations entre frères et sœurs ne sont peut-être pas aussi harmonieuses qu'on ne le pensait auparavant chez deux primates sociaux monotoques à longue durée de vie, les babouins chacma et les mandrills. Nous montrons que le conflit mère-enfant et la compétition dans la fratrie peuvent survenir autour de la reproduction suivante de la mère, et que les frères et sœurs continuent à se disputer le toilettage et l'attention de la mère tout au long de leur période de développement, et même à l'âge adulte chez les femelles. De plus, la compétition entre frères et sœurs peut prendre des formes subtiles, comme des sollicitations maternelles ou des interférences non agressives qui ne sont détectables que lorsqu'on se concentre sur les contextes et les relations triadiques. Ainsi, la compétition fraternelle chez les primates peut être très différente dans ses formes de la compétition fraternelle chez d'autres espèces – comme les espèces d'oiseaux siblicides polytoques ou les hyènes tachetées, ou les otaries et lions de mer monotoques des Galápagos – et plus similaire aux querelles observées chez les enfants humains. Cette thèse est un travail exploratoire sur les relations entre frères et sœurs qui, je l'espère, attirera l'attention et permettra des investigations plus approfondies sur la compétition entre frères et sœurs chez les primates. En particulier, les frères et sœurs sont des partenaires sociaux importants tout au long de la vie chez de nombreuses espèces vivant en groupe, et comprendre comment leurs relations peuvent dériver d'une interaction complexe entre coopération et compétition peut être une étape clé nécessaire pour apprécier pleinement les effets du soutien des frères et sœurs sur la valeur sélective, et l'évolution des sociétés népotiques. Mon travail met également en évidence l'aspect émotionnel potentiel de la compétition entre frères et sœurs chez les primates, ce qui pourrait raviver l'intérêt pour l'étude des états émotionnels secondaires tels que la jalousie chez les animaux non humains, ainsi que pour son développement, en fournissant un contexte social pertinent pour étudier son occurrence, et qui pourrait avoir contribué à son évolution.

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Appendices

Appendix 1: Texte de vulgarisation scientifique publié à The Conversation Junior

« Pourquoi l'être humain est-il plus évolué que les autres animaux ? »

Tous les organismes présents sur Terre, dont les êtres humains, ne sont pas apparus tels qu'on les connaît aujourd'hui. Leurs formes actuelles sont le résultat de nombreux changements qui se sont accumulés au cours du temps : c'est ce qu'on appelle l'évolution des espèces. Aujourd'hui, on pense que toutes les espèces descendent d'un unique organisme : on l'appelle LUCA, dont les initiales en anglais veulent dire « Dernier Ancêtre Commun Universel ». Ce lointain ancêtre aurait vécu il y a environ 3,5 milliards d'années puis ses descendants auraient progressivement donné naissance aux diverses lignées d'organismes que tu connais : les bactéries, les plantes, les animaux, etc. Tu es donc un cousin très éloigné du chêne !

Mais comment une espèce évolue-t-elle ? A la naissance, les individus d'une même espèce ne sont pas tous identiques. Par exemple, imaginons que dans une population de singes, un individu naisse avec une forme de main différente qui lui permette de mieux grimper aux arbres : il pourra mieux se nourrir et s'abriter des prédateurs. Cette main bizarre lui permettra de vivre plus longtemps, donc d'avoir plus de petits que les autres. Si ses petits héritent de la même main, ils vont eux-mêmes faire plus de petits avec une main bizarre, et ainsi de suite jusqu'à ce que tous les singes de cette forêt possèdent cette « différence ». Cela s'appelle la sélection naturelle, et c'est le moteur de l'évolution. Petit à petit, lorsque deux populations se retrouvent séparées par un obstacle ou une distance infranchissable, de telles différences s'accumulent jusqu'à obtenir deux espèces distinctes.

Peut-on alors dire qu'une espèce est plus évoluée qu'une autre selon les différences qu'elle possède ? Non ! Le plus souvent, ces différences ne sont des avantages que dans certains environnements. Par exemple, savoir grimper aux arbres est avantageux en forêt, mais pas dans le désert. A force de s'adapter à la grande diversité d'environnements présents sur Terre, les lignées du passé se sont diversifiées en d'innombrables espèces, à l'origine de notre biodiversité. On ne peut donc pas dire qu'une espèce est plus évoluée qu'une autre, seulement qu'elle est mieux adaptée à son environnement.

Les humains seraient-ils donc les meilleurs car capables de s'adapter à tout type d'environnement ? Pas forcément. Par exemple, les fourmis d'Argentine sont aussi présentes presque partout sur Terre, et bien plus nombreuses que nous. C'est sans doute parce que, comme les humains, elles forment des sociétés complexes et ont trouvé des solutions astucieuses : par exemple, elles ont commencé à élever des pucerons des millions d'années avant que les humains ne fassent de même avec les vaches. D'autres espèces survivent là où aucun humain ne le pourrait, comme les minuscules tardigrades qui supportent des températures qui vont de -272 à +150°C, et même le vide spatial !

Mais les humains sont quand même une espèce à part, capable de parler, d'écrire, d'accumuler et de transmettre beaucoup d'information ou encore de construire des fusées : ne sont-ils pas les plus intelligents ? Pas si sûr, car chaque jour, de nouvelles découvertes nous dévoilent d'extraordinaires capacités chez les autres espèces, qui partagent beaucoup des nôtres. Par exemple, certains chimpanzés sont capables de mémoriser une suite de nombres si rapidement qu'ils battent tous les humains entraînés au même exercice (voir ici). Certains animaux possèdent des cultures, des systèmes de communication très efficaces, une capacité à se projeter dans le futur, ou encore de l'humour ; ils peuvent créer et manier des outils (comme les pieuvres), ressentir des émotions complexes comme la jalousie et le deuil, ou encore faire preuve d'une intelligence remarquable pour manipuler leurs congénères ou résoudre des problèmes complexes (comme les corbeaux).

Une chose est sûre, il est impossible de mesurer si une espèce est « plus évoluée » qu'une autre ! Chaque espèce possède des caractéristiques qui la rendent unique, et il nous reste encore beaucoup à apprendre sur les autres espèces. Qui sait, peut-être que toi aussi, un jour, tu feras des découvertes sur leurs étonnantes capacités ?

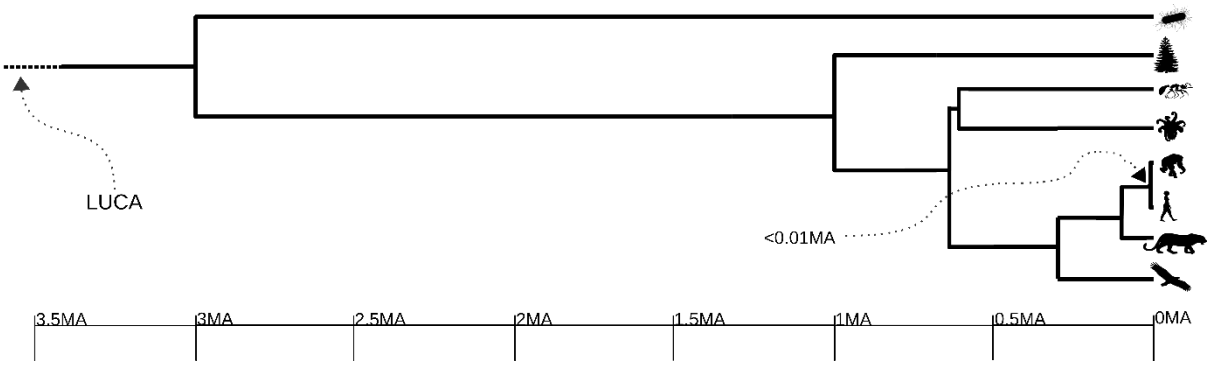

Figure 9: Evolution des espèces actuelles depuis le "Dernier Ancêtre Commun Universel". MA: Millards d'années. Silhouettes adaptées d'après Phylopic.

Appendix 2: A couple of baboon stories

At the end of each field seasons, we ask field assistants to write a little story about their time in Tsaobis. It can give you a little idea of the ups and downs of field work, and how crazy people can become spending their days with baboons.

Journey to becoming a certified baboon groupie, by Josephine Amwaalwa

After a week of quarantine, a gruesome COVID test and 2/6 necessary inoculations, I finally had my first day tracking baboons. The day commenced at the wee hour of 05:15, when my first of 3 alarms rang. 10 minutes later, I was out of my tent and headed to kudu, the bungalow in which we keep our field backpacks, electronics and oh – the kitchen. Armed with a PDA (glorified phone), GPS, satellite radio, first aid kit (random medical appliances is a more appropriate term), whistle, baboon ID notebook, water and lunch, we headed out at 06:20, half an hour before sunrise towards Baboon Hill. I have seen baboons before, but it is an entirely different marvel being surrounded by them. I felt equally excited and terrified – on one hand, I get to see them up close – on the other, these are wild animals and if I disregard their space, it could easily go downhill. I was on J Troop on my first day and I remember Jules clearly drilling into me that one of the things you never do is flinch when a baboon is approaching you. I flinched when two juvenile baboons both chased after a locust that flew in my direction. Conversely, I also didn't flinch when Schtroumpf came barrelling towards me, swerved left a metre just before he reached me and swerved back right to continue chasing a female baboon.

You see, baboons do not have such a great reputation in Namibia, they are one of the four officially declared 'problem animals' and nearly all the stories I heard of them was coming from that perspective. What a welcome surprise. I completely shed that perception of them. They all have so many different personalities and over time, I got to know which baboons were friends, who likes to eat what, how each one sleeps, the instigator of fights (Kalahari, always)… It was amazing to see that just like humans, even the parents had different rearing styles. Yersinia is the unbothered, free-range mother. Zika is the young adult in the peak of her 20s who accidentally got knocked up and is clearly cross about it. Bruise is the ladies' man who gets around a bit too much – Zika can attest – but he is evidently a great father because

his children are around him 24/7. Unsurprisingly the award for best mother, according to the 2021 volunteers, goes to Verruca.

I went to Tsaobis with no clue what the field time would be like and came back with one of the best experiences of my life. The soft hums, moo-grunts, barks, gecks and wahoos became the background soundtrack to my life and as I'm sure some of my teammates will mention, renouncing of the primitive human ways of communication to adopt the more eloquent language baboons use is a rite of passage. Tsaobis to me is babies throwing tantrums, males with ego complexes, fierce females, curious juveniles and getting lost at night on our way back to camp because the baboons decided that the closest sleeping cliffs were too mediocre for the gentry. It is also the little bit of passion you lose for existence because it's time for phenology again, playing broken telephone on the sat radio with the team at camp; magnificent geological features and the privilege of watching baboon society play out in front of me. Most importantly, Tsaobis is Cooties with his adorable, green-tinged muzzle from eating too many Salvadora berries. It is the *'you have got to be kidding me'* piercing stare a baboon gives you that makes you feel ashamed of your humanity.

<u>The mountain quest, by Esa Ahmad</u>

What follows is a tale of J-troop, whose intrepid spirit and total lack of sound leadership led to an afternoon odyssey containing the most exasperating and uplifting moments of my season. It was this daring episode which cemented my love for those ridiculous baboons. No crag could concern, nor peak perturb, nor terrain trouble the heart of a J-troop baboon, and for these plucky papionins the onrush of night was simply inducement to push ever further beyond the horizon.

Perhaps the political turbulence of J-troop is relevant. The decision-making process of ababoon troop is not easily discernible, but I like to think that it was a wag-the-dog policy decision by some high-ranking individual, seeking to distract from the scandals of scuffling and shrieking, the fights and chases, of that anarchic afternoon, which caused them to rise with sudden resolve and forge ahead into the far-flung hills.

Helen and I stopped mid-lunch to follow them to what we assumed would be one of their predictable set of favourite locations. First past Leopard Quelle. 'That's a curveball', we

thought. Through an unfamiliar tributary. 'Very interesting', said we. Then to the Python Valley Road and, to our concern, along the inclining slope and up Buttberg's precipitous haunch. 'This is weird, but it won't get any weirder', we reassured each other with wavering voices. Over the following hours the baboons led us implacably across the highest hills in their range and skirted ever closer to the looming lip of Potberg. This summit, clearly visible from almost every part of Tsaobis, we had climbed as a group on a communal day off for the very reason that we expected never to do so with the baboons.

From their early afternoon departure to their final resignation on a makeshift sleeping cliff in the shadow of the mountain, J-troop never stopped. Once we accepted this, there was joy in the journey. There was great fun in it as the day cooled and we puzzled our way across inscrutable geology. Walking amongst forty baboons along a lofty ridge, the shadows lengthening and the plains spread below me, I found one of my very favourite moments of the season.

Whatever J-troop was searching for, they never found it. As the sun dipped and the light turned golden, as a twilight wind poured in and a mumbling of anxious grunts flurried across the hillside, we abandoned the baboons to their fate. During our quest, we had caught intermittent bursts of radio communication from which the hills usually shielded us. Unable to make ourselves heard, our dismay had grown at the prospect of not having a lift to camp. It was only as we bum-slithered down a darkening tributary that we came into radio contact with Vittoria, desperately enunciated the words '*Pot-berg*' into the crackling airways, and were met with the deadpan response:

'You are joking'.

I don't think it was until we showed our GPS points to the team that the drama of our excursion was entirely believed.

Elisa Fueyo

I remember my first day in the field with the baboons as a very exciting but also a bit scary one. I had never been close to a wild animal before, so it was very surprising to see how close to us the baboons would walk and do their life without caring about us. However, very soon I learned how careful and respectful you have to be while being around them. That morning

a juvenile female screamed because a juvenile male had scared her; the other volunteer was in front of them and a juvenile male came from behind and slapped him because he thought the volunteer had been the one scaring the female. Everything seemed really complicated that day and also during the first month; I will be honest and say that I had some moments of self-doubt, as I had never been able to imagine how hard fieldwork with wild animals was before I arrived at Tsaobis. However, working at the Tsaobis Baboon Project turned out to be the most interesting and amazing thing I have done in all my life.

Being able to observe the lifes of 120 wild baboons from so close and on a daily basis is such a unique thing that I could not describe it with words. Not only I got to know baboon personalities, such as Zica 'the super careless mum', Lupus 'the philosopher' or Djuba 'the baboon everyone wants to play with', but I also did things I would never imagine I was able to do, like climbing a cliff while Byron (a very cheeky baboon) was looking down at me from the top or hiking 1 hour in the darkness to find the troop before they woke up. I would say that this experience has taught me as much about baboons as about what I am capable of (which is for sure much less than what a baboon is capable of!).

Although baboons are of course the main characters of this story, the human team I worked with at Tsaobis was as important or more. I am extremely thankful to Axelle and Vittoria for leading the field site so well and for making us feel at home all the time. I have so many good memories from the time I spent at Tsaobis thanks to the great and supportive team I was part of. Discussions during dinner were one of my favourite moments, going from baboon gossip and putting the toilet seat down to 'what Tsaobis Baboon would you be?' and nightmares about baboons or phenology. We are aware that this particular experience with the same group of people and baboons will not happen again, but at least we can go back to it every time we meet and our conversation slowly turns to our Tsaobis memories.

Ben Kawam

Living with the Tsaobis baboons is an unconventional human experience. Our life-style there is odd in many ways. We are in a remote place, and share kitchen with crickets. We follow the cycle of the sun. We see our standards for food drastically change, such that instant noodles become delicious. And all of this is still somewhat tangible. Many of us, Tsaobis alumni, are now back to a more classic lifestyle, and, every time we see a sunset, or eat some questionable

food, we might think: “oh, this reminds me of Tsaobis”. These aspects are also the easiest to share with others, who never lived in the desert or shared their days with the baboons.

However, in my opinion, the most striking, the most baffling, aspect of life at Tsaobis is of a different nature. It is difficult to describe it explicitly. Perhaps because so few elements of “real life” are attached to it. Maybe it is so odd, almost taboo, that the topic usually remains enclosed to the narrow circle of us who have known baboons. I am, of course, speaking about our *baboon metamorphosis*.

When we arrived in Namibia for the first time, all of us were standard humans. With a human spoken language, and a human body language. We were interested in topics related to humanity. For example, most of the gossips we shared were about human people. However, as we woke up from uneasy IDing dreams, mornings after mornings, we gradually found ourselves transformed into gigantic baboons.

Pop culture became baboon pop culture. Two Tsaobis volunteers, Esa and Helen, started to elaborate baboon memes. Their obscure British pop culture references got supplanted by L-troop jokes, shared and understood by all field workers. We discussed which baboon was the most famous influencer, which juvenile was promised to which career, and which sort of YouTube channel some of the baboons were running.

We discussed baboon politics. The social status of the J-troop adult males was standard source of polarisation among the volunteers. Schtroumpf and Narco, two large males, were competing for the alpha status. As in many human political systems, no candidate was a good candidate, and we were to pick the least terrible one. Both males were violent and, to some extent, stupid. Some theories argue that Schtroumpf and Narco were also engaged in a tumultuous romance, igniting the conflict.

Some days, our transformation was leading us to behave in peculiar ways. Competition for salt or water around the dinner table was materialised into baboon-inspired threats. Many times, volunteers were seen lipsmacking and presenting to each other. Showing intent of affiliation was made easy, for volunteers could connect using a set of social convention they found themselves comfortable with.

Today, most of us, ex-Tsaobis baboons, are back, roaming around the human world. Only in our dreams, or when meeting together, can we embrace who we once were, and greet each other with a “hey baboon”.

All the small things, by Axelle Delaunay

It is very hard to find a single story to tell about Tsaobis: there’s always something happening, whether it’s the baboons doing something weird/funny/cute/scary; a car breaking down; someone getting bitten; someone getting lost without radio contact with the others; Helen’s ripping her trousers… But I think that what makes Tsaobis so special is the range of emotions baboons make you feel every single day:

Hatred, when J troop decides at 1pm when it’s hottest to run back to Leopard Quelle through the hills because they’re thirsty while you were hoping to take a sneaky post-lunch nap in a shade; dispair, when you’re running after them running after locusts in the hills and the only thing you can see is the last one of the troop disappearing two hills ahead of you; fun, when you’re in front of a bunch of infants playing all together on a cliff, occasionally falling from several meters; wonder, when you’re quietly walking with the baboons and suddenly a female kudu and her baby join the troop and stay with them without bothering for you for more than 1h; relief, when after running for 4 hours in the morning to forage, L troop finally settle down to nap; boredom, when the only thing you can see is sleeping baboons lying flat on the ground/hiding in cracks and you can’t identify anyone; panic, when you realized all of your team fell asleep at lunch and there’s no baboons in sight anymore; anger, when two adult males don’t want to fight between each other to decide who is the strongest and instead start attacking and traptreeing innocent females, who will, most annoyingly, groom them just after; thrill, when an alpha female decides that she is not the one to be attacked because a male has ego’s problem and fight back, getting support from all her matriline (I truly found myself in a stadium mood, internally shouting “JK! JK! JK!” in my mind); disgust, when Rubella with her swelling 6 is mating with her brother daddy Bruise right next to where you’re sitting; also disgust, when Shelley had such a big swelling that she couldn’t deal with salvadora’s diarrhoea anymore, and her entire back legs and swellings where covered in poop, as well as Narco’s balls; sympathy, when you see that Bobo is so used to be rejected and abandoned by his mom, that he always keeps a hand on her back to be

ready to jump on her if ever she tries to run away from him; sadness, when you watch an infant baboon die in front of you; frustration, when one of "the rich kids" wants to steal food from a lower ranking individual, and instead of fighting for it himself, just scream to call his mom; fear, when one of the baby rich kid decides to come sit on your shoe and play with your shoe laces and all the adults around stop and watch you; also fear, when one of the adult male makes it an habit to retaliate aggression toward you whenever he loses a fight (you become very careful to not be the smallest one in the team); affection, when one of the female you were following four years ago just gave birth to her first baby (you understand how every grandma in the world must feel); sweetness, following the perfect couple Scurvy and Vitiligo and their baby, watching him climb on Scurvy's head to play; weird envy when watching the perfect moms Kinsh, Freetown or Verruca spending their entire time grooming their offspring one by one and feeling that if you had to pick a baboon mom, it would be one of them; pure love, when you see your 2 favorite individuals in each troop (Coeur Coeur Coeur sur vous Cooties and Djuba) meeting, playing and grooming each other during an ITI (this was truly my happiest moment in Tsaobis, I was smiling at the thought of it the entire evening after); and this list could go on and on forever as you could add a new story every day! Cheers to all the baboons for giving me so much joy(ce) and so many memories during 7 months!

A lively evening in the baboon kingdom, by Vittoria Roatti

It was a wonderful (as always) summer evening at Tsaobis, and we were gladly walking back to camp with J troop at a decent time to be on the cliff well before dark. Happy to avoid almost-dark panicking runs to bed that had been a recurring nightmare of J troop teams, I followed Kinshasa (a mature lady, whose leadership I trust blindly) up the riverbed side of Baboon Hill. Soon afterwards, the guys (how I like to call baboons) were grooming on the hillside, kissed by the sunset orange/pink light that one could only dream of in Europe.

I was doing proximity scans and I quickly got stuck in finding the same social groups grooming/cuddling together. At one point, I saw Gao throwing one of his best tantrums to JK, while Turkana was threatening him to be the one closest to the mother. JK got annoyed and attacked the poor Turkana, who started screaming like crazy, plumping her mother's rage. JK, who is not a particularly good mother (as you may have sensed already), is a very aggressive female, whom even bigger subadult males pass by with cautiousness. That evening it was the turn of Amboseli: he passed a few meters from the scene, almost tiptoeing, and accidentally served as a perfect target for JK's redirected aggression, who started to scream immediately after, as if he'd been the one attacking her.

After taking a good 5 minutes to record all these odd dominance interactions, I decided it was time for fresher air (and avoid falling victim of JK myself!) and climbed further up where my beloved Consanguin was grooming with his big sister Tanganyika. Those human-sniffing specialists are among my favourites in J troop. Unfortunately, the so-called baby criminal Byron was not far, alone and bored, looking for someone to bother. Since I had just said that he was behaving better, I didn't want to give him the chance of prove myself wrong and I kept walking towards the edge of the hill. "Oh perfect" I thought: L troop was on the other side of the hill, so I could collect scans on them as well.

Without a second thought, I left the not-so-recommendable J atmosphere to join the L vibes (who scored a little lower in the number of "problematic" – to use a gentle word – individuals at the time). While cursing myself for not having been born baboon, which would have made my climb down much more straightforward (literally – instead of zig-zagging around looking for a slightly more stable rock to put my foot on), the nasty rock betrayed me, and I brutally fell on the hard and edgy hillside less than 1 metre below. It had been a bad fall, but, after a few seconds checking that nothing was broken, I looked around to make sure that (1) my field partner and (2) the baboons hadn't seen me falling. The latter was hopeless: those smart furry balls were pitifully looking at me like I was some sort of old/sick animal. Well, the damage was done, but I still managed to (painfully) stand up quickly enough to fade some doubt about my, undoubtfully compromised, physical abilities: "I'm still alive, you cannot take my backpack yet".

Still willing to get some work done during that last hour of light, I scanned the surroundings looking for the top individuals on the proximity list that I had memorized before. None was nearby, but Lupus, my (and everybody's really) favourite subadult male in L troop, was grooming his little sister Munchausen: what a perfect scene to record. I tapped on my pocket, looking for the PDA (the smartphone we use to collect data) and felt nothing but my leg underneath. At the same time, I saw that Munch was hugging a rectangular object with a blue cover and Lupus was probably grooming her to have a closer look at it, while keeping the other baboons away at the same time. A group of juveniles interested in the object was gathering around (Herpes of course – Munch's paternal sister and best friend; a bunch of males: Plague, Pots, Parkinson; and the little Myxo). Munch, the small survivor daughter of Ringworm (who must have died when she was barely weaned), wouldn't have stood a chance without Lupus' support. Two thoughts hit my brain at the same time: (1) Lupus, who could have just supplanted Munch to have the PDA like any other subadult male would have certainly done, is amazing (!), and (2) I am completely screwed. Maybe there was a small chance to get the smartphone back, but I had to act quickly before it got in the mouth of someone with bigger teeth than the little Munch, who was already gently biting the soft cover.

"What if I trade the PDA with something else?". It was risky and certainly not covid-friendly, but she already had the smartphone anyway. So, I looked for things that I could have used: the personal alarm maybe not; the crisps' empty bag, the pencil, and the hand sanitizer

were the safest options. I got a bit closer, to avoid that other naughty guys ruined my plan, and pretended to drop the pencil. Munch quickly grabbed the new, unexpected toy and started chewing the tip, while holding the PDA with the other hand. Then, it was the turn of the plastic bag, which she promptly collected and held with her foot (of course, I should have known that I needed 4 items to get all her opposable thumbs busy!). Starting to think that the previous fall must had seriously damaged my brain, Munch saw a little plastic bottle falling at her feet, and she loved it more than anything else. I don't know what made that hand sanitizer special, but the pretty princess dropped the PDA and I calmly picked it up before another baboon did as if it was the most normal thing in the world. It worked: I was alive, no baboon had threatened me, and I had the smartphone back. In the meanwhile, Lupus had been distracted by the PDA cover, which Munch had taken proficiently out better than we were ever able to do (it was a hard one to remove!), and he was proudly walking away with the soft plastic in his mouth. I got that one back as well a few minutes later, when he dropped it to chase someone for apparently no reason (well, I only said that he was nice to his sister, not to everybody…).

At the end of another adventurous day in the baboon kingdom, the sun had set over a happy Munchausen, and we discovered that a hand sanitizer is more valuable than a smartphone, at least for a baboon! The PDA involved also acquired a special value among us since it had been saliva-autographed by our special VIBs (Very Important Baboons).

Sibling competition in two social primate species, chacma baboons and mandrills

Parental care is widespread in the animal kingdom and refers to any parental trait that enhances an offspring fitness. Yet, the amount of parental care that can be devoted to each offspring is limited, conflicts may therefore arise between the different family members with diverging evolutionary interests. Sibling competition has been extensively studied by behavioural ecologists who focused on competition over parental resources between same-age offspring in species producing broods or litters, or by psychologists who focused on children from Western societies. Hence, little is known on competition between different-age siblings in non-human species producing one offspring at a time (i.e. monotocous). In this thesis, we investigated the causes and mechanisms of sibling competition in two social primate species, chacma baboons (*Papio ursinus*) and mandrills (*Mandrillus sphinx*). These two species both produce one offspring at a time and share many similarities in their social organization but mandrills are seasonal breeders living in equatorial, food-rich forests while chacma baboons reproduce non-seasonally and live in a challenging arid environment. In the first two chapters, I investigate the dynamics of maternal care and mother-offspring relationships during an intriguing milestone, the birth of a younger sibling, in both species. I show that young chacma baboons solicit their mother more often and show more signs of anxiety after the birth of their younger sibling although they are already weaned and do not suffer from reduced maternal investment. This result suggests a discrepancy between the amount of maternal care provided by the mother and the amount requested by the juvenile (*manuscript 1*). In contrast, in mandrills, the birth of a younger sibling induces an abrupt decrease in maternal care toward the older sibling which, yet, does not trigger any detectable signs of conflicts. In addition, juvenile mandrills show sex-specific reactions, with females increasing their affiliations toward the mother while males become more rapidly independent than females (*manuscript 2*). Finally, as sibling competition in humans is often characterized by children's attempts to disrupt affiliative interactions between their mother and their siblings, the last chapter investigates offspring interferences in grooming interactions between the mother and a sibling. I show that grooming interferences occur in contexts eliciting sibling competition, are most frequent against siblings with whom competition is more intense, and are generally unsuccessful at granting access to maternal grooming (*manuscript 3*). These results suggest that grooming interferences may reflect spontaneous emotional reactions to affiliation between the mother and a sibling rather than strategic attempts to gain maternal grooming. This work extends our understanding of sibling competition in long-lived, monotocous social mammals by showing that sibling conflict can extend beyond nutritional dependency, over post-weaning maternal resources such as maternal grooming and attention, and can take subtle forms. In addition, this thesis provides new insights on the potential emotional aspect of sibling competition and the evolution of secondary emotional states in non-human primates.

Keywords: sibling competition; parental investment; post-weaning maternal care; transition to siblinghood; jealousy

Compétition dans la fratrie chez deux espèces de primates sociaux, les babouins chacma et les mandrills

Les soins parentaux sont très répandus dans le règne animal et désignent tout trait parental qui améliore la santé de la progéniture. Cependant, la quantité de soins parentaux qui peut être consacrée à chaque enfant est limitée. Des conflits peuvent donc survenir entre les différents membres de la famille dont les intérêts évolutifs divergent. La compétition entre frères et sœurs a été largement étudiée par les écologistes comportementaux qui se sont concentrés sur la compétition pour les ressources parentales entre enfants de même âge chez les espèces produisant des couvées ou des portées, ou par les psychologues qui se sont concentrés sur les enfants dans les sociétés occidentales. Par conséquent, on sait peu de choses sur la compétition entre frères et sœurs d'âges différents chez les espèces non humaines produisant un seul enfant à la fois (c.à.d. espèces monotoques). Dans cette thèse, nous avons étudié les causes et les mécanismes de la compétition entre frères et sœurs chez deux espèces de primates sociaux, les babouins chacma (*Papio ursinus*) et les mandrills (*Mandrillus sphinx*). Ces deux espèces produisent un seul petit à la fois et partagent de nombreuses similitudes dans leur organisation sociale, mais les mandrills sont des reproducteurs saisonniers vivant dans des forêts équatoriales riches en nourriture, tandis que les babouins chacma se reproduisent de manière non saisonnière et vivent dans un environnement aride difficile. Dans les deux premiers chapitres, j'étudie la dynamique des soins maternels et des relations entre la mère et sa progéniture lors d'une étape intrigante, la naissance d'un petit frère ou d'une petite sœur, chez les deux espèces. Je montre que les jeunes babouins chacma sollicitent plus souvent leur mère et montrent plus de signes d'anxiété après la naissance de leur petit frère ou petite sœur, bien qu'ils soient déjà sevrés et ne souffrent pas d'une diminution de l'investissement maternel. Ce résultat suggère un décalage entre la quantité de soins maternels fournis par la mère et la quantité demandée par le juvénile (*manuscrit 1*). En revanche, chez les mandrills, la naissance d'un frère ou d'une sœur plus jeune induit une diminution abrupte des soins maternels envers le frère ou la sœur plus âgé(e) mais, pourtant, ne déclenche aucun signe de conflit détectable. De plus, les mandrills juvéniles montrent des réactions spécifiques au sexe, les femelles augmentant leurs affiliations envers la mère tandis que les mâles deviennent plus rapidement indépendants que les femelles (*manuscrit 2*). Enfin, comme la compétition entre frères et sœurs chez les humains est souvent caractérisée par les tentatives des enfants de perturber les interactions affiliatives entre leur mère et leurs frères et sœurs, le dernier chapitre étudie les interférences de la progéniture dans les interactions de toilettage entre la mère et un frère ou une sœur. Je montre que les interférences de toilettage se produisent dans des contextes suscitant la compétition entre frères et sœurs, qu'elles sont plus fréquentes contre les frères et sœurs avec lesquels la compétition est plus intense, et qu'elles ne réussissent généralement pas à donner accès au toilettage maternel (*manuscrit 3*). Ces résultats suggèrent que les interférences de toilettage peuvent refléter des réactions émotionnelles spontanées à l'affiliation entre la mère et un frère ou une sœur plutôt que des tentatives stratégiques pour obtenir le toilettage maternel. Ce travail élargit notre compréhension de la compétition entre frères et sœurs chez les mammifères sociaux monotoques à longue durée de vie en montrant que le conflit entre frères et sœurs peut s'étendre au-delà de la dépendance nutritionnelle, sur des ressources maternelles post-sevrage telles que le toilettage maternel et l'attention, et peut prendre des formes subtiles. En outre, cette thèse fournit de nouvelles perspectives sur l'aspect émotionnel potentiel de la compétition entre frères et sœurs et sur l'évolution des états émotionnels secondaires chez les primates non humains.

Mots-clés : compétition entre frère et sœur ; investissement parental ; ressources maternels post-sevrage ; transition vers la fratrie ; jalousie