

Understanding Constraints on Horizontal and Vertical Information Transmission in Baboons: Implications for the Evolution of Culture

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University College London

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Cover photo: Baboons ready to run for food at sunrise, Tsaobis (Namibia).

Photo credit: Vittoria Roatti.

DECLARATION OF ORIGINALITY

I, Vittoria Roatti, confirm that the work presented in my thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis. Author contributions for each research chapter are provided in a dedicated section at the end of the thesis. The pictures shown in this thesis are my own unless otherwise stated.

London, 15/03/2024

Vittoria Roatti

ABSTRACT

Culture involves the social transmission of information between individuals. Immature individuals may have a fundamental role in the formation of culture because they learn socially more than adults. This learning facilitates both information spread at the group level and its maintenance across generations. Baboons, group-living primates, represent an interesting study case because they innovate and readily learn socially, but they are not generally considered a species with culture (Chapter 1). In this thesis, I addressed the possible constraints on social learning in wild immature chacma baboons (*Papio ursinus*). I describe how social networks, and thus opportunities for social learning, change during development and are influenced by maternal social features (Chapters 2 and 3); how social learning evolves throughout the immature period and from whom immatures learn (Chapter 4); and how maternal warmth, a component of maternal style linked to social learning propensity, influences the offspring's tendency to acquire social information (Chapter 5). Immature baboons tended to both associate and learn from members of their matriline (close maternal kin), potentially limiting information spread at the group level. Juvenile males could intensify matrilineal clustering by associating and learning from same-sex peers more than females. The steep dominance gradient present in most baboon species may further hinder social information diffusion by promoting learning from close kin. There was no effect of maternal warmth on an offspring's tendency to learn socially. Overall, I argue that the emergence of group-level cultures in baboons, and other female-philopatric primates, may be constrained by the social clustering of their matriline-based networks. However, the question remains

about whether behaviours that are socially transmitted and maintained within matrilineal groups qualify as culture, as is the case for socially transmitted and maintained group behaviours.

IMPACT STATEMENT

This thesis increased our understanding of which factors may constrain social information transmission, and potentially the formation of culture, in chacma baboons and other species. The research has relevant impacts both inside and outside academia.

Inside academia, this research helped to fill important gaps in our knowledge and may inspire further studies aiming to understand cultural evolution. Baboons live in well-connected multi-male-multi-female social groups and readily learn socially. Nevertheless, there is little evidence of culture in baboons. We address this paradox by investigating how the opportunities to learn from others change in immature age classes, who are known to learn socially more than adults. Indeed, while social learning has been studied in a variety of taxa, there is still little knowledge on how this develops in infants and juveniles, particularly in species that do not use tools.

In terms of academic output, this thesis is structured as a series of papers that are either published or in preparation for submission to a journal. Importantly, the results found in this observational research have various implications on the formation of culture in wild groups, thus setting the bases for further studies testing the hypothesised limitations on social information transmission experimentally. Because baboons are considered a model species for understanding the selection pressures on early hominin evolution, information on the limitations on social learning in baboons may also stimulate new hypotheses on the evolution of cumulative culture in humans. Indeed, Dr Alecia Carter and I have been awarded a Leakey Foundation Research Grant to conduct

experiments testing the constraints on individual and social learning of tool use, and potentially the formation of tool-use cultures, in baboons.

This research is also likely to attract non-academic interest, which may benefit conservation. Because culture is a fundamental characteristic of humanity, it is a concept widely explored outside academia, thus providing opportunities for public engagement. The public's involvement in research strengthening the evolutionary link between baboons and humans could increase people's benevolence towards baboons, who are generally considered pests across Africa. This may contribute to the adoption of non-violent solutions to the human-baboon conflict, which may promote conservation both by (1) improving the status of species sharing baboons' ecological environment and (2) generally increasing people's sensibility towards other animals, potentially enhancing the allocation of funds towards conservation initiatives.

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Vittoria Roatti: conceptualisation, formal analysis, data curation, writing (original draft), visualisation.

Guy Cowlshaw: writing (review and editing), project administration, project funding.

Elise Huchard: writing (review and editing), project administration, project funding.

Alecia Carter: conceptualisation, formal analysis, writing (review and editing), supervision, project administration, project funding.

4. In which chapter(s) of your thesis can this material be found?

Chapters 2 and 3

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Date: 04/02/2024

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1 CHAPTER 1: GENERAL INTRODUCTION

1.1 INTRODUCTION

Culture is a fundamental characteristic of humanity, but it is rarely found in other social animals (Tennie *et al.* 2009, Dean *et al.* 2012), despite social learning, a critical mechanism for the formation of culture, being widespread in the animal kingdom (Laland 2004, Dall *et al.* 2005). Social learning can allow the rapid dissemination of novel information among group members and has been widely implicated in the formation of culture (Laland and Janik 2006, Whiten 2017). Although our knowledge regarding the evolution of social learning and culture has increased exponentially in recent years, there are still important fundamental gaps (Street *et al.* 2017, Whiten and van de Waal 2017). In particular, we have very little understanding of why some cultural traits spread quickly and become established in a social group (van de Waal *et al.* 2013, Aplin *et al.* 2015) while others do not (van de Waal and Bshary 2011, Ladds *et al.* 2017). To understand the causes of the different patterns of diffusion and fixation, we should consider that cultural traits arise through a multi-step process: (1) novel information has to be produced (innovation), (2) the information has to spread between most individuals in a social group (transmission), and (3) the information has to be maintained for a period of time (maintenance) (McGrew 1998, Perry and Manson 2003). Innovation stems from individual learning and has been defined as the production of novel information, the expression of novel behaviours, or the use of known behaviours in a novel context (Ramsey *et al.* 2007, Bandini and Harrison 2020). Importantly, the other two steps in this process, namely transmission and maintenance, entail social learning. The

transmission phase regards horizontal social learning, i.e., information is passed from peer to peer (Allen *et al.* 2013, Hobaiter *et al.* 2014), while the maintenance phase involves vertical social learning, i.e., information is passed from older to younger individuals (Sargeant and Mann 2009, Lamon *et al.* 2017). Culture may or may not arise because of differences in who learns from whom during these phases (van Schaik 2010). This chapter focuses on which factors enhance or constrain horizontal and vertical transmission of information, and thereby promote or limit cultural evolution.

1.2 SOCIAL LEARNING AND CULTURE

1.2.1 Definitions and evolution

Social learning is widespread in the animal kingdom (see Table 1.1 for definitions) and its evolution and implication in the formation of culture have been a major focus of recent research (Whiten and van de Waal 2017, Schuppli and van Schaik 2019), with potential implications for species' conservation (Brakes *et al.* 2019, 2021). The ability to learn from others has been documented in a variety of animal taxa, mainly vertebrates, but also invertebrates (Whiten 2017, Allen 2019). Among vertebrates, studies on social learning and culture focused mostly on non-human primates (hereafter primates), in which social learning seems to 'pervade' most aspects of their development and sociality (Whiten and van de Waal 2017, 2018). Other taxa that have been a major focus of social learning and culture studies are cetaceans, songbirds, and fish (Laland and Janik 2006, Allen 2019). Whilst humans may be the only species to have evolved cumulative culture (i.e., where novel innovations are built on previous innovations (Tennie *et al.* 2009, Dean *et al.* 2012); but see Schofield *et al.* 2018, Garland *et al.* 2021,

Whiten *et al.* 2021), studies on non-human great apes (hereafter apes; see §1.2.2) and cetaceans question whether culture can be considered a distinctive hallmark of humanity (Sommer and Parish 2010, Whiten 2019). Indeed, many believe the difference between human and non-human culture is more of quantity rather than quality (Whiten 2017, Schuppli and van Schaik 2019).

Table 1.1: Examples of definitions of **social learning** (in ascending chronological order).

Definition	Reference
"Learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products."	Heyes 1994, p. 207
" (...) any information that is generated by the behaviour of another organism."	Dall <i>et al.</i> 2005, p. 187
"Any process through which one individual ('the demonstrator') influences the behaviour of another individual ('the observer') in a manner that increases the probability that the observer learns."	Laland 2008, p. 368

Social learning can be adaptive because: (1) individuals save the time and energy required for individual learning by using information produced by others; and (2) learning certain kinds of information individually, such as food edibility (Boinski and Frigaszy 1989, Landová *et al.* 2017) or predator avoidance (Shier and Owings 2007, Griesser and Suzuki 2017), would be too costly (Laland 2004, Dall *et al.* 2005). Relying on social information (e.g., on patch quality), however, entails some risks because it can be unreliable, or it can quickly become outdated (Giraldeau *et al.* 2002). Therefore, individuals trade-off between gaining information socially and individually, and could switch from one to the other depending on the context and their behavioural plasticity (Kendal *et al.* 2005, Mesoudi *et al.* 2016).

In order to demonstrate that a behaviour relies, at least in part, on socially transmitted information, researchers have used observational evidence, experiments, and mathematical models (Whiten 2000, Laland 2008). First,

observational evidence has been claimed when it was possible to track the diffusion of a novel behaviour among group members (McGrew 1998). Famous examples are potato-washing and wheat-sluicing invented by a Japanese macaque (*Macaca fuscata*) (Schofield *et al.* 2018). Second, experiments showed how individuals who had witnessed a demonstrator (i.e., the individual to whom they pay attention) trained to solve a task were more likely to either solve the task or manipulate the same object parts compared to controls (who did not witness a demonstrator) (Reader and Biro 2010). For instance, compared to controls, observer great tits (*Parus major*) were more likely to solve a hidden-food task (Aplin, Sheldon, *et al.* 2013) and vervet monkeys (*Chlorocebus pygerythrus*) to interact with the same object parts that a demonstrator touched in a tool-use task (van de Waal and Bshary 2011). Third, new mathematical models allow the assessment of the likelihood of social and asocial information transmission (i.e., Network-Based Diffusion Analysis). In social transmission models the rate of information acquisition depends on individuals' social networks, while in asocial ones, information acquisition is independent from social connections (Hoppitt *et al.* 2010). These models have been applied, among others, to chacma baboons (*Papio ursinus*) (Carter, Torrents Ticó, *et al.* 2016), humpback whales (*Megaptera novaeangliae*) (Allen *et al.* 2013), and songbirds (Paridae family) (Aplin *et al.* 2012).

Studies on social learning have also focused on the strategies adopted to maximize the benefits of acquiring social information and on the mechanisms through which information is transmitted (Whiten 2000, Laland 2008). First, because evaluating the current value of social *versus* individual learning could require time and relatively high cognitive abilities, individuals may adopt 'learning strategies' that favour the acquisition of social information when and from whom

it is most beneficial (Laland 2004, Kendal *et al.* 2005). For example, the prevalence of social learning in immature individuals (Carter *et al.* 2014, Noble *et al.* 2014) is consistent with a ‘copy when uncertain’ strategy (see §1.3.1) and an attentional bias towards older group members (Mann *et al.* 2007, Barrett *et al.* 2017) reflects a ‘copy knowledgeable individuals’ strategy (see §1.4.1) (Laland 2004). Second, social information can be acquired through different mechanisms, which can be divided into two categories, ‘high fidelity’ and ‘low fidelity’, based on the faithfulness of the information transmitted (Tennie *et al.* 2009, Bandini *et al.* 2020). When learning through high-fidelity mechanisms, most of the information is transmitted socially (Horner and Whiten 2005, Whiten *et al.* 2009), while low-fidelity mechanisms involve a large part of individual learning following the acquisition of few social cues (Bandini and Tennie 2020, Tennie *et al.* 2020). The social learning mechanisms adopted by a species may require different cognitive abilities and have implications on information transmission at the group level (Lewis and Laland 2012, Meulman *et al.* 2013) (see §1.3.2).

In some cases, social learning leads to the formation of culture (see Table 1.2 for definitions). As mentioned, culture is a multi-step process involving the innovation, transmission, and maintenance of a novel behaviour (McGrew 1998, Perry and Manson 2003). Transmission and maintenance involve, respectively, horizontal (between peers) and vertical (from older to younger individuals) social learning (van Schaik 2010). For example, following the innovation of potato-washing and wheat-sluicing by a juvenile female Japanese macaque, these new behaviours were first transmitted among other juveniles and eventually to adult females, who then passed it to their infants (Schofield *et al.* 2018). Culture has thus been proposed as a ‘second inheritance system’ because, even though it involves the transmission of social, rather than genetic, information, it has the

potential to produce evolution similarly to the primary genetic system (Whiten 2017).

Table 1.2: Examples of definitions of **animal culture** (in ascending chronological order).

Definition	Reference
"Culture is considered to be group-specific behaviour that is acquired, at least in part, from social influences. (...) <i>Prima facie</i> evidence of culture comes from within-species but across-group variation in behaviour (...)."	McGrew 1998, p. 305
"Cultural behaviour is one that is transmitted repeatedly through social or observational learning to become a population-level characteristic."	Whiten <i>et al.</i> 1999, p. 682
"A behavioural practice that is relatively long-lasting (i.e., is performed repeatedly over a period of time) and that is shared among members of a group in part through social learning."	Perry and Manson 2003, p. 71
"All group-typical behaviour patterns, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information."	Laland and Janik 2006, p. 542
"The cultural traditions of non-human primate species (...) represent behavioural biases of different populations, all within the respective species' ZLS, generated by founder effects, individual learning, and product-oriented (rather than process-oriented) copying."	Tennie <i>et al.</i> 2009, p. 2413
"An individual's cultural repertoire is the sum of all socially learned skills and knowledge."	Schuppli and van Schaik 2019, p. 5

Several definitions of culture have been proposed but there is still no full consensus over which is most suitable (Table 1.2). As a result, studies applying different definitions may not be comparable (Schuppli and van Schaik 2019). All culture definitions agree that the presence of social learning is an essential requisite for the formation of culture, although the possible influence of genetics and ecology is recognized (Laland and Janik 2006). Yet, the mere presence of social learning is not enough to fulfil most definitions (but see Schuppli and van Schaik 2019), and a behaviour needs to be shared by most group members (McGrew 1998, Whiten *et al.* 1999) and to be maintained through time (Perry and Manson 2003) in order to qualify as cultural. However, some authors argue that the role of social learning in animal culture is limited, compared to its importance in human culture, because information transmission is mainly sustained by individual learning within a species' 'Zone of Latent Solutions' (ZLS; i.e., all innovations that are achievable by a species based on its cognitive abilities).

According to this hypothesis, animal social learning involves only low-fidelity mechanisms, leading them to almost ‘reinvent solutions’ from the observed products of others’ behaviours (Tennie *et al.* 2009) (see also §1.3.2).

Cultural behaviours can be ascribed to four domains (Sapolsky 2006): (1) material culture, which relates to the manufacture of tools and shelters (Mann *et al.* 2012, Koops *et al.* 2015); (2) foraging, which refers to the techniques employed for food acquisition, processing, and consumption (van Schaik *et al.* 2003, Sargeant and Mann 2009); (3) communication, which includes vocal, olfactory, and gestural communication (Briseño-Jaramillo *et al.* 2015, Garland *et al.* 2021); and (4) social customs, which regard arbitrary (i.e., non-subsistence) behaviours (e.g., social interactions) (Perry *et al.* 2003, Nakamura and Uehara 2004).

To determine the presence of culture, primate studies have largely applied the ‘Method of Exclusion’ (MoE), which defines culture as behaviours that cannot be explained by genetic or ecological factors and are therefore dependent on social learning (Whiten and van de Waal 2017). This method has the advantage to detect the presence of culture indirectly (Laland and Janik 2006). Indeed, direct documentation of culture is limited to rare long-term studies witnessing both the transmission and the maintenance of innovations (Japanese macaques (Schofield *et al.* 2018), olive baboons *P. anubis* (Sapolsky and Share 2004)). To rule out that a common genetic ancestry underlies candidate cultural behaviours, the MoE considers only behaviours found in some (allowing for independent innovation) but not all populations (or subspecies) of the same species. As a result, for a behaviour to be considered socially learnt and cultural, this method requires that within-group variation in behaviour is smaller than between-group variation (McGrew 1998). In addition, the MoE excludes behaviours that could be

absent due to different local ecologies. For example, high predation risk could explain the absence of ground-nesting in some chimpanzee (*Pan troglodytes*) communities. Therefore the behaviour cannot be considered cultural because it is unknown whether communities with no ground-nesting would display it in the absence of predators (Whiten *et al.* 1999).

The MoE has been criticized for several reasons. First, it may be impossible to rule out all the ecological factors that could determine the absence of a behaviour (Laland and Janik 2006). In addition, the method does not consider that genetics (e.g., different populations of the same species sharing similar cognitive abilities (Kamilar and Marshack 2012)) and ecology (e.g., different biting ant species shaping ant-dipping techniques (Möbius *et al.* 2008)) may be intertwined with social learning and contribute to the formation of culture (Koops *et al.* 2013, Schuppli and van Schaik 2019). As a consequence, many basic subsistence behaviours (e.g., food processing), in which social learning has an important role (though genetics and ecology also contribute) are excluded as cultural variants (Santorelli, Schaffner, Campbell, *et al.* 2011, Schuppli, Meulman, *et al.* 2016). Furthermore, being a comparative method, the number of cultural behaviours detected depends on the number of populations studied. Finally, the MoE assumes a greater between-group variation, but social learning does not necessarily increase within-group behavioural homogeneity (Laland and Janik 2006, Schuppli and van Schaik 2019). For instance, multiple socially transmitted food processing variants co-exist in social groups of banded mongooses *Mungos mungo* (Müller and Cant 2010) and vervet monkeys (van de Waal and Whiten 2012, van de Waal *et al.* 2012).

Other than the MoE, the ability of a species to sustain a cultural behaviour has been assessed in other ways. First, experiments have seeded a novel

behaviour in a group and determined its (potential) transmission and maintenance (Whiten and Mesoudi 2008). For example, two demonstrators, each trained to solve a tool-use task in either of two ways, were introduced in two different captive chimpanzee groups (trials), while in another group (control) the tool was provided with no demonstrator. The two novel behaviours spread only in the trial groups and persisted when tested two months later (Whiten, Horner, and De Waal 2005). Second, more recently an alternative method has been proposed: the 'Socially Learnt Skills' (SLS) method quantifies culture as the sum of all behaviours acquired through social learning. This approach has been applied to wild Bornean *Pongo pygmaeus* and Sumatran *P. abelii* orangutans (hereafter orangutans), detecting a far larger number of cultural behaviours than the MoE (Schuppli and van Schaik 2019). Finally, other studies have quantified the proportion of use of universal behaviours (i.e., present in all groups) arguing that these also constitute cultural variants (Santorelli, Schaffner, and Aureli 2011, Tournier *et al.* 2014) (see §1.2.2).

Conclusions

In summary, the taxa in which social learning and culture have received the most attention by researchers are also the ones that show the most evidence of culture (McGrew 1998, Whiten and van de Waal 2017). In general, authors agree that apes exhibit a cultural repertoire whose complexity is outmatched only by our own species (Whiten *et al.* 1999, van Schaik *et al.* 2003) (see §1.2.2). Despite the difficulties of observing marine animals in the wild, cetaceans are thought to have a comparably wide range of cultural behaviours (Rendell and Whitehead 2001), such as hunting techniques (Mann *et al.* 2012, Allen *et al.* 2013) and song dialects (Marcoux *et al.* 2007, Garland *et al.* 2021).

Because species who live in social groups comprising both kin and non-kin individuals, have a relatively greater brain size, and extended life history (relatively long life span and late age at first reproduction), also tend to have a 'higher' cultural status, these characteristics may have coevolved in primates and potentially other taxa (van Schaik and Burkart 2011, Street *et al.* 2017). Nevertheless, among primates, monkeys seem to be less culturally able compared to apes (see §1.2.2). However, this conclusion could arise from our current knowledge being biased towards apes (Perry and Manson 2003, Whiten and van de Waal 2017). Indeed, studies on taxa as diverse as mammals and insects made clear that culture is not an all-or-nothing trait, but rather there is variation on a continuum from a narrow to a wide cultural repertoire. For many taxa this repertoire is still broadening as new evidence is being gathered (Whiten 2017, Allen 2019).

1.2.2 Culture in apes and monkeys

The greater variety of cultural behaviours reported in the wild for apes compared to monkeys could be explained by several factors (Whiten and van de Waal 2017). First, due to the rarity of long-term studies on the majority of monkey taxa many cultural behaviours may have been overlooked (Perry and Manson 2003, Perry *et al.* 2017). Cultural studies in the wild (hereafter in Chapter 1 examples refer to wild populations unless 'captive' is specified) have focused on five main primate taxa: chimpanzees, orangutans, gorillas (*Gorilla* spp.), 'gracile' (*Cebus* spp.) and 'robust' (*Sapajus* spp.) capuchins, and macaques. Among those, chimpanzees have been the most well-studied (McGrew 1998, Whiten and van de Waal 2017). Second, material culture, which makes a large part of ape cultures (Whiten *et al.* 1999, van Schaik and Pradhan 2003), may have attracted

more attention from researchers, perhaps because humans greatly rely on technology themselves (Tennie *et al.* 2009), or because it is more easily detectable (Schuppli and van Schaik 2019). However, most monkeys do not use tools (van Schaik *et al.* 1999, Perry and Manson 2003). Finally, cultural behaviours in the social and communication domains have been studied in monkeys relatively more recently, and more cases may be reported in the future (Santorelli, Schaffner, Campbell, *et al.* 2011, Briseño-Jaramillo *et al.* 2015).

Apes include chimpanzees, orangutans, gorillas, and bonobos (*P. paniscus*) (Groves 2017). Among them, chimpanzees and orangutans present the greatest variety of cultural behaviours and are thought to be the two taxa most similar to humans from a cultural perspective (Whiten and van de Waal 2017). In chimpanzees, the MoE (Method of Exclusion) identified 39 cultural variants (i.e., likely sustained by social learning) out of 65 behaviours (Whiten *et al.* 1999). The fact that the authors sampled across two different subspecies (western *P. t. verus* and eastern *P. t. schweinfurthii* chimpanzees) has led to the critique that the differences observed were (at least partly) explicable by genetic divergence (Laland and Janik 2006). However, subsequent studies confirmed these results by comparing neighbouring chimpanzee communities of the same subspecies (Luncz *et al.* 2012, Koops *et al.* 2015). For example, a study compared three neighbouring communities of western chimpanzees, who crack nuts using stone and wooden hammers. If chimpanzees selected hammers based on their availability and differences in nut hardness, all three communities would have preferred stone hammers at the beginning of the season, when nuts are harder, and wooden hammers at the end, when the wooden hammers are more abundant than stone hammers. Instead, chimpanzees' choices seem to not be determined by optimal foraging efficiency but rather by group-specific norms (Luncz *et al.*

2012, 2018), which were maintained for at least 25 years (Luncz and Boesch 2014).

In orangutans, six groups of the Sumatran and the Bornean species were compared finding 24 cultural variants out of 36 behaviours (van Schaik *et al.* 2003). The same communities were then analysed using the SLS (Socially Learnt Skills) method, which revealed, respectively, 195 and 122 cultural behaviours (Schuppli and van Schaik 2019). To detect social learning, the method assesses the presence of behaviours indicative of social information acquisition: for instance, observing others is associated to increased subsequent exploration of the items manipulated by the demonstrator (Schuppli, Meulman, *et al.* 2016). Both in chimpanzees and orangutans, most cultural variants regard subsistence activities, mainly related to tool use for foraging and, secondarily, to the building of shelters and night-nests (Whiten *et al.* 1999, van Schaik *et al.* 2003). In addition, both taxa possess arbitrary traits (social customs) (Sapolsky 2006). For example, eastern chimpanzees engage in hand-clasp grooming (where groomers each hold one arm in contact with their partner's in different positions) (Nakamura and Uehara 2004), and orangutans do spluttering vocalizations during nest building (van Schaik *et al.* 2003).

Gorillas and bonobos show fewer cultural behaviours compared to chimpanzees and orangutans, potentially due to the lower information available (Hohmann and Fruth 2003, Robbins *et al.* 2016). In gorillas, 23 cultural traits out of 41 behaviours were identified between five groups of western lowland (*G. gorilla gorilla*) and mountain (*G. beringei beringei*) gorillas. Of these, only 12 variants had no clear species-specificity (excluding a genetic origin). Compared to chimpanzees and orangutans, cultural traits regarding foraging activities are underrepresented (only one trait) and none involve tool use (Robbins *et al.* 2016).

In bonobos, the behaviours observed during a long-term study at Lomako (Congo) were compared with information from four other sites and with the cultural variants previously described in chimpanzees. Among different bonobo communities, six out of nine behaviours were considered cultural. In addition, the equivalents of 14 chimpanzee cultural variants were found in bonobos at Lomako. Despite a considerable overlap with chimpanzee culture, bonobo culture is relatively more biased towards communication behaviours (Hohmann and Fruth 2003).

Monkeys include New World monkeys (e.g., capuchins, marmosets, spider monkeys) and Old World monkeys (e.g., baboons, macaques, vervet monkeys) (Groves 2017). Despite diversity in species, cultural studies have focused mainly on two taxa: Japanese macaques, where the diffusion of innovations was tracked in long-term studies; and white-faced capuchins (*C. capucinus*), where groups were compared through the MoE (Perry and Manson 2003, Whiten and van de Waal 2017). More recently, studies on tool use in long-tailed macaques (*M. fascicularis*) (Tan *et al.* 2015, Proffitt *et al.* 2018) and robust capuchins (Falótico *et al.* 2018, Falótico 2023) have argued that these constitute cultural behaviours despite the influence of genetic and ecological factors (Malaivijitnond *et al.* 2007, Ottoni and Izar 2008). Several cultural behaviours have been reported in Japanese macaques and white-faced capuchins, mainly related to foraging (Perry and Manson 2003). For example, comparing 60 foods eaten by white-faced capuchins, 20 were processed differently across three social groups (Panger *et al.* 2002). However, these differences could be partly accounted for by ecological differences among the study sites (O'Malley and Fedigan 2005a, 2005b). In addition, in food-provisioned Japanese macaques, foraging cultures (e.g., potato-washing and wheat-sluicing) have been criticised because their

onset was facilitated by human interference (McGrew 1998). Nevertheless, striking examples of monkey culture come from a set of arbitrary behavioural patterns detected by applying the MoE (Whiten and van de Waal 2017).

Social customs were found in both Japanese macaques and white-faced capuchins. In Japanese macaques, 45 variants of stone handling resulted from the comparison of 10 provisioned groups. Each group possesses a distinctive set of stone handling patterns, which seem to be a form of solitary play (e.g., carrying, rubbing, throwing, gathering stones into piles, and clacking them together). Stones are never used as tools in this context, thus none of the stone handling behaviours is related to subsistence activities (Leca *et al.* 2007a, 2007b). In white-faced capuchins, a study compared 13 groups reporting five cultural patterns performed in pairs: hand-sniffing, sucking of body parts, and three types of games. The latter involves the capture in the mouth of one player of the other's fingers, tuft of hair, or of an object, while the other partner tries to retrieve it. All these behaviours entail a certain degree of discomfort and risk (e.g., fingers inserted into nostrils, fingers or tails placed between teeth), which may serve to test the quality of social bonds (Perry *et al.* 2003).

Cultural behaviours have also been described to a lesser extent in other monkey taxa, such as Geoffroy's spider monkeys (*Ateles geoffroyi*), vervet monkeys, and baboons (Whiten and van de Waal 2017). The MoE was applied to five social groups of Geoffroy's spider monkeys reporting 22 cultural variants out of 62 behaviours. More than a half of these variants are related to the communication domain (e.g., greeting and substrate-marking behaviours), which may facilitate membership recognition in a fission-fusion society (Santorelli, Schaffner, Campbell, *et al.* 2011). A second study on the same groups focused on intergroup differences in the proportional use of universal behaviours. These

behaviours are displayed in all groups, but they are used with different frequencies, indicating local preferences. Out of 14 'community preferred' variants, six were considered likely to be maintained through social learning. These six add to the previously-identified ones for a total of 28 cultural behaviours (Santorelli, Schaffner, and Aureli 2011).

In vervet monkeys, variants in diet compositions were reported for six neighbouring groups. Overall, there is a positive correlation between local abundance of tree species and their proportions in the diet. However, in some cases, groups eat similar amounts of a tree species even though its abundance is significantly different in the respective home ranges, while, in other cases, groups eat significantly different amounts of a tree species that is equally abundant in the two home ranges. This suggests that dietary habits are not entirely dependent on resource availability, but they are also influenced by local cultures (Tournier *et al.* 2014). Dietary differences between neighbouring groups have also been reported in taxa showing (in addition) more 'traditional' examples of culture, such as orangutans (Bastian *et al.* 2010).

In baboons, two cases of culture have been reported in two different groups of olive baboons (*P. anubis*) (Strum 1975, Sapolsky and Share 2004). The first case regards a predatory strategy characterized by cooperative hunting and meat sharing. Predation was at first performed almost exclusively by adult males, who were also the ones doing most of the eating. A few years later, the proportion of adult females and juveniles who participated to the hunting and eating had increased. In addition, the predatory technique evolved through time until prey chasing became cooperative and more successful. Eventually, this culture appeared to be transmitted to the next generation. Infants still in close association with the mother or related to the adult male who consumed the majority of the kill

were more likely to obtain meat scraps. When older, the same infants also attended kills more often than peers (Strum 1975). The second case regards a 'pacific culture' characterized by a relatively more relaxed dominance hierarchy and higher rates of affiliation within and between the sexes of one group. Due to an epidemic of tuberculosis spread through consumption of infected meat, almost a half of the males of the group died, producing a sex ratio greatly in favour of females. Since only males who could successfully compete for meat were infected, it was the most aggressive ones who died, leaving a population of less aggressive survivors. A decade later, when none of the original male survivors were present, this pacific culture persisted and had been adopted by new immigrant males. The comparison with other groups with an equally skewed sex ratio suggests that a simple higher proportion of females cannot explain the onset of these behavioural patterns, supporting a social learning transmission (Sapolsky and Share 2004).

Conclusions

In summary, for chimpanzees and orangutans over 150 and 26 years of observation have been respectively accumulated and these two taxa also provide the most evidence for culture (Whiten *et al.* 1999, van Schaik *et al.* 2003). This higher cultural status tends to be extended to apes in general (Whiten and van de Waal 2017), even though many fewer data are available for gorillas and bonobos (Hohmann and Fruth 2003, Robbins *et al.* 2016). Therefore, the question whether apes' enhanced culture derives (at least partially) from the larger dataset available compared to monkeys remains (Perry and Manson 2003).

Concerning the variety of the cultural repertoire, in all apes and in some monkeys, communities present multiple cultural traits simultaneously. In monkeys, other than the well-studied macaques and capuchins (Perry and Manson 2003), a relatively broad cultural repertoire has been described in spider monkeys (Santorelli, Schaffner, and Aureli 2011, Santorelli, Schaffner, Campbell, *et al.* 2011). However, vervet monkeys and baboons still provide little evidence of culture (Whiten and van de Waal 2017). The baboon case is particularly striking given the abundance of long-term studies (Cheney and Seyfarth 2007, Alberts 2019), which argues against the lack of data as a possible explanation. Therefore, to understand why culture has a greater role in some primate species than in others, it may be informative to determine which factors constrain or enhance horizontal and vertical transmission of social information (van Schaik 2010).

1.3 CONSTRAINTS ON HORIZONTAL INFORMATION TRANSMISSION

1.3.1 Social information use

Social information use involves three sequential steps: the acquisition of information, its application, and the exploitation of its benefits (Carter, Torrents Ticó, *et al.* 2016). Even though only the first step involves social learning, the other two are equally important for information spread at the group level because they determine who can act as a demonstrator for others (Drea and Wallen 1999, Leca *et al.* 2007b).

The acquisition of social information

The acquisition of social information can be defined as using social cues, such as the position or the activity of a demonstrator, to gain information about the environment (Laland 2004, Dall *et al.* 2005). For example, an individual who sees another foraging in a patch obtains information about the location of a food resource (Carter, Torrents Ticó, *et al.* 2016). Information acquisition may be influenced by individuals' propensity to obtain information individually (i.e., behaving as 'producers') or socially (i.e., behaving as 'scroungers') (Giraldeau *et al.* 2002, Lee *et al.* 2016). Producer-scrounger dynamics could depend on several factors (Lee *et al.* 2016), including: (1) individuals' phenotype, such as their age, sex, dominance rank, social integration, and personality; and (2) aspects related to the social group as a whole and/or a species, such as group size and structure, and social tolerance. These factors are addressed in turn focusing in particular on the acquisition of information from others (scrounging).

Age

Individuals' age predicts their experience with the environment and may thus affect their tendency to behave as information producers or scroungers. On the one hand, older individuals may be more likely to produce information because their relatively greater experience may facilitate innovation (Reader and Laland 2001). Indeed, innovation rates are higher in adult than in immature primates (Reader and Laland 2001, Amici, Widdig, *et al.* 2019). On the other hand, immature individuals, who lack experience, may be more likely to learn from others, which is consistent with a 'copy when uncertain' strategy (Laland 2004) (see §1.2.1). In general, both observational studies and experiments showed that immature age classes pay relatively more attention to social information

(Rapaport and Brown 2008, Whiten and van de Waal 2018). For example, immature long-tailed macaques observe and interact with individuals cracking shelled seafood more than adults (Tan *et al.* 2018) and juvenile chacma baboons watched others interacting with a novel food and a hidden food task more than older age classes (Carter *et al.* 2014).

Despite young age classes' general propensity to use social information, juveniles may produce information when they are not limited by the lack of experience. In this case, younger individuals may be facilitated by their relatively greater curiosity about the environment (Biro *et al.* 2003, Amici, Widdig, *et al.* 2019). For example, juvenile chacma baboons tended to discover experimental food patches individually rather than socially when all group members were equally naïve about the patches' locations (Cambefort 1981, Carter, Torrents Ticó, *et al.* 2016). However, because the juveniles involved were mainly males, their tendency to learn individually may have depended also on their sex and, consequently, on their social integration (Cambefort 1981, Carter, Torrents Ticó, *et al.* 2016) (see below).

Sex

Individuals' sex may affect their propensity to be information producers or scroungers because of the sexual dimorphism present in most primate species. In general, male primates are larger than females and socially dominant over them. Because of the need to sustain a larger body, males may be more willing to discover potentially higher pay-off foraging opportunities because, if unsuccessful, they could scrounge food from a lower-ranking individual (Reader and Laland 2001, Carter, Torrents Ticó, *et al.* 2016). Accordingly, several studies reported that male primates tend to produce information more than females

(Reader and Laland 2001, Amici, Widdig, *et al.* 2019), including a long-term observational study on white-faced capuchins (Perry *et al.* 2017) and an experiment on chacma baboons (Carter, Torrents Ticó, *et al.* 2016).

Females, on the other hand, tend to learn from others more than males (Reader and Laland 2001, Amici, Widdig, *et al.* 2019). For example, in social groups including a majority of adults, female vervet monkeys learnt socially twice as fast as males how to open a baited box (Canteloup *et al.* 2020) and captive chimpanzee females were more likely to use social information to solve several experimental tasks than males (Watson *et al.* 2018). However, this general pattern is not clear for immature-only age classes: studies obtained contrasting results on the two sexes' tendencies to learn tool use from others, probably reflecting species-specific adult proficiency in using tools (Gruber *et al.* 2010, Falótico and Ottoni 2014) (see 'application' below).

Females' reproductive state may also affect information use. For instance, pregnant and lactating chacma baboons are more likely to join a patch occupied by a male (scrounging information from him) than females in other reproductive states (King *et al.* 2009). Pregnant and lactating females may either have relatively higher energetic demands (Altmann 1980, Barrett *et al.* 2006) and thus scrounge to reduce the costs of searching for food individually, or they may follow the father of their infant as an infanticide counterstrategy (King *et al.* 2009) (see §1.5.3).

Dominance rank

Individuals' dominance rank may influence producer-scrounger dynamics because the likelihood to obtain a resource depends on one's position in the group's hierarchy (King *et al.* 2008, Majolo *et al.* 2012). Subordinates could

benefit more from innovation because their ability to exploit resources is reduced by receiving agonism from dominant conspecifics (Reader and Laland 2001). Indeed, low- and middle-ranking primates are more likely to innovate than higher-ranking ones (Reader and Laland 2001, Perry *et al.* 2017). Conversely, higher-ranking individuals tend to scrounge relatively more because they can monopolize the resources discovered by subordinates (King *et al.* 2008). For example, dominant chacma baboons tend to use the presence of a conspecific in a patch to infer the location of food more than subordinate ones (King *et al.* 2009, Carter, Marshall, *et al.* 2013). Accordingly, chacma baboons prefer to associate with subordinates, from whom they can scrounge, during foraging (King, Clark, *et al.* 2011, Marshall *et al.* 2012).

Despite the general tendency of dominant individuals to learn from others more than subordinates, contrasting results have been reported. For instance, dominance rank was positively related to individual discovery of experimental food patches in chacma baboons (Carter, Torrents Ticó, *et al.* 2016) and lower-ranking captive chimpanzees showed a relatively higher propensity to acquire social information about the opening of a baited box (Kendal, Hopper, Whiten, Brosnan, Lambeth, *et al.* 2015). However, in the first case, dominant baboons tended to be males and thus more likely to innovate (see above); in the second case, the lower competition in a captive *versus* a wild environment may have reduced aggression from dominants and thus facilitated scrounging by subordinates (Carter, Torrents Ticó, *et al.* 2016).

Social integration

Individuals' social integration can be assessed by calculating social networks. These refer to the social connections, measured through spatial

proximity or social interactions (e.g., affiliations or dominance interactions), among the individuals in a social group (Croft *et al.* 2008, Brent, Lehmann, *et al.* 2011). Social networks could affect information transmission both at the individual and the group level.

At the individual level, individuals' connections may influence their social information acquisition in at least three ways: (i) individuals cannot acquire information from others with whom they do not associate (e.g., in fission-fusion societies (Sueur *et al.* 2011)), (ii) individuals who have a central position in the network (i.e., who have diverse and frequent social connections (Sosa *et al.* 2021)) have relatively more opportunities to access social information (van Boekholt *et al.* 2021), and (iii) individuals may prefer to learn from group members in their proximity (Grampp *et al.* 2019) or from those with whom they share strong affiliative bonds (e.g., grooming) (Coelho *et al.* 2015). Proximity and affiliation networks are different because, while individuals may be in proximity of close affiliates, they do not necessarily interact with all the conspecifics in their proximity (Castles *et al.* 2014). Alternatively, individuals may select the group members from whom to learn based on other phenotypic characteristics, irrespective of their position in the network (Lonsdorf and Bonnie 2010) (see §1.4.1).

Several studies showed how individuals central in the proximity and/or affiliation networks acquire information more than peripheral ones. For example, socially central chacma baboons were relatively more likely to acquire information about the location of experimental food patches while foraging naturally (Carter, Ticó, *et al.* 2016). Similarly, captive ring-tailed lemurs (*Lemur catta*) who were relatively more central in the affiliation network were also more likely to acquire information about the opening of a baited box (Kulahci *et al.* 2018a). In addition,

social learning and network position may have a bi-directional relationship (Kulahci and Quinn 2019). Lemurs who were frequently observed solving the task experienced an increase in approaches and grooming received, becoming even more central in the network. This change in network position persisted after the end of the experiment and was independent from immediate benefits (e.g., social tolerance during foraging; see below) for the conspecifics who affiliated with the 'knowledgeable' lemurs (Kulahci *et al.* 2018a).

At the group level, information transmission could be affected if individuals tend to associate together based on their phenotype (Carter *et al.* 2015). Across primate taxa, immatures tend to associate with same-sex peers (homophily) (Lonsdorf 2017, Amici, Kulik, *et al.* 2019). Given the fact that immatures tend to learn socially more than adults and females may acquire information from others more than males (see above), homophily by age and sex may limit information transmission in primate groups: the individuals who produce information (adults and males) are socially separated from those who acquire information (immatures and females) (Carter *et al.* 2015). Because, in female-philopatric primates (i.e., females remain in their natal group for life while males disperse at maturity), females tend to be more socially integrated than males (Lehmann and Ross 2011, Sosa 2016), homophily by sex could constrain group-level information transmission more than in male-philopatric primates (opposite sex-driven dispersal patterns than above) (van de Waal *et al.* 2012). That is, females may have both a greater tendency and greater opportunities to learn from others by being socially central, while males may have both a greater propensity and chances to discover novel information by being at the edges of the group (King *et al.* 2009, Carter, Torrents Ticó, *et al.* 2016).

Personality

Personality refers to within-individual consistency in behaviour (Sih *et al.* 2004, Réale *et al.* 2007). Although personality may partially depend on individuals' phenotype (e.g., change with age (Manson and Perry 2013, Rosati *et al.* 2020)), between-individual variation in personality traits persists through time and is repeatable across contexts (Carter *et al.* 2012a, Kulahci *et al.* 2018b). Personality traits vary along a continuum between two extremes: for example, the boldest and the shyest individuals represent the opposite ends of a 'boldness' dimension (Carter, Feeney, *et al.* 2013).

Personality can predict individuals' propensity to acquire social information and/or their opportunities to do so (Krause *et al.* 2010, Carter, Marshall, *et al.* 2013). First, individuals' tendency to produce information or acquire it from others may depend on certain personality traits. For instance, both boldness (i.e., the tendency to explore novel objects or situations) and anxiety (i.e., the tendency to inspect threats) measures, which were repeatable over a 3-year period (Carter *et al.* 2012b, 2012a), predicted chacma baboons' propensity to produce or scrounge during field experiments (Carter, Marshall, *et al.* 2013, Carter *et al.* 2014). Second, sociability (i.e., the tendency to initiate social interactions) could enhance individuals' centrality in the group's network and thus their opportunities to learn from others (Krause *et al.* 2010, van Boekholt *et al.* 2021) (see above). An individual's position in the social network can reflect sociability because direct indices of connectivity are consistent over time and different contexts: ring-tailed lemurs (Kulahci *et al.* 2018b) and vervet monkeys (Canteloup, Puga-Gonzalez, *et al.* 2021) who are more central in the grooming network are also more central in the dominance network.

Group size and structure

Group size and structure could affect social information transmission through individuals' opportunities to learn from others. First, larger groups may offer more opportunities for social learning than smaller ones (King and Cowlshaw 2007). In addition, the positive correlation between primate group size and relative brain size suggests that living in larger groups selected for relatively higher cognitive abilities, due to the challenges of tracking a greater number of social relationships (Dunbar 1998, 2003). Larger group size and relative brain size are also associated with higher levels of social learning (van Schaik and Burkart 2011, Street *et al.* 2017). Indeed, more 'socially intelligent' primates may be able to adjust their social relationships in order to gain better access to social information: species living in relatively larger groups and having larger brains have more 'efficient' social networks, i.e., that would allow faster information transmission through a smaller number of individual connections (Pasquaretta *et al.* 2014).

Second, group cohesion and dominance structure could affect social learning. For example, the transmission of information regarding the presence of experimental food patches was more rapid in chacma baboons and mandrills (*Mandrillus sphinx*) than in vervet monkeys. Compared to vervet monkeys' groups, baboons' and mandrills' groups are more cohesive and show greater asymmetry in the dominance hierarchy (Cambefort 1981). Group cohesiveness may make social information travel more quickly (Pasquaretta *et al.* 2014). In addition, dominance asymmetry could mean that (i) individuals show relatively higher vigilance for threat, and may thus monitor social cues in general more; and (ii) dominant individuals can easily acquire information from subordinates (Cambefort 1981, King *et al.* 2008). However, the fact that higher dominance asymmetry may favour social information transmission contrasts with the

opposite hypothesis that social tolerance enhances the acquisition of information from others (see below).

Social tolerance

Social tolerance may enhance information acquisition because individuals who are tolerated in close proximity may be able to observe others better (Ottoni and Izar 2008, Rapaport and Brown 2008). This could be particularly important for the use of ‘complex’ information (see also ‘application’ below), such as tool-use (see §1.3.2), that requires a longer period of time in close proximity compared to ‘simpler’ information, such as the location of food (van Schaik *et al.* 1999, Koops *et al.* 2014). In addition, social tolerance could facilitate information spread at the group level (Pasquaretta *et al.* 2014, van Boekholt *et al.* 2021). Therefore, tolerance may have an important role on social learning both within and between-species.

Within species, social tolerance may affect who is more likely to acquire social information and from whom. First, primates are more tolerant of the proximity of young immatures compared to older age classes, both in despotic (Tarnaud and Yamagiwa 2008) and more egalitarian (Ottoni *et al.* 2005) species (see below). This may contribute to infants’ and young juveniles’ relatively greater tendency to learn from others in addition to their inexperience (Rapaport and Brown 2008) (see above). Second, social affiliates may be relatively more tolerant of each other’s proximity and thus be preferred as learning partners, particularly in despotic societies (Tan *et al.* 2018) (see below). Social affiliates may include both kin and non-kin individuals. For instance, Japanese macaques tend to forage together with close kin (Chapais and Belisle 2001), while chacma baboons

scrounge information from close grooming partners independently from genetic relatedness (King, Clark, *et al.* 2011).

Between species, the degree of social tolerance may affect how much primate taxa rely on socially acquired information. Tolerant societies are characterized by a more relaxed dominance hierarchy and a weaker influence of kinship, while more despotic ones have a steeper dominance gradient and stronger nepotism (Thierry 2013, 2022). Other than potentially allowing for greater between-individual average proximity (and thus higher information acquisition; see above), social tolerance may affect group structure and thus information transmission (Pasquaretta *et al.* 2014). Information may travel relatively faster in the social groups of tolerant species because a higher number of individuals have a central position in the group (and are thus connected to most group members). In contrast, in despotic species, individuals tend to be clustered in sub-groups based on kin relationships (Pasquaretta *et al.* 2014, van Boekholt *et al.* 2021), which may retain social information and limit its spread to the group level (van de Waal *et al.* 2012). For example, following the introduction of a novel food in vervet monkey groups, similarity in food-cleaning techniques emerged at level of matriline with no behavioural homogeneity at the group level (van de Waal *et al.* 2012).

The application of social information

The application of social information refers to performing actions directly related to the acquired information. For example, an individual who sees a demonstrator feeding and moves to the same patch is applying the acquired information about food location (Carter, Torrents Ticó, *et al.* 2016). Because, in observational studies, it is difficult to determine whether individuals acquire any

information by watching others, individual practice following others' observation indicates that some information has been acquired (Ottoni and Izar 2008, Schuppli and van Schaik 2019).

Since information application follows the acquisition phase, it tends to be enhanced or constrained by similar factors: the individuals who acquire information more also apply it more. For example, juvenile chacma baboons, who were the age class paying more attention to others performing a novel food item and a hidden food task, also showed the greatest improvement in applying, and eventually exploiting, the acquired social information (Carter *et al.* 2014). However, the time spent acquiring social information is not always correlated to its application, suggesting that other factors, such as dominance rank, affect specifically the application, and, consequently, the exploitation, phases of social information transmission (Carter *et al.* 2014, Carter, Torrents Ticó, *et al.* 2016) (see 'exploitation' below).

Age

As for acquisition, the application of social information is higher in younger than in older individuals. For instance, infant and young juvenile common marmosets (*Callithrix jacchus*) and orangutans pay attention to demonstrators more than older juveniles (Schiel and Huber 2006, Schuppli, Meulman, *et al.* 2016). After conspecifics' observation, common marmosets either approach or forage in proximity to the demonstrator, or manipulate a food item dropped by the demonstrator (Schiel and Huber 2006), and orangutans increase the manipulation rates of the same type of item (e.g., food or nest-building material) handled by the demonstrator (Schuppli, Meulman, *et al.* 2016).

Sex

Similar to what is reported for age, the sex that acquires social information more may also apply it more. This has been observed in immature individuals. As mentioned, studies reported opposite tendencies for the two sexes in the acquisition and the application of social information. Despite spending similar amounts of time with the respective demonstrators, eastern chimpanzee daughters observe their mothers more than sons while termite-fishing (Lonsdorf *et al.* 2004) and juvenile male bearded capuchins (*S. libidinosus*) watch adult males using probes to displace hidden preys more than female peers (Falótico *et al.* 2021). Perhaps as a consequence, female chimpanzees spend relatively more time attempting to fish when in proximity of a termite mound and male capuchins manipulate probes at relatively higher frequencies (Lonsdorf *et al.* 2004, Falótico *et al.* 2021).

As for acquisition, female reproductive state may influence social information application when intragroup competition is high. For instance, pregnant and lactating chacma baboons tended to join and feed on experimental food patches less than males, independently from their dominance rank. Because, as mentioned, females may have relatively higher energetic demands, they could be less willing to forego more secure natural foraging opportunities to compete for small food patches (Carter, Torrents Ticó, *et al.* 2016).

Social tolerance

Social tolerance may facilitate both the acquisition (see above) and the application of social information. As mentioned, the role of tolerance may be most important in the use of information that requires extensive practice in close proximity. This may regard both tool use and certain social customs (van Schaik

et al. 1999, Bonnie and de Waal 2006). For example, immature western chimpanzees (Biro *et al.* 2003) and tufted capuchins (*S. apella*) (Ottoni *et al.* 2005) are allowed to explore the tools used for nut cracking, the nuts gathered by adults and those already opened, and to feed on the adults' scraps. In addition, the degree of affiliation between pairs predicted captive chimpanzees' acquisition of hand-clasp grooming from experienced group mates over a 12-year period (Bonnie and de Waal 2006).

The exploitation of social information

The exploitation of social information refers to the access to a resource through the application of the acquired information. For example, an individual who had seen another forage in a patch and joined the latter in the same location, then starts to forage in the patch, thus exploiting the benefits of the acquired information about food location (Carter, Torrents Ticó, *et al.* 2016). As for information application, the likelihood to exploit the benefits of social information may depend not only on individuals' performance in the previous steps of information use (acquisition and application), but also on additional factors that can limit the access to a resource (Carter, Torrents Ticó, *et al.* 2016, Visalberghi *et al.* 2016).

Age

Despite acquiring and applying social information, immature individuals may be constrained in exploiting such information when it requires high manual dexterity or strength. Indeed, in species that use tools to crack embedded foods, juveniles reach adults' success at extracting the edible parts after years of practice (Fragaszy *et al.* 2004, Visalberghi *et al.* 2016). For example, in bearded

capuchins, higher body mass and older age predict the efficiency (number of strikes required) in cracking palm and cashew nuts (Visalberghi and Addessi 2013). For cashew nuts, which are protected by caustic chemicals, higher body mass is positively related to success in opening fresh nuts (for which physical strength is more important than dexterity), while older age, and thus experience, is linked to shorter processing times of both fresh and dry nuts (Visalberghi *et al.* 2016).

Sex

Although age may limit information exploitation, individuals who apply more the acquired social information may then be able to exploit it sooner and more efficiently (see also ‘application’ above). Juvenile female eastern chimpanzees learn to fish for termites about two years earlier than male peers and obtain a higher number of termites per dip (Lonsdorf *et al.* 2004). As adults, female chimpanzees are generally more proficient in using tools than males (Gruber *et al.* 2010). Similarly, the fact that probe tool use is almost exclusively practiced by adult male bearded capuchins in the absence of a strong sex-driven diet bias (Falótico and Ottoni 2014) could be explained by juvenile males learning the behaviour from others more than female peers (Falótico *et al.* 2021).

Dominance rank

As mentioned, dominance rank may affect information application and exploitation even though the relevant information to solve a task has been acquired. For example, shyer and calmer chacma baboons were less likely to apply and to exploit social information, despite having spent more time in acquiring it than, respectively, bolder and more anxious individuals (Carter *et al.*

2014). The reasons behind this discrepancy could be that: (i) individuals did not acquire the information; or (ii) individuals refrain from applying (and thus exploiting) the acquired information because of the presence of dominant competitors, presumably to avoid losing their reward to them (Carter et al. 2014, Carter, Torrents Ticó, et al. 2016). The results of experiments on captive monkeys support the latter explanation (Drea and Wallen 1999, Lonsdorf *et al.* 2016). For instance, rhesus macaques, who acquired information on colour cues indicating the presence of food, were tested in two conditions: with all individuals present (joint) and with dominant and subordinate individuals separated (split). While the performance of the dominant individuals was not affected by the test condition, subordinates spent less time in the baited zone (information application) and, consequently, obtained less food (information exploitation) than the dominants in the joint condition. Instead, in the split condition, both subordinate and dominant individuals were equally successful in applying and exploiting the acquired information (Drea and Wallen 1999).

Social tolerance

While dominance interactions may inhibit social information exploitation, social tolerance may enhance it. For example, independently from dominance rank, chacma baboons central in the affiliation (grooming) network could exploit social information about experimental food patches more than peripheral individuals (Carter, Torrents Ticó, *et al.* 2016). This may be because subordinates who have strong social bonds with higher-ranking individuals are relatively less likely to receive aggression during foraging (Marshall *et al.* 2015). Accordingly, chacma baboons tend to groom dominant individuals early in the morning in order to gain tolerance ahead of the day's foraging (Sick *et al.* 2014). Experiments

further confirmed primates' flexible social strategies: vervet monkeys quantitatively distributed grooming according to the benefits (amount of food reward) that they could gain from other group mates (Fruteau *et al.* 2009, Borgeaud and Bshary 2015).

Conclusions

In summary, the constraints on social information use have been investigated by various studies, but these have sometimes yielded contrasting results that need further explanation (e.g., the roles of age and dominance rank on information acquisition) (Carter, Torrents Ticó, *et al.* 2016). In other cases, individuals may be unable to use social information for reasons other than the factors explored in this section. For example, vervet monkeys were able to open a baited box by performing the single action witnessed from a trained demonstrator (van de Waal and Whiten 2012, van de Waal *et al.* 2015). However, when a similar task required two sequential actions, the observer monkeys were not able to open the box despite not being limited by their manual dexterity (they performed the required actions, but not in the right sequence) or dominance dynamics (the experimental design minimised monopolisation) (van de Waal and Bshary 2011). In this case, the monkeys' failure may be attributed to limits in their cognitive abilities (van de Waal and Bshary 2011).

1.3.2 Cognitive abilities

To understand differences in primate cultures, it may be useful to consider species' and individuals' cognitive abilities involved in the use of 'complex' information (i.e., information that requires more than one step to apply it (Matsuzawa 1996)) (Tennie *et al.* 2009, Dean *et al.* 2012). A relevant example

regards tool-use behaviours because their diffusion can be studied through dedicated experiments (Visalberghi and Tomasello 1998, Dean *et al.* 2012). Importantly, these behaviours are likely to be recognised as cultural by the Method of Exclusion (MoE), which has been the most applied method in primate cultural studies (Whiten and van de Waal 2017) (but see Ottoni and Izar 2008, Schuppli and van Schaik 2019).

Based on how culture is defined (see §1.2.1), cultural traits can derive from information that is long-lasting and whose independent discovery is unlikely (Laland 2004, Whiten and van de Waal 2017). Indeed, information that rapidly becomes outdated cannot be maintained through time: the location of a novel food patch will no longer be useful once it has been depleted (Giraldeau *et al.* 2002). In addition, independent innovation will not produce between-group variation, which is a prerequisite of traditional definitions of culture (McGrew 1998). Although basic subsistence skills are transmitted socially within groups, and could therefore be considered cultural, they are 'simple' enough to be reinvented by all the populations of the same species, and thus excluded by the MoE (Laland and Janik 2006, Schuppli and van Schaik 2019). On the other hand, innovations regarding material culture (e.g., the choice and modification of twigs as termite-fishing tools in chimpanzees (Koops *et al.* 2015)) and novel social interactions (e.g., the social games of white-faced capuchins (Perry *et al.* 2003)) represent life-long skills. These innovations are relatively rare, as documented in long-term studies (Nishida *et al.* 2009, Perry *et al.* 2017). Indeed, these behaviours may require a cognitive effort (at least for species without genetic predispositions; see below) both to be innovated and to be transmitted socially (Dean *et al.* 2012, Mesoudi *et al.* 2016).

Tool use, defined as the use of an object as an extension of a body part to achieve a goal, is limited to a few non-human animals (St Amant and Horton 2008). Only in some species the transmission of tool-use behaviours occurs socially and gives rise to a tool-use culture, while in others social learning is not necessary to learn to use tools, suggesting rather a genetic predisposition (e.g., woodpecker finches *Geospiza pallida* (Tebbich *et al.* 2001)) (Bandini *et al.* 2020). In primates, all apes but gorillas (Lonsdorf *et al.* 2009), robust capuchins (Falótico *et al.* 2018, Falótico 2023), and long-tailed macaques (Tan *et al.* 2015, Proffitt *et al.* 2018) have a culture of tool use. Constraints on the formation of a tool-use culture could derive from (1) the ability and/or (2) the opportunity to innovate tools (van Schaik *et al.* 1999, Koops *et al.* 2014), and (3) the possibility to transmit those innovations socially (van de Waal and Bshary 2011, Bandini and Tennie 2018). The latter, depending on the social learning mechanism adopted, may also involve individual learning (Tennie *et al.* 2009, Bandini and Tennie 2020).

The absence of a culture of tool use in many primate species could derive from the lack of tool-use innovations. However, both the observation of innovations and tool-use related cognitive abilities in primate species that do not regularly use tools (hereafter non-tool-using species) argue against this explanation. First, spontaneous tool use was reported in, e.g., individual baboons, both in captivity and in the wild (Beck 1974). In captivity, four individual baboons (one hamadryas *P. hamadryas*, one Guinea *P. papio*, and two olive baboons) learnt to use objects (e.g., a hooked stick) to draw food within their reach (Beck 1972, 1973a, 1973b, Benhar and Samuel 1978). In the wild, an olive baboon used a twig to extract stone fragments from a clay matrix prior to chewing them (Oyen 1979) and two other olive baboons used objects (e.g., a stone) as 'napkins' to wipe their mouths (van Lawick-Goodall *et al.* 1973). Second, cognitive

experiments showed that at least a few non-tool-using species understand spatial and abstract associations between stimuli (Fagot *et al.* 2015, Petit *et al.* 2015), and tool functional properties (Santos *et al.* 2006, Fichtel *et al.* 2020). For example, given two options, cotton-top tamarins (*Sanguinus oedipus*) and vervet monkeys chose the tool of the right material to retrieve food out of their reach more than expected by chance (Santos *et al.* 2006).

An alternative explanation to the rarity of tool-use cultures in the wild may be that innovations are rare due to the lack of environmental objects suitable to serve as tools or because tools are unnecessary to exploit the available resources (van Schaik *et al.* 1999, Koops *et al.* 2014). For instance, object manipulation by wild chacma baboons is more common in a swamp environment (where more diverse objects are available) compared to a desert environment (Hamilton *et al.* 1978, Hamilton and Tilson 1985). Nevertheless, the lack of opportunity or benefits in using tools may not be an exhaustive explanation for why species such as baboons do not have a culture of tool use. Indeed, baboons who share the same environment of tool-using chimpanzees (e.g., at Gombe) would presumably benefit from using tools to access a wider variety of resources (Beck 1974). In addition, tool use is expected in omnivorous foragers who process food prior to eating it (Parker and Gibson 1977, van Schaik *et al.* 1999) and should be facilitated by terrestrial habits (Meulman *et al.* 2012, Falótico and Ottoni 2023), characteristics that both apply to baboons (Fischer *et al.* 2019).

Other constraints on the formation of a tool-use culture may lie in a species' social learning abilities. In particular, based on the amount of information that individuals are able to acquire socially, understanding the physical mechanisms underlying object movements may be more or less necessary to successfully use a tool (Beck 1974, Bandini *et al.* 2020). In the first case, social learning has little

role in low-fidelity learning mechanisms because observers only acquire social information on the importance of a specific location or stimulus, but they then need to explore individually the remaining information necessary to solve the task (Tennie *et al.* 2009, Bandini and Tennie 2020). In the second case, high-fidelity learning mechanisms allow the social acquisition of most (or all) of the information related to a task, such as the relationship between stimuli or the sequence of actions performed by the demonstrator (Horner and Whiten 2005, Whiten *et al.* 2009).

Inability to learn socially multi-step tasks though high-fidelity learning mechanisms may limit the formation of tool-use cultures in monkey species, despite the presence of tool innovations. Indeed, most tool-use behaviours in the wild require the interaction of at least two objects (e.g., a twig inserted in a termite mound) (Matsuzawa 1996). The ability to learn multi-step tasks socially has been reported in species that sustain tool-use cultures, but not in non-tool-using ones. For example, captive chimpanzees were able to copy sequences of multiple actions in order to open a baited box (Horner and Whiten 2005). Instead, as mentioned, vervet monkeys were not able to copy the two sequential actions performed by a demonstrator to open a box (van de Waal and Bshary 2011). Nevertheless, an experiment on captive long-tailed macaques, who regularly use tools in the wild, failed to confirm that they can innovate and/or socially learn to use tools, raising further questions on the factors underlying the onset of tool-use cultures (Bandini and Tennie 2018).

Conclusions

In summary, there are constraints on both individual and social learning of 'complex' information. In particular, the case of species that do not transmit tool-

use behaviours socially despite being able to innovate tools is particularly interesting. This is because innovation and social learning are positively correlated in primates, suggesting that these abilities are based on the same cognitive processes (van Schaik and Burkart 2011, Street *et al.* 2017). For instance, social learning of one option to open a baited box favoured the individual discovery of the other option in vervet monkeys (Canteloup *et al.* 2020). Studies in naturalistic settings would allow the exploration of both the constraints related to cognitive abilities and the social environment (Laidre 2008) (see §1.3.1). However, these are rare because of the challenges of carrying out tool-use experiments in the wild (Harrison *et al.* 2022).

An alternative, or complementary, approach to performing experiments on social information transmission in the wild may be that of studying how immature primates develop their species-specific behavioural repertoire (e.g., the progressive learning of ant-dipping in western chimpanzees (Humble *et al.* 2009)). This may help to identify which behaviours are likely acquired through social learning, and hence are cultural (Ottoni and Izar 2008, Schuppli, Meulman, *et al.* 2016). In addition, studying constraints on social learning during ontogeny, that is, on vertical information transmission, may be important to understand the cultural dimension of primates because information would eventually extinguish if not passed to the next generation (van Schaik 2010).

1.4 CONSTRAINTS ON VERTICAL INFORMATION TRANSMISSION

1.4.1 The ontogeny of social learning

The immature phase of primate's life represents a period of intense learning, and the presence of knowledgeable older individuals is a fundamental source of social information (Rapaport and Brown 2008, Whiten and van de Waal 2018). Young primates need to learn how to navigate their physical and social environment (Altmann 1980). In particular, because post-weaning provisioning is rare, primates need to learn what to eat, where to find food, and how to process it in order to become nutritionally independent by weaning (Bray *et al.* 2018, Carvajal and Schuppli 2022). The foraging knowledge to be acquired may be vast (Carvajal and Schuppli 2022). For instance, yellow baboons (*P. cynocephalus*) at Amboseli (Kenya) can consume more than 250 types of food (Alberts 2019). Immatures could acquire foraging information by observing others and, then, inspecting and eating the same food items, and by sniffing the muzzles of other group mates (Brown *et al.* 2004, Rapaport and Brown 2008).

The ontogeny of primate social learning can be divided in two main sequential phases, characterized by learning from primary caring figures and other group members (Lonsdorf and Bonnie 2010, Whiten and van de Waal 2018). During the first phase, young primates may learn mostly from individuals in their proximity (Grampp *et al.* 2019). For example, young juvenile vervet monkeys tend to watch more often the individuals within 5 m during foraging, which mostly includes their matriline members (the mother and maternal siblings) (Grampp *et al.* 2019). Similarly, infant western chimpanzees focus their attention

on the mother during nut-cracking (Biro *et al.* 2003). During the second phase, young primates may actively look for other kinds of demonstrators (de Resende *et al.* 2004, Coelho *et al.* 2015). Accordingly, older juvenile vervet monkeys and chimpanzees have a relatively lower kin bias in their learning preferences (Biro *et al.* 2003, Grampp *et al.* 2019). Therefore, immature individuals can adopt different social learning strategies (Laland 2004): (1) acquire information from individuals in proximity and (2) target demonstrators with a specific phenotype independently from their proximity.

Learning from individuals in proximity

The individuals who are most often in spatial proximity may change depending on immatures' age and sex. When young, immatures of both sexes share their mother's network, including close kin, and unrelated maternal social partners (Berman 1982a, 1982b, de Waal 1996). As they age, immatures differentiate their social networks from the maternal one by forming their own relationships (Berman 1982a, 1982b, Kulik *et al.* 2015). As mentioned, in general, older juvenile primates associate with same-sex peers and the philopatric sex tends to be more integrated in the group's network (Lonsdorf 2017, Amici, Kulik, *et al.* 2019). Finally, in some cases, immature females and males could bias their proximity towards same-sex adult demonstrators, which may facilitate the acquisition of sex-specific behaviours (Agostini and Visalberghi 2005) (see also 'sex' below).

Although immatures of all ages could learn from demonstrators closer in their proximity network, this may be relatively more common in young immatures (Whiten and van de Waal 2018). Indeed, the demonstrator choices of infants and young juveniles are constrained by the presence of close kin, who provides care

and protection (Altmann 1980, Lehmann *et al.* 2006). First, infants are dependent on primary caring figures for nutrition and transport (Altmann and Samuels 1992, Barrett *et al.* 2006). Apart from cooperatively breeding species (e.g., Callitrichids) (Snowdon 1996, Tecot and Baden 2015), mothers are the individuals taking care of infants the most (Maestripieri 2018). In addition, even when independent from the mother, young juveniles may benefit from the presence of close kin for agonistic support when their rank is not yet established (Pereira 1989, Prud'Homme and Chapais 1993). By learning from spatially close individuals young immatures may acquire information mainly from close maternal kin, primarily the mother (Maestripieri 2018, Whiten and van de Waal 2018), but they could also learn from other individuals associated with their mothers (Huchard *et al.* 2013, Lynch *et al.* 2020).

Close maternal kin

Information transmission from mother to offspring has been described in several studies (Whiten and van de Waal 2018). For example, infant orangutans' diets largely overlap with those of their mothers. Mothers have different diets, and these are not correlated to maternal home ranges' food availability, thus suggesting a social transmission of dietary preferences from mother to offspring (Jaeggi *et al.* 2010). In addition, when groups of vervet monkeys were given a novel food (grapes) covered in sand, the range of cleaning techniques (sometimes more than one) used by infants matched those of their mothers more than those used by different individuals. Importantly, infants who manipulated the grapes for the first time adopted the cleaning technique they had just observed from their mothers, supporting a social transmission explanation (van de Waal *et al.* 2014).

Social information transmission from close maternal kin may lead to similarities in behaviour at the matriline level (van de Waal *et al.* 2012). In vervet monkeys, the proportions of each grape cleaning technique used were more similar between mothers and their immature offspring compared to adult full sisters, thus favouring a social learning over a genetic explanation. Similarities persisted in a follow-up session more than a year later (van de Waal *et al.* 2012). In addition, both in chimpanzees (Wrangham *et al.* 2016) and in Japanese macaques (Tanaka 1995) the frequencies of use of different grooming styles are more similar within than across matriline, suggesting a fidelity to the maternal grooming style despite the exchange of grooming with different matriline (Tanaka 1995, Wrangham *et al.* 2016).

Although matriline may be pivotal centres of information acquisition for young immatures, the restriction of behaviours to the matriline level may limit the formation of group-level cultures, as mentioned previously (van de Waal *et al.* 2012). Social information clustering within matriline may occur particularly in female-philopatric societies because (i) older juvenile males, who may produce information more than female peers (Amici, Widdig, *et al.* 2019) (see §1.3.1), tend to be relatively less bonded to their maternal kin (Amici, Kulik, *et al.* 2019), thus limiting the introduction of novel information inside their matriline; and, (ii) although juvenile males are less socially focused on their matriline, and may thus act as information ‘bridges’ across different matriline, they are less likely to act as demonstrators than females because they are the dispersing sex (van de Waal *et al.* 2010) (see also ‘sex’ below).

Other individuals

Other than close maternal kin, young immatures' regular spatial associates may include other maternal social partners (Amici, Kulik, *et al.* 2019). Because infants are attractive to others, they receive affiliations from several group mates (Silk 1999, Dunayer and Berman 2018), who may widen the social network of new mothers (Silk, Rendall, *et al.* 2003, Frank and Silk 2009). In addition, mothers may interact with unrelated adult females and their offspring, with whom infants may bond (Owens 1975, de Waal 1996), and with adult males, whom new mothers may follow as an infanticide counterstrategy (Nguyen *et al.* 2009, Baniel *et al.* 2016). These males are often the biological fathers of the offspring and may provide paternal care in the form of affiliation (e.g., tolerated proximity) and agonistic support (Buchan *et al.* 2003, Murray *et al.* 2016).

Other than in cooperatively breeding primates, where fathers commonly provision their offspring (Snowdon 1996), associating with their fathers may provide social learning opportunities for young primates in general (Huchard *et al.* 2013, Lynch *et al.* 2020). For example, owing to adult males' high dominance status, juvenile chacma baboons can access relatively higher quality food patches by foraging with their fathers whilst potentially acquiring information from them (Huchard *et al.* 2013). In addition, the presence of fathers may widen young juveniles' social networks by connecting them to their paternal siblings (Lynch *et al.* 2017). Paternal siblings may constitute important social partners both for females (Smith *et al.* 2003, Schülke *et al.* 2013) and for males (Kulik *et al.* 2015, Widdig *et al.* 2016). Compared to maternal siblings, paternal siblings may be of similar age and thus form potentially long-lasting bonds (Altmann 1979, Silk *et al.* 2010a). Fathers may thus have a role in connecting different matrilineal lines (Silk *et al.*

al. 2017), which may be important to mitigate the negative effects of matrilineal clustering on group-level information transmission (see above).

Learning from specific demonstrators

Older juveniles, who are relatively more independent from the care and protection of their close kin, can actively select the individuals from whom to acquire information rather than simply observing conspecifics in their proximity (Coelho *et al.* 2015). Although looking for specific demonstrators may be more common for older rather than younger immatures (Grampp *et al.* 2019), infants and young juveniles may also show learning preferences when different demonstrators are within their spatial proximity group (Estienne *et al.* 2019). In particular, immatures may bias their attention towards demonstrators that possess characteristics indicative of their knowledge (e.g., older age) or that could provide better learning opportunities (e.g., more successful in exploiting a resource) (Laland 2004, Lonsdorf and Bonnie 2010). Multiple learning biases can be present at once (Coelho *et al.* 2015, Tan *et al.* 2018) and may flexibly change depending on the context (Bono *et al.* 2018). Because these learning biases influence who learns from whom, they may also contribute to determine which novel information spreads in a group. For example, although males tend to learn individually more than females (Amici, Widdig, *et al.* 2019) (see §1.3.1), their innovations may be unlikely to spread in female-philopatric societies because individuals may prefer to acquire information from the philopatric sex, that is females (van de Waal *et al.* 2010) (see below).

Demonstrators' age

Juveniles may preferentially acquire information from older individuals (Laland 2004). Because older individuals benefit from a relatively greater experience, the social information acquired from them may be of 'higher quality', thus allowing observers to gain greater foraging benefits (Barrett *et al.* 2017) (see also 'success' below). However, this tendency may depend on which kind of information is acquired. For example, older individuals may be targeted to acquire food processing techniques in which age, and thus experience, is predictive of higher foraging proficiency (Visalberghi *et al.* 2016). When a novel food was introduced in naïve social groups, younger white-faced capuchins tended to adopt the processing techniques of older individuals, who were also those most efficient in extracting the edible kernels (Barrett *et al.* 2017). Similarly, juvenile long-tailed macaques (Tan *et al.* 2018) and robust capuchins (Coelho *et al.* 2015) observe older, more proficient, conspecifics during tool use.

On the other hand, the expertise of older individuals may be less necessary for foraging on foods that do not require specific extractive techniques or the use of tools. In this case, individuals may prioritise other characteristics in choosing from whom to learn (Grampp *et al.* 2019). For example, juvenile vervet monkeys tend to forage in proximity to other juveniles rather than adults and demonstrators' age does not predict social attention. Immature individuals, with whom juveniles may share stronger bonds compared to adults (Amici, Kulik, *et al.* 2019), may be preferred as learning partners for their relatively higher social tolerance (Grampp *et al.* 2019) (see also 'affiliation' below). These results are not due to a species-specific preference for younger demonstrators because individuals from the same population biased their attention towards adults *versus* immatures when

given a novel food that adults were relatively more efficient in extracting (Canteloup, Cera, *et al.* 2021).

Demonstrators' sex

Demonstrators' sex may affect juveniles' learning choices because they may learn either from individuals of the philopatric sex or same-sex individuals. First, compared to the dispersing sex, the philopatric sex could have a more accurate knowledge of the local resources (van de Waal *et al.* 2010). For instance, juvenile common marmosets (Schiel and Huber 2006) and vervet monkeys (Grampp *et al.* 2019) observe females, the philopatric sex, more than males during natural foraging. Experiments with male and female demonstrators further confirmed these results in vervet monkeys: individuals attended relatively more to the behaviour of female demonstrators while opening baited boxes and opened the boxes from the same side as the demonstrator only when the latter was a female (van de Waal *et al.* 2010, Bono *et al.* 2018). This sex bias seems to be independent from the demonstrator's dominance rank (Renevey *et al.* 2013).

Information acquisition from the dispersing sex may be relatively less common, but it may still occur in some cases. For example, the number of cultural traits in different chimpanzee communities is predicted by the number of females, the dispersing sex, rather than by the number of males or the overall group size (Lind and Lindenfors 2010). This may be at least partially explained by immigrant females introducing behaviours performed in their natal group into their new community (Lind and Lindenfors 2010), as reported for the predation of a new ant species (O'Malley *et al.* 2012). In addition, individuals from the dispersing sex may be relatively more flexible in their learning strategies and learn from the

philopatric or the dispersing sex depending on which behaviour gives the higher pay-offs (Bono *et al.* 2018) (see also ‘success’ below).

Second, juveniles may learn from the same sex when they acquire sex-typical behaviours. As mentioned, a bias towards being in spatial proximity to same-sex individuals may facilitate learning from them (Pereira 1988a, Agostini and Visalberghi 2005). For instance, juvenile male black capuchins (*S. nigritus*) are both more often in proximity to adult males and pay more attention to them than female peers, which may lead to sex-differentiated diets in adulthood (Agostini and Visalberghi 2005). However, juveniles may also actively look for demonstrators of the same sex despite social connections being similar between sexes: as mentioned, juvenile female eastern chimpanzees (Lonsdorf *et al.* 2004) and juvenile male bearded capuchins (Falótico *et al.* 2021) learn to use tools from, respectively, the mother and adult males more than peers of the opposite sex.

Demonstrators’ rank

Studies have reported both a learning bias towards higher-ranking and towards lower-ranking individuals since there may be advantages in acquiring information from both. On the one hand, individuals may gain benefits by learning from dominant demonstrators because they could provide (i) relatively ‘better’ information, such as the presence of high-quality food that they monopolised, and (ii), in some cases, food scrounging opportunities. For example, in vervet monkeys, the information regarding the technique used to open a baited box was transmitted from high- to low-ranking individuals in the social network (Canteloup *et al.* 2020). In addition, foraging with a dominant individual who is tolerant of an observer’s presence may allow access to high-quality resources (e.g., juvenile

chacma baboons foraging with their father (Huchard *et al.* 2013); see above). On the other hand, individuals may acquire information relatively more from lower-ranking group mates. Indeed, unless social affiliation allows lower-ranking individuals to be tolerated by higher-ranking ones (Sick *et al.* 2014) (see also ‘affiliation’ below), individuals are relatively more likely to approach and to scrounge food from subordinates (e.g., chacma baboons foraging with lower-ranking individuals and close social affiliates (King, Clark, *et al.* 2011); see §1.3.1).

Demonstrators’ success

In a foraging context, more successful demonstrators are those who extract food more efficiently. Acquiring information from more efficient individuals can thus be considered a pay-off biased strategy (Laland 2004). More successful demonstrators may be, as mentioned, older individuals because they are more experienced (Barrett *et al.* 2017), or dominant individuals because they can access higher-quality resources (Huchard *et al.* 2013). Individuals could prioritize a pay-off learning bias over other biases depending on their flexibility, as mentioned above. For example, when a male vervet monkey was given more food upon opening one side of a baited box than a female demonstrator, who opened the other side, male observers, but not female ones, copied more often the male demonstrator. Instead, when demonstrators were given the same amount of food independently from their sex, observers of both sexes copied relatively more the female demonstrator (Bono *et al.* 2018).

Individuals may pay attention to successful demonstrators because they could increase their own foraging success by (i) learning an efficient foraging technique (e.g., white-faced capuchins processing a novel food (Barrett *et al.*

2017); see above) and, as mentioned, (ii) scrounging food from those demonstrators. In particular, food scrounging has been suggested to facilitate learning by positive reinforcement (Caldwell and Whiten 2003, Ottoni and Izar 2008). Indeed, attending the nut-cracking behaviour of relatively more successful demonstrators maximises the food scrounging pay-offs of immature long-tailed macaques (Tan *et al.* 2018) and robust capuchins (Coelho *et al.* 2015). Obtaining food from others is also facilitated by social tolerance (Ottoni *et al.* 2005) (see below).

Social affiliation

Social affiliates may be preferred learning partners because they are tolerant of each other's proximity, which is known to facilitate social information use (see §1.3.1) and, as mentioned, may allow food scrounging (van Schaik *et al.* 1999, Ottoni *et al.* 2005). Strong social bonds may be formed with close kin and with unrelated individuals. First, as mentioned, close maternal kin preferentially associate together (Langergraber *et al.* 2009, Silk *et al.* 2010a) and are the primary learning targets of young immatures (Whiten and van de Waal 2018) (see above). However, older individuals may also learn from close kin, independently from their spatial proximity. For example, moss-sponging, an innovation involving the use of moss to collect water, first spread through a proximity network (Hobaiter *et al.* 2014) and subsequently within matriline (Lamon *et al.* 2017). Because moss-spongers did not associate more with each other *per se*, matriline-based transmission was not a by-product of association with kin (Lamon *et al.* 2017). Learning from close kin may be relatively more important in despotic societies (with a strong nepotistic bias; see §1.3.1) and, for older juveniles in general, it may be advantageous because the social tolerance of unrelated

individuals could be lower towards older compared to younger immatures (Pereira 1988a).

Second, unrelated individuals may share strong bonds through affiliative interactions. These bonds are often maintained by subordinates who affiliate with dominant individuals in order to gain social tolerance (Sick *et al.* 2014) (see also §1.3.1). For example, juvenile long-tailed macaques (Tan *et al.* 2018) and robust capuchins (Coelho *et al.* 2015) pay relatively more attention to close social partners using tools. As mentioned, chacma baboons tend to associate with close social partners during foraging, independently from their genetic relatedness (King, Clark, *et al.* 2011). While grooming is the main form of affiliation among adult primates (Dunbar 1991, 2010), immature individuals also bond with each other through play (Palagi 2018). Social play generally decreases throughout the immature period, while grooming increases (Shimada and Sueur 2014, 2017), and it is prevalent in juvenile males compared to female peers (Förster and Cords 2005, Lonsdorf, Markham, *et al.* 2014).

The majority

Another social learning strategy is to copy the majority, referred to as conformity (Laland 2004). This happens when individuals refrain from applying their personal knowledge if it is different from the group's norm and, instead, converge their behaviour to what most individuals in the group do (Whiten, Horner, and de Waal 2005). For instance, a novel behaviour was seeded in groups of vervet monkeys by providing two differently coloured variants (pink and blue) of the same food, one of which was made unpalatable. Individuals from different groups first learnt to avoid the distasteful food colour (e.g., pink); when the two options were presented months later coloured but both palatable, naïve

infants adopted the maternal preference for the originally palatable option (e.g., blue). Importantly, although low-ranking individuals discovered that the pink food was now edible, they ate the group-preferred blue option whenever it was not monopolised by dominant individuals (van de Waal *et al.* 2013).

Conformity could contribute to the maintenance of cultural behaviours and hinder the transmission of novel behaviours (Whiten, Horner, and de Waal 2005). Indeed, in the vervets' experiment, nine out of 10 immigrant males coming from groups where the originally palatable option was of the opposite colour than in the group in which they immigrated, switched their choice towards their new group's colour preference (van de Waal *et al.* 2013). Colour preferences were maintained for years, even after group split (van de Waal *et al.* 2017). In addition, a long-term study on western chimpanzees showed that neighbouring communities maintained cultural diversity in the selection of nut-cracking tools over a period of 25 years despite frequent immigrations of adult females. The case of an immigrant female progressively shifting her nut-cracking technique towards that of her new group suggests that conformity promotes chimpanzees' cultural diversity (Luncz and Boesch 2014).

Conclusions

In summary, the ontogeny of social learning has been explored in some primate species, but there is still little knowledge on many taxa without material culture (i.e., most monkeys) (Whiten and van de Waal 2018). Since social attention is not always correlated to the acquisition of information (Humble and Snowden 2008, Canteloup *et al.* 2020), it may be easier to determine when social learning occurs in species with material culture because individuals' observation could be followed by an increase in manipulation of the same objects used by the

demonstrator (Schuppli, Meulman, *et al.* 2016, Lamon *et al.* 2018). However, because several behaviours have now been linked to social information acquisition in species leaving artefacts from their subsistence activities (Rapaport and Brown 2008, Schuppli and van Schaik 2019), these behaviours may be explored in other taxa as indicative of social learning (Alberts 2019).

Other than studying immatures' learning from others in general, understanding the specific role of mothers in shaping their offspring's social learning may contribute to unravel primates' cultural development. Mothers are the primary learning model for infants and young juveniles, leading the intergenerational flow of social information (Maestriperi 2018). Even though the learning process continues in the juvenile phase, this first source of maternal information is fundamental for infants, who need to become nutritionally independent by weaning (Whiten and van de Waal 2018, Carvajal and Schuppli 2022).

1.4.2 The role of mothers

Mothers are the sole individual responsible for their infants' survival in most primate species (Maestriperi 2018) and maintain strong bonds with their offspring beyond weaning (Samuni *et al.* 2020, Delaunay *et al.* 2023). Mothers can influence immatures' behavioural development both through genetic inheritance and non-genetic mechanisms (Wolf and Wade 2009, Von Borell *et al.* 2019). First, examples of genetic inheritance of behaviour include immatures' temperament (Von Borell *et al.* 2019). For example, the age at first grooming of wild infant yellow and yellow-olive baboons (Lange *et al.* 2023) and the exploration tendency of infant captive rhesus macaques (Fawcett *et al.* 2014) are heritable. Second, epigenetics may be a main form of non-genetic intergenerational transmission of

behaviour: early rearing experiences may have consequences on gene expression, and ultimately affect individuals' neuroendocrine system and behaviour (Champagne 2010, English *et al.* 2015). Both genetic and non-genetic maternal influences were confirmed by cross-fostering experiments (Maestriperi 2018): when becoming mothers themselves, captive rhesus macaques were more similar to their foster mothers than to their biological mothers in the rates of maternal rejection and grooming, while the rates of making contact with their infants were relatively more similar to those of their biological mothers (Maestriperi *et al.* 2007). Importantly, mothers may enhance or constrain immatures' social learning by (1) actively facilitating learning of certain skills, (2) shaping their social connections and thus their opportunities to learn from others, and (3) influencing their propensity to acquire personal or social information.

Learning facilitation

Mother-offspring information transmission mainly occurs passively through the offspring's observation of the mother's behaviour (see §1.4.1), but mothers could also actively create social learning opportunities for their offspring (Maestriperi 2018). This has been documented in chimpanzee mothers during tool use (Musgrave *et al.* 2016, Estienne *et al.* 2019). For example, in central chimpanzees (*P. t. troglodytes*), mothers allow their infants to explore the materials they gathered before and during their nut-cracking and termite-fishing activities. Mothers are the only individuals allowing extensive interruptions of their tool-use activities and they experience a cost in terms of reduced feeding efficiency. On the offspring's side, more occasions to practice with the mother's tools increase tool-use proficiency and, consequently, feeding rate compared to before the 'tool transfer' (Musgrave *et al.* 2016). Similarly, central chimpanzee

mothers facilitate learning of a tool-use technique to extract honey from underground bee nests by sharing tools and spending time inactive at the nests, thus allowing their infants to practice. Mothers decrease inactive time as their infant daughters age, while the opposite happens with sons, possibly as a consequence of earlier learning in female infants compared to male peers (Estienne *et al.* 2019).

Maternal sociality

A mother may shape her offspring's social connections through (i) passive exposure to her social partners, (ii) her degree of sociability, and (iii) active encouragement or dissuasion to associate with certain social partners. Maternal social connections may provide bonding opportunities for her offspring and affect both with whom and with how many social partners immatures familiarise (Brent 2015, Maestripieri 2018). As mentioned, young immatures, who spend most of the time in proximity to their mothers, share the maternal social network (Berman 1982a, 1982b). Even when differentiating their relationships, maternal social connections may continue to affect the immatures' ones (Kulik *et al.* 2015, Jarrett *et al.* 2018). In female-philopatric Cercopithecine monkeys, this process has been defined as the 'inheritance' of maternal social networks, which occurs through familiarity beyond the attraction towards close maternal kin (de Waal 1996). For example, the associations between pairs of wild juvenile Japanese macaques (Nakamichi 1996) and captive rhesus macaques (de Waal 1996) are largely a reflection of those between their mothers.

Mothers may have numerous social connections because many individuals interact with them and because they themselves socialise with many individuals (Krause *et al.* 2010, Sosa *et al.* 2021). First, both a mother's matriline size and

dominance rank could determine to how many social partners her offspring is exposed. A greater number of maternal siblings may widen immatures' networks by providing indirect social connections (i.e., 'friends of friends' (Brent 2015)). Because of the attraction towards dominant individuals (to gain social tolerance; see §1.3.1), offspring of higher-ranking mothers may associate with relatively more maternal partners (Barrett *et al.* 1999, Sick *et al.* 2014) and, by inheriting the maternal rank (Holekamp and Smale 1991), have more social partners themselves (Wooddell *et al.* 2020, Liu *et al.* 2022). Second, more sociable mothers may have a relatively higher social integration by directly engaging in social interactions (Kulahci *et al.* 2018b) (see §1.3.1). In both cases, social exposure during early life may affect immatures' sociability (Thompson and Cords 2020, Wooddell *et al.* 2020). For instance, in Stuhlmann's blue monkeys (*Cercopithecus mitis stuhlmanni*), the more a mother groomed with other females during her offspring's infancy, the less juvenile females play with peers and the more juvenile males engage in social play. Instead, maternal sociability throughout the whole immature period does not predict the offspring's play tendencies (Thompson and Cords 2020).

Finally, in some cases, mothers actively influence the proximity of their offspring to certain social partners (Maestriperi 2018). On the one hand, mothers may promote their infants' association with group members whose affiliation may be advantageous (e.g., to learn sex-specific behaviours (Murray *et al.* 2014) or for agonistic support and social tolerance (de Waal 1990)). For example, in eastern chimpanzees, mothers of sons, compared to mothers of daughters, spend more time in larger parties (i.e., temporary groups resulting from other groups' fission or fusion) and parties that contain adult males during the first six months of infants' life. Because infants below six months of age are always in the

same party as their mothers, these associations are unlikely to be driven by the offspring's own social preferences (Murray *et al.* 2014). On the other hand, mothers may limit the association of their offspring with individuals who may pose a threat to infants (Maestriperi 2018). For instance, captive rhesus macaque mothers are intolerant of infant handling from females who may kidnap their infants (Maestriperi 1995) and wild yellow baboon mothers with young infants avoid the proximity of potentially infanticidal males (Palombit *et al.* 2001). This may also depend on a mother's degree of protectiveness (Sekizawa and Kutsukake 2019) (see below).

Maternal style

Maternal style refers to between-individual variation in infant care behaviours that persist across different infants and contexts (Berman 1980, Fairbanks 1996). Although maternal style behaviours tend to be consistent within individuals, maternal phenotype (e.g., parity, dominance rank), infant characteristics (e.g., age, sex) (Dura *et al.* 2018, Arlet *et al.* 2019), and the social context (e.g., threats to the infants) (Fairbanks and McGuire 1987, Maestriperi 2001) can condition maternal behaviour. Maternal style has been studied mainly in Cercopithecine monkeys in captivity (Maestriperi 2018), in which both the behavioural and physiological aspects of maternal behaviour have been documented (Bardi *et al.* 2003, Nguyen *et al.* 2012), as well as their knock-on effects on the offspring's own physiology and behaviour (Bardi and Huffman 2006, Maestriperi *et al.* 2009).

In Cercopithecines, maternal style has been described as varying along two main independent dimensions, named 'protectiveness' and 'rejection'. Protectiveness reflects a mother's tendency to maintain contact and/or proximity with her infant, and to prevent the infant from leaving her contact and/or proximity

(Maestriperi 2001, Sekizawa and Kutsukake 2019). Rejection reflects a mother's tendency to break contact and/or proximity with her infant and prevent the infant from making contact with her (Schino *et al.* 1995, Liu *et al.* 2018). Combinations between different degrees (high or low) of protectiveness and rejection lead to four possible maternal styles: 'controlling' mothers are characterized by high protectiveness and rejection, while 'laissez-faire' ones have low values of both factors; the 'protective' style is typical of highly protective and low rejecting mothers, while the 'rejecting' one is attributed to low protective and high rejecting mothers (Fairbanks 1996, Maestriperi 1999).

In addition to protectiveness and rejection, some studies reported a third maternal style dimension, termed maternal 'warmth'. Warmth correlates with being in ventral-ventral contact with the infant, cradling and grooming the infant, and allowing nursing (Hinde and Simpson 1975, Maestriperi *et al.* 2009). This dimension may be similar to human parental responsiveness (Maestriperi 1999) and, similarly to humans, it may determine primate infants' attachment security, i.e., a measure of how much a caregiver represents a secure base from which to explore the surrounding environment (Mason and Mendoza 1998, Maestriperi and Roney 2006). As for humans, securely attached primate infants may be more willing to leave the proximity of their mothers and explore the environment surrounding them compared to insecurely attached ones (Kondo-Ikemura and Waters 1995, McCormack *et al.* 2015).

Maternal style may have both short- and long-term effects on the offspring's development (Maestriperi 2018). For example, in captive vervet monkeys, infants of protective mothers have fewer opportunities to explore the environment beyond their mother's reach compared to those whose mothers are less protective (Fairbanks and McGuire 1987). When juveniles, infants who had

protective mothers spent relatively less time looking outside their enclosure and had a relatively higher latency to enter a novel enclosure (Fairbanks and McGuire 1988, 1993). Maternal protectiveness experienced early in life may continue to affect the offspring's behaviour up to adolescence: subadult vervet monkeys who had protective mothers were also more cautious in approaching and inspecting a foreign adult male (Fairbanks 1996).

A direct influence of maternal style on the offspring's social learning was reported only in captive brown rats (*Rattus norvegicus*) (Lindeyer *et al.* 2012). Maternal licking-grooming, a behaviour associated with warmth, is consistent across litters in individual mothers (Champagne *et al.* 2003). When adult, rats who received more maternal grooming as pups learn conspecifics' food preferences more than those who were maternally deprived (Lévy *et al.* 2003, Melo *et al.* 2006) or who received less maternal grooming (Lindeyer *et al.* 2012). In primates, maternal style could influence immatures' social learning by shaping (i) their propensity to collect social information and (ii) their opportunities to learn from others.

Social learning propensity

Maternal style could shape the immatures' propensity to acquire either social or individual information (or both) through indirect effects on their behaviour. For example, maternal style may affect the offspring's tendency to explore the environment and the ability to cope with stress (Maestripieri 2018). First, greater exploration may enhance both social and individual learning. By exploring the physical and social environment around them, immatures may discover novel information (Biro *et al.* 2003) and have opportunities to acquire social information (van Boekholt *et al.* 2021) (see also §1.3.1 and below). Indeed, the attraction

towards novelty (i.e., boldness (Carter *et al.* 2012c)) in chacma baboons was linked to higher social learning in the presence of reliable cues (Carter *et al.* 2014) but higher individual learning when information is unreliable (Carter, Marshall, *et al.* 2013). Second, better abilities to cope with stress translate in lower vigilance for threat during stressful situations (stress levels) or in general (i.e., anxiety (Carter *et al.* 2012c)). Lower stress levels are linked to better social and individual learning in mammals (Bangasser and Shors 2010). However, higher anxiety predicted a relatively greater reliance on social information about a novel food in chacma baboons (Carter *et al.* 2014).

Different maternal style dimensions may have opposite effects on the offspring's exploration and stress-coping abilities. First, higher maternal protectiveness appears to constrain exploration, while higher rejection and warmth seem to enhance it (Maestriperi 2018). For instance, in captive Japanese macaques (Bardi and Huffman 2002) and vervet monkeys (Fairbanks 1996), protective mothers had juvenile offspring who showed relatively less interest in the external environment and who were more cautious towards novelty (see also above). Opposite effects were reported for offspring of rejecting mothers (i.e., higher exploration) both in captive Japanese and rhesus macaques (Bardi and Huffman 2002, 2006) and in captive vervet monkeys (Fairbanks 1996). Finally, in captive Japanese macaques, securely attached infants, who have warm mothers, explore the environment surrounding their mothers more than insecurely attached ones (Kondo-Ikemura and Waters 1995).

Second, higher maternal protectiveness and rejection may generally constrain the development of stress-coping abilities in the offspring (but see below), while higher maternal warmth may favour it (Maestriperi 2018). For example, infant rhesus macaques who had protective mothers spent relatively

more time looking to a picture of a conspecific's threatening face compared to a neutral face, which may indicate social anxiety (Mandalaywala *et al.* 2014). Similarly, in captive rhesus macaques (Maestriperi *et al.* 2006) and white-faced marmosets (*C. geoffroyi*) (Birnie *et al.* 2013), offspring who had experienced higher rejection also showed higher stress levels when up to two years old. However, contrasting results on higher maternal rejection improving stress-coping abilities up to adulthood were reported in captive Japanese macaques (Schino *et al.* 2001). Finally, higher maternal warmth was associated with lower stress levels in captive juvenile baboons (Bardi *et al.* 2005) and macaques (Bardi and Huffman 2006).

Social learning opportunities

Maternal style could influence immatures' social learning opportunities by enhancing or limiting their social connections (van Boekholt *et al.* 2021). A mother's maternal style may affect both the social interactions that her offspring receives and those that s/he gives. First, as mentioned, protective and controlling mothers may directly limit their infants' social interactions by restraining them and retrieving them when not in contact. As a consequence, infants of protective and controlling mothers may experience fewer social interactions when young than infants of rejecting and laissez-faire mothers (Altmann 1980, Maestriperi 2018). For example, infants of protective Japanese macaque mothers receive relatively less handling and grooming from other group mates (Sekizawa and Kutsukake 2019).

Second, maternal style may influence the offspring's propensity to interact with others (Maestriperi 2018). For example, in captive Japanese and rhesus macaques, infants who had protective mothers engage in relatively fewer social

interactions when older, while infants who had rejecting mothers initiate relatively more social interactions (Bardi and Huffman 2002, 2006). As mentioned, securely attached infants may have both more opportunities and a greater willingness to socialise compared to insecurely attached ones. Indeed, in captive Japanese macaques, securely attached infants tend to leave the mother's proximity relatively more often, which exposes them to more social partners (Kondo-Ikemura and Waters 1995). In addition, in captive bonnet (*M. radiata*) and pigtail (*M. nemestrina*) macaques, juveniles who had experienced a relatively higher maternal warmth socialised more with others when transferred in a peer-only group (Weaver *et al.* 2004). However, contrasting results on lower maternal warmth favouring infants' interactions with others have also been reported (Bardi and Huffman 2006).

Conclusions

In summary, mothers may have an important role in enhancing or constraining their offspring's social learning opportunities and their propensity to learn from others. While learning facilitation may be limited to certain taxa and particular circumstances (Musgrave *et al.* 2016), the influences of maternal sociality and maternal style on immatures' social learning seem relatively more widespread across primate species (Maestriperi 2018). Nevertheless, most studies have focused on macaques and, in general, on provisioned or captive social groups (Lonsdorf 2017, Amici, Kulik, *et al.* 2019), which may experience different social and environmental constraints compared to wild ones (Hill 1999, Haslam 2013). In addition, the potential role of different maternal style dimensions in shaping immatures' social learning needs to be clarified (Maestriperi 2018). In

particular, little is known on maternal warmth, which was linked to social learning in brown rats (Lindeyer *et al.* 2012).

The next section (§1.5) reviews the social system of baboons, the taxon on which this study focuses, and explains why baboons are an ideal taxon to study the constraints on horizontal and vertical information transmission, and hence the formation of culture, in primates. Finally, building on the gaps in our knowledge outlined above, I present the aims of the current study and describe the study site (§1.6).

1.5 BABOONS

1.5.1 Taxonomy and distribution

Cercopithecine (Old World) monkeys belonging to the genus *Papio* are known as baboons (Groves 2017). The genus counts six species (Table 1.3) distributed across sub-Saharan Africa (Zinner *et al.* 2013). The Guinea, olive and hamadryas baboons are found in central Africa and the Arabian Peninsula. The Guinea baboon inhabits a small area on the western side of Africa, while the hamadryas baboon is located on the eastern side and its range includes the south-western tip of the Arabian Peninsula. The olive baboon is the most wide-ranging, spreading across equatorial sub-Saharan Africa. The other three species range in central-south Africa. The yellow and kindia baboons are distributed across the eastern and western sides, respectively, of northern Southern Africa, sandwiched between the ranges of olive baboons to the north and of chacma baboons to the south. Chacma baboons are found all across Southern Africa (Fischer *et al.* 2017, 2019). No baboon species is of conservation

concern, except for the Guinea baboon, who is considered 'near threatened' (IUCN 2023).

Table 1.3: Species' and common names of baboons (Zinner *et al.* 2013).

Common name	Species' name
Chacma baboon	<i>Papio ursinus</i>
Guinea baboon	<i>Papio papio</i>
Hamadryas baboon	<i>Papio hamadryas</i>
Kinda baboon	<i>Papio kindae</i>
Olive baboon	<i>Papio anubis</i>
Yellow baboon	<i>Papio cynocephalus</i>

Adult baboons have a marked sexual dimorphism. Adult males are approx. twice the size of adult females. They also have a longer muzzle and long sharp canines. For example, in chacma baboons (the largest among the baboon species), males weigh on average 30 kg and females 15 kg (Fischer *et al.* 2019) (Figure 1.1). While females pass directly from the juvenile to the adult phase when they start cycling (i.e., ovulating), males have an intermediate subadult phase after they reach sexual maturity and before achieving full adult size (Table 1.4).

Figure 1.1: A lactating female chacma baboon grooms an adult male. Like in the other baboon species, sexual dimorphism is marked. Photo credit: Axelle Delaunay.



Table 1.4: Classification of individual baboons according to age class and sex. The correspondent approximate age is shown (Altmann *et al.* 1981, Alberts and Altmann 1995a, 1995b, Altmann and Alberts 2003, Cheney *et al.* 2004, Dezeure, Dagorrette, *et al.* 2021).

Age class	Sex	Age	Description
Pink infant	Female/ Male	0–3 months	Young baboon before weaning age. At birth s/he has a black coat and pink skin, which starts turning grey by the 3 rd month of age. By the 6 th month of age, the infant has both the coat and the skin completely grey and starts turning to the adult colour by the 7 th month of age. This transition to the adult colour is completed by the end of the 1 st year of age.
Grey infant		4–7 months	
Black infant		8–12 months	
Juvenile	Female/ Male	13 months to 5 years	Young baboon fully weaned. A female has two separate ischial callosities, while a male has an unbroken ischial callosity. Sexual dimorphism in size is not marked yet.
Subadult	Male	6–8 years	A male larger than an adult female who has reached sexual maturity but is still growing. He may emigrate to other troops.
Adult	Female	> 5 years	A female who has completed growth and is cycling. Upon reaching menarche she undertakes a period of subfertility, after which she conceives her first infant around six years old. A female can live for > 20 years.
	Male	> 8 years	A male who has completed growth. He is about twice the size of an adult female and has long sharp canines. He may still emigrate to other troops until about 11 years old. A male generally lives < 15 years old.

1.5.2 Socio-ecology

Baboons are predominantly terrestrial and are behaviourally flexible, allowing them to inhabit a variety of habitats, from open savannahs to woodlands and hills, including urban environments (Hoffman and O'Riain 2011, Stone *et al.* 2013). Baboons are omnivorous and spend about a half of their daytime feeding. Although predominantly herbivorous, they occasionally eat insects and small vertebrates (Altmann 1980, Cheney and Seyfarth 2007). In addition, groups close to human settlements can feed opportunistically on farm crops, for which they are widely considered as pests (Hill 2000, Fehlmann *et al.* 2017).

Mortality in the wild is mainly due to predation for adults and juveniles, while common causes of infant mortality include also infanticide and pathologies (Cheney *et al.* 2004, Alberts 2019). The main predators for baboons are lions (*Panthera leo*) and leopards (*P. pardus*) (Cowlshaw 1994). Mortality rates are relatively low for juveniles and adult females, while for adult and subadult males (see Table 1.4), these are less clear because their sudden disappearance can be due to emigration rather than death. Infants are the most vulnerable age class (Altmann and Alberts 2003, Cheney *et al.* 2004). For example, at Amboseli, yellow baboons' mortality in the first year of life can reach up to 60%, while survival is over 90% for nearly adult individuals (Alberts 2019).

Baboons live in cohesive groups, known as troops, which vary greatly in size, from a few to over 100 individuals. In general, because of their larger size, males are socially dominant over females (Cheney and Seyfarth 2007). However, the fine social organisation of baboon troops varies depending on the species. Chacma, olive, kindia, and yellow baboons (called 'COKY') live in multi-male-multi-female societies where females are philopatric and they mate with multiple males in the group (Fischer *et al.* 2019). In contrast, hamadryas and Guinea

baboons have multi-level societies with female-biased dispersal: hamadryas baboons' groups present multiple one-male units formed by a male and a variable number of females (Swedell and Plummer 2019); Guinea baboons' groups comprise multiple units formed by a primary breeding male, a variable number of females, and secondary males (Fischer *et al.* 2017). In these two species, interactions are concentrated at the unit's level, but occur also between units in the same group (Fischer *et al.* 2019). Further descriptions regard the most common social and mating system found in the genus *Papio*, that of COKY baboons.

Female baboons form the 'core' of baboon society (Cheney and Seyfarth 2007). They share strong and stable bonds with their close maternal kin (Silk, Alberts, *et al.* 2006, Silk, Altmann, *et al.* 2006), but they also interact frequently with similarly-aged paternal half-sisters (Smith *et al.* 2003, Silk *et al.* 2010a). Females form a stable and linear dominance hierarchy, maintained through maternal kin support (Pereira 1988b, Silk *et al.* 2004), with offspring attaining their mother's rank (Cheney 1977, Pereira 1989). Between-matriline rank reversals are rare, but, within the same matriline, females shift in rank whenever a new daughter is born because she inherits a rank just below her mother's (Samuels *et al.* 1987, Engh *et al.* 2009).

Female competition takes mainly the form of supplant (i.e., when a subordinate individual gives up a resource to a dominant one) (Cheney and Seyfarth 2007). High-ranking females have priority of access to food resources (King *et al.* 2008, Marshall *et al.* 2015), mating opportunities (Huchard and Cowlshaw 2011, Baniel *et al.* 2018a), and social partners (Palombit *et al.* 2001, Baniel *et al.* 2018b). As a result, dominant females have shorter interbirth intervals than subordinate females (Altmann and Alberts 2003, Cheney *et al.*

2004), and their offspring grow at a relatively higher rate (Johnson 2003) and reach sexual maturity sooner (Alberts and Altmann 1995a, Altmann and Alberts 2005).

Males remain in the natal troop until they reach sexual maturity (sub-adulthood), when they tend to disperse to other troops (Alberts and Altmann 1995a, 1995b). The male dominance hierarchy is dynamic since contests frequently arise among males of adjacent ranks, who often engage in non-violent displays and, occasionally, physical fights (Fischer *et al.* 2004, Kitchen *et al.* 2005). Males compete over mating opportunities, which is reflected in their stress levels (Bergman *et al.* 2005). For instance, in chacma baboons, high-ranking males' stress levels increase during periods of instability in the hierarchy and during a consortship (i.e., when a male guards a cycling female and mates exclusively with her) (Bergman *et al.* 2005).

As a result of their female monopolisation abilities, males' rank is a predictor of their short-term reproductive success (Altmann and Alberts 2003, Alberts *et al.* 2006). In addition, males can have other reproductive strategies, such as being sexually coercive and committing infanticide. Sexual coercion is common in chacma baboons, where males are more likely to consort with a female they harassed during her previous peri-ovulatory period (Baniel *et al.* 2017, 2019). Infanticide is prevalent in high group density conditions, where a male rarely holds the alpha position for more than one year, and is generally perpetrated by new immigrant males (Cheney *et al.* 2004, Zipple *et al.* 2017). Infant killing can reduce postpartum sterility by up to 13 months, creating more mating opportunities for males (Altmann *et al.* 1978).

1.5.3 Reproduction

Baboons have a polygynandrous mating system in which both sexes mate with multiple partners (Cheney and Seyfarth 2007). Baboons are non-seasonal breeders, with no distinct mating and birth seasons (Cheney *et al.* 2004, Dezeure, Baniel, *et al.* 2021). Females' fertility (Higham *et al.* 2008) and quality (health condition) (Huchard, Courtiol, *et al.* 2009) are signalled by the size of their sexual swellings (i.e., inflation of the perineal skin around ovulation). Swellings peak in size near the ovulation day and deflate thereafter: ovulation is most likely to occur during the five days preceding swelling deturgescence (Higham *et al.* 2008). As a consequence, females with peak-size swellings tend to be in consortship with high-ranking males (Weingrill *et al.* 2000, Huchard, Courtiol, *et al.* 2009).

Sexual swellings may have evolved as a strategy to promote paternity certainty, and hence increase paternal care (Alberts and Fitzpatrick 2012). In contrast with this hypothesis, however, the individually-recognisable female copulation calls signal proximity to ovulation and the rank of the male partner (Semple 2001, Semple *et al.* 2002), which could promote sperm competition and confuse paternity (O'Connell and Cowlshaw 1994). Male competition serves to obtain high-quality sperm, while creating paternity uncertainty could be one of the strategies employed by females to reduce infanticide risk (O'Connell and Cowlshaw 1994, Cowlshaw and O'Connell 1996). In addition, to avoid infanticide, females typically form 'friendships' with their infants' fathers (Nguyen *et al.* 2009, Huchard *et al.* 2010).

Friendships in baboons are heterosexual relationships outside of a mating context (Palombit *et al.* 1997). These are largely maintained by females, who follow and groom their male friends, even though males also contribute by, e.g., initiating post-conflict reconciliation behaviours (Webb *et al.* 2019). In accordance

with the infanticide avoidance hypothesis, females tend to befriend their infants' fathers (Huchard *et al.* 2010, Moscovice *et al.* 2010), who are likely to defend them in case of aggression (Palombit *et al.* 1997, Bergman *et al.* 2005); friendships are more likely to form when infanticide risk is highest (presence of an alpha immigrant male) (Palombit *et al.* 2001, Beehner *et al.* 2005); they last throughout pregnancy and lactation and end soon after females resume cycling, when either the infant has died or is no longer at risk of infanticide (Palombit *et al.* 2001, Baniel *et al.* 2016). On the males' side, they do not seem to have future mating benefits from their female friends, but they have the opportunity to provide paternal care, and hence enhance their fitness (Nguyen *et al.* 2009) (see also §1.5.4).

1.5.4 Infant care and development

Female baboons typically give birth to a single infant every two years after approx. six months of pregnancy (Gesquiere *et al.* 2018, Dezeure, Baniel, *et al.* 2021). As mentioned, births can occur all year round, but they tend to be seasonally concentrated to maximize infants' survival (Cheney *et al.* 2004, Dezeure, Baniel, *et al.* 2021). Infants are generally considered as individuals $\leq$ 12 months of age, although they can be nursed up to 18 months of age (Huchard *et al.* 2013, Carboni *et al.* 2022). After this point, weaned baboons are classified as juveniles until they reach sexual maturity around five years of age (Altmann and Alberts 2003, Cheney *et al.* 2004) (see Table 1.4 above).

Infants undertake three main developmental phases (see Table 1.4 above), marked by transitions in coat and skin colours (Figure 1.2), which correspond to changes in locomotive abilities and feeding independence (increasing consumption of solid food) (Altmann 1980, Dezeure, Dagorrette, *et al.* 2021).

While newborn 'pink' infants are totally dependent on the mother for nutrition and transport, by four months of age, 'grey' infants explore the environment at increasing distances from their mother and feed on solid food (Altmann and Alberts 2005). In this period, maternal rejection increases as infants start to be weaned. At first, infants feed on food items that do not require processing, such as flowers, berries, leaves, and scraps left by adults. By eight months, 'black' infants are generally able to sustain the day's travel on their own and to provide most of their nutrition through solid food (Altmann 1980, Altmann and Samuels 1992).

Figure 1.2: Infants' **colour transitions** in chacma baboons. Top: a pink infant (left) and a grey infant (right). Bottom: two black infants (left and right) and a juvenile (middle).



Immature baboons experience a wide variety of social interactions from an early age. First, infants receive affiliations from other group members from birth, even though they spend most of the time in contact with their mothers (Silk, Rendall, *et al.* 2003, Frank and Silk 2009). Older infants and juveniles bond with the offspring of their mothers' social partners (Owens 1975, Cheney 1978a) and with unrelated adults (Cheney 1978b, Pereira 1988a). While the time spent with the mother decreases with age, immatures maintain strong bonds with their close maternal and paternal kin (Smith *et al.* 2003, Silk *et al.* 2010b), and with their behavioural father (i.e., their mother's male friend) (Buchan *et al.* 2003, Huchard *et al.* 2013). As mentioned, a behavioural father is generally also the genetic father of the infant (Huchard *et al.* 2010, Moscovice *et al.* 2010), but not necessarily (Moscovice *et al.* 2009, Nguyen *et al.* 2009). Nevertheless, because the costs of paternal care are trivial compared to those of maternal care, fathers still provide care to their probable offspring (Huchard *et al.* 2013, Alberts 2019).

Fathers may play an important role in immatures' development. Other than offering protection from infanticide (see §1.5.3), males show high rates of affiliation with their infants and sometimes carry them (Palombit *et al.* 1997, Cheney and Seyfarth 2007). As juveniles, baboons still associate with their mothers' former male friends (Buchan *et al.* 2003, Huchard *et al.* 2013). Because adult males outrank all adult females, juveniles can receive agonistic support from their fathers irrespective of their maternal rank (Buchan *et al.* 2003, Moscovice *et al.* 2009) and access high quality food patches by foraging with their fathers (Huchard *et al.* 2013, Lynch *et al.* 2020). As a result, the father's presence during juvenile years may accelerate immatures' attainment of sexual maturity (Charpentier *et al.* 2008), thus having long-term fitness benefits (Altmann and Alberts 2005). Finally, the father's presence can strengthen the social bonds

among paternal half-siblings (Lynch *et al.* 2017, Silk *et al.* 2017), who tend to be of similar age (Altmann 1979) and may thus form long-lasting bonds, further enhancing individuals' fitness (Silk *et al.* 2010b, 2010a) (see §1.5.5).

1.5.5 Sociality

Social bonds, mainly mediated by grooming, are a fundamental part of baboon lives that goes beyond close kin relationships (Cheney and Seyfarth 2007). Even though females form strong bonds with close kin (Smith *et al.* 2003, Silk *et al.* 2010a), social bonds are better predictors of collective movements (King, Sueur, *et al.* 2011) and co-feeding preferences (King, Clark, *et al.* 2011) than genetic relatedness. The important role of social bonds in baboon society is exemplified by their tolerance and fitness benefits, and by individuals' social awareness (Silk *et al.* 2010b, Seyfarth and Cheney 2013).

Social bonds can have both short- and long-term benefits for baboons. In the short term, grooming favours can be traded for tolerance during foraging. For example, individuals who have stronger grooming bonds receive less agonism during foraging (Marshall *et al.* 2015). Dominant social partners are preferentially groomed in the early morning, perhaps to negotiate tolerance ahead of the day's foraging (Sick *et al.* 2014). In the long term, social bonds influence individuals' physiology and, ultimately, fitness. For instance, socially isolated baboons have higher stress levels (Sapolsky *et al.* 1997, Seyfarth *et al.* 2012). The loss of a close relative also increases stress levels in females, who respond by seeking more social relationships (Engh *et al.* 2006). Finally, social connectedness enhances females' reproductive success by increasing the offspring's survival (Silk *et al.* 2009, Cheney *et al.* 2016), and females' own survival and lifespan (Silk

et al. 2010b, Archie *et al.* 2014), which are predictive of lifetime reproductive success (Altmann and Alberts 2003, Cheney *et al.* 2004).

Because of the fundamental role sociality has in their lives, baboons have a high degree of social awareness (Seyfarth and Cheney 2013). For example, baboons keep track of both relatively stable and more transient social relationships between all troop members. First, baboons know their group mates' relative dominance rank and kinship relationships. Subordinate female chacma baboons responded more strongly to the playback vocalisations of a recent attacker's relative compared to those of a control female from a different matriline: a playback mimicking kin support led to a greater avoidance of that matriline (Wittig, Crockford, Seyfarth, *et al.* 2007), while a playback simulating kin-mediated reconciliation made females more tolerant of the attacker's and her relative's proximity (Wittig, Crockford, Wikberg, *et al.* 2007). Second, individuals may monitor their group mates' short-term relationships, such as consortships. In chacma baboons, the playbacks of a male's grunt and a female's copulation call played from different directions (mimicking the female's copulation with a different male) elicited greater attention from other males when these two individuals were in consortship (new information indicating the consortship's end) compared to when the consortship had already ended (redundant information on the consortship's end) (Crockford *et al.* 2007a).

1.5.6 Baboons as model species

Baboons may represent an interesting case to study constraints on horizontal and vertical information transmission because they are highly social (Cheney and Seyfarth 2007, Fischer *et al.* 2019), show a striking social awareness (Seyfarth and Cheney 2013), and readily learn socially (Carter *et al.* 2014, Carter, Torrents

Ticó, *et al.* 2016). Nevertheless, only two cases of culture have been reported in baboons (Strum 1975, Sapolsky and Share 2004). In addition, because long-term studies on baboons provided a solid baseline knowledge of their socio-ecology (Cheney and Seyfarth 2007, Alberts 2019), more specific questions on social information transmission in baboon groups can be addressed. Importantly, baboons are considered model species for understanding the selection pressures on early hominin evolution because they may live in similar ecosystems (Codron *et al.* 2008) and have similar social systems as early hominins' (Swedell and Plummer 2012). Therefore, information on the limitations on social learning and the formation of culture in baboons may provide insights on the evolution of human culture (Fischer and Zinner 2020, King 2022).

1.6 THE CURRENT STUDY

1.6.1 Aims

Social learning and culture have been studied in many primate species, but there are still fundamental gaps in our knowledge (Whiten and van de Waal 2017). In order to understand what constrains the formation of culture in some species compared to others, it may be useful to investigate individuals' opportunities and propensity to learn from others during the immature period, which is characterised by an intense learning activity (Rapaport and Brown 2008, Whiten and van de Waal 2018). While studies on social learning in immature age classes have increased in recent years, there is currently little information on some wild primate species (Whiten and van de Waal 2018). Indeed, the development of immatures' social connections, which may determine their opportunities for social learning (van Boekholt *et al.* 2021), has been mainly

studied in provisioned macaque populations (Amici, Kulik, *et al.* 2019). In addition, the ontogeny of social learning has been mostly described in species that show material culture (e.g., orangutans (Schuppli, Meulman, *et al.* 2016)), but relatively less is known about primates that do not use tools (most monkeys) (Whiten and van de Waal 2018). Finally, while maternal behaviour has been extensively studied in captivity, the role of mothers in shaping their offspring's behaviour in the wild, and, specifically, immatures' tendency to learn from others needs to be clarified (Fairbanks 1996, Maestriperi 2018).

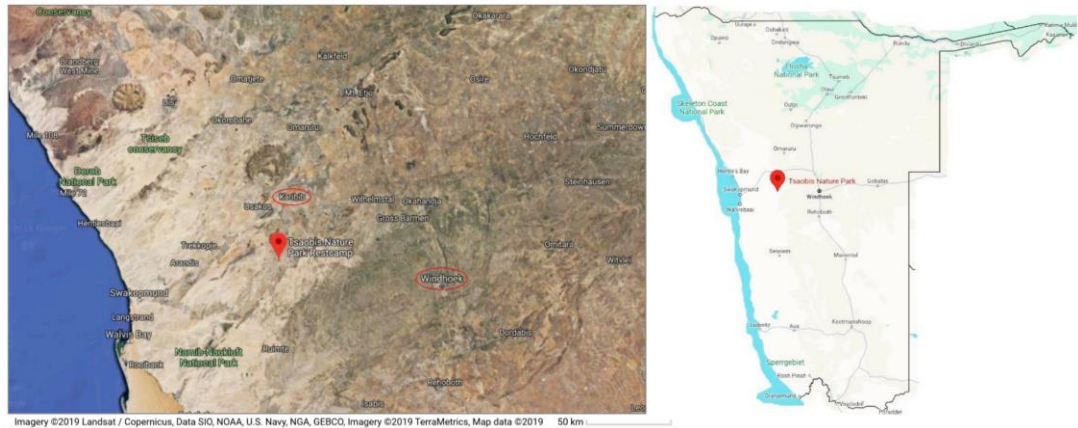
The main objective of this research was to understand the constraints on horizontal and vertical social information transmission in wild chacma baboons, focusing on immature individuals. I first investigated how social networks change with age and differ by sex during the immature period (Chapter 2). At the same time, I assessed the role of maternal characteristics in shaping immatures' social network development (Chapter 3). Then, I studied how social learning changes with age and differs by sex during the immature period (Chapter 4). Finally, I tested whether maternal behaviour affects the immatures' tendency to learn from others (Chapter 5). I discussed my general findings highlighting which factors could constrain the formation of culture in baboons (Chapter 6).

1.6.2 The Tsaobis Baboon Project

This research has been carried out at the Tsaobis Baboon Project (TBP), a long-term, individual-based study of the behaviour, ecology, genetics, and health of a chacma baboon population (TBP 2019). The study has been ongoing annually since 2000. The field site is located at Tsaobis (22°23'S, 15°45'E), an area including Tsaobis Nature Park (45 ha) and the surrounding farmland.

Tsaobis is on the edge of the Namib Desert in central Namibia, approx. 4 h drive from the capital Windhoek and 1.5 h from the nearest town, Karibib (Figure 1.3).

Figure 1.3: Location of **Tsaobis Nature Park** from a full map of Namibia (right) and a closer satellite view of the area (left) where the nearest town, Karibib, and the capital, Windhoek, are circled in red.



Tsaobis is a semi-desertic landscape. The main features comprise the sandy riverbeds of ephemeral rivers and the surrounding rocky hills and plains, ranging between 683–1445 m in altitude (Figure 1.4). The Swakop River, which runs from east to west for 350 km across central Namibia, is the main river crossing the centre of the baboons' ranges. In the riverbeds, tall trees and large shrubs dominate in large patches of woodland. The predominant tree species are *Faidherbia albida*, *Prosopis glandulosa*, and *Salvadora persica*. In the hills and plains, instead, the vegetation is scarce and scattered, comprising herbs, small shrubs, and dwarf trees (Figure 1.5). The most common shrubs found in the hills/plains are *Monechma cleomoides* and *Sesamum capense*, while *Commiphora virgata* is a typical dwarf tree (Cowlshaw and Davies 1997).

Figure 1.4: A view of the landscape at Tsaobis showing the dry Swakop River by the campsite, bordered on both sides by dense woodland, and the open desert of the surrounding hills and plains.



Figure 1.5: Baboons foraging under the trees of the riverbed woodland (top) and in the semi-desertic hills (bottom).



The weather at Tsaobis is seasonal, characterised by a long dry season during the austral winter (April to September) and a shorter period of rains that occur sporadically during the austral summer (October to March). Rainfall is relatively low (on average 85 mm/year, N = 5 years), concentrated between January and March. As is typical of deserts, the temperature varies markedly between day and night and throughout the year. For example, a maximum of 40°C may be recorded in the shade in summer and a minimum of 0°C in winter (Cowlshaw and Davies 1997).

During the course of this research, the TBP has studied up to three baboon troops. Between 2014–2016, two troops ('J' and 'L') were followed (Carter, Torrents Ticó, *et al.* 2016). A part of J troop then fissioned forming 'M' troop, which was studied between 2017–2019. In 2021, troops J and M fused together again, so that two troops, 'J-M' and L (as originally), were followed in 2021–2022. The study troops are habituated to the presence of observers on foot, allowing the collection of detailed behavioural data. The majority of the individuals are recognizable from a unique combination of ear marks (Figure 1.6). The troops have partially overlapped ranges, with J-M troop spending more time in the south-west side of Tsaobis and L troop more on the north-east side (Figure 1.7). Because of the scarce vegetation cover at Tsaobis (see above), visibility is often excellent to perform both individual and group observations.

Baboons at Tsaobis move and rest together as a cohesive group (King and Cowlshaw 2009a, 2009b), but they can spread over up to 1 km² while foraging (Carter, Torrents Ticó, *et al.* 2016). While woodland food patches can contain multiple foraging individuals, in the open desert patches can rarely host more than one individual (Cowlshaw 1999). Baboons' diet consists mainly of berries, flowers, pods, and immature leaves from five plant species: *F. albida*, *P.*

glandulosa, *S. persica*, *Acacia erioloba*, and *Tapinanthus oleifolius* (Cowlshaw 1997a). During the night, the troops sleep on cliffs as an anti-predatory behaviour (Cowlshaw 1997b, 1997a). The risk of predation for this population is, however, low, since the leopard, their primary predator at Tsaobis, is relatively rare (Cowlshaw 1994).

Figure 1.6: Two juvenile Tsaobis baboons identifiable through a unique combination of ear marks.



2 CHAPTER 2: SOCIAL NETWORK INHERITANCE AND DIFFERENTIATION IN WILD BABOONS

2.1 ABSTRACT

Immatures' social development may be fundamental to understand important biological processes, such as social information transmission through groups, that can vary with age and sex. Our aim was to determine how social networks change with age and differ between sexes in wild immature baboons, group-living primates that readily learn socially. Our results show that immature baboons inherited their mothers' networks and differentiated from them as they aged, increasing their association with partners of similar age and the same sex. Males were less bonded to their matriline and became more peripheral with age compared to females. Our results may pave the way to further studies testing a new hypothetical framework: in female-philopatric societies, social information transmission may be constrained at the matrilineal level by age- and sex-driven social clustering.

2.2 INTRODUCTION

For group-living species, social connections can affect fitness by influencing health and survival (Snyder-Mackler *et al.* 2020). For example, strong social bonds enhance longevity, and both adult and offspring survival in wild baboons (*Papio* spp.) (Silk, Alberts, *et al.* 2003, Silk *et al.* 2009, 2010b, Archie *et al.* 2014, Cheney *et al.* 2016), killer whales (*Orcinus orca*) (Ellis *et al.* 2017), and spotted hyenas (*Crocuta crocuta*) (Ilany *et al.* 2021). Yet, despite the importance of an

individuals' social connectedness in many social species (but see eastern grey kangaroos *Macropus giganteus* (Menz *et al.* 2020)), the mechanism driving this relationship is unclear. An individual's position in the social network could affect a range of biological processes influencing fitness, such as the acquisition of information from knowledgeable group members (i.e., social learning) (Brakes *et al.* 2019, 2021). Social connections may be particularly important for immature age classes, who could benefit from social information more than adults due to their inexperience with the environment (Laland 2004, Whiten and van de Waal 2018).

Social learning can be adaptive because it allows access to vital information without expending the time and energy needed for individual learning (Giraldeau *et al.* 2002, Laland 2004) and can lead to variations in fitness (McComb *et al.* 2001, Marcoux *et al.* 2007). For instance, older African elephant (*Loxodonta africana*) matriarchs have relatively greater conspecific call discrimination abilities, which can affect the behavioural responses of their family group and, consequently, enhance their reproductive success (McComb *et al.* 2001). Social learning is closely tied to social connections: the number and characteristics of individuals' connections set an upper limit on social learning *opportunities* (Whiten and van de Waal 2018, Alberts 2019, Kulahci and Quinn 2019, van Boekholt *et al.* 2021), and often predict information transmission. For example, socially central chacma baboons (*P. ursinus*) have better access to social information (e.g., about the location of food) because they have a larger number of social partners to provide that information compared to peripheral ones (Carter, Torrents Ticó, *et al.* 2016). Recent studies have quantified social connections using social network analysis, which can account simultaneously for all the

interactions occurring in a group, determining both an individual's direct and indirect connections in the network (Pinter-Wollman *et al.* 2014).

Social connections can be characterized through proximity (i.e., individuals are associating if they share similar spatial positions) or interactions (i.e., individuals are associating if they are observed interacting) (Croft *et al.* 2008, 2011). Proximity may be important because individuals could acquire information more easily from others that are in visual contact. For example, spatial associations predict the discovery of foraging tasks by threespine sticklebacks (*Gasterosteus aculeatus*) (Atton *et al.* 2012) and experimental food patches in sympatric tits (Family *Paridae*) (Aplin *et al.* 2012). Alternatively, or concurrently, individuals may be more attentive to those with whom they share strong bonds. For instance, ring-tailed lemurs (*Lemur catta*) (Kulahci *et al.* 2018a) and ravens (*Corvus corax*) (Kulahci *et al.* 2016) who are more central in an affiliation network are more likely to acquire information about the solution of a foraging task. Although our knowledge of social networks has increased dramatically in recent years (Webber and Vander Wal 2019), few studies have focused specifically on immature age classes, and little is known about how their social networks, and social learning opportunities, develop with age (Whiten and van de Waal 2018).

Understanding how social networks change during immatures' development may give important insights into which factors constrain or enhance group-level social learning. Immatures may both be more socially active than adults and rely more on social learning than individual learning compared to adults (Laland 2004, Whiten and van de Waal 2018). A greater tendency to seek social opportunities was reported in juvenile Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Krzyszczuk *et al.* 2017), mantled howler monkeys (*Alouatta palliata*) (Rodrigues 2007), and rhesus macaques (*Macaca mulatta*) (Liao *et al.* 2018). Because

immatures may have social networks differentiated from those of adults (Colombian spider monkeys *Ateles fusciceps rufiventris* (Boeving *et al.* 2020)), they can play an important role in the group's network, to the point that their analytical exclusion changes the group's structure, as reported for olive baboons (*P. anubis*) (Fedurek and Lehmann 2017). In addition, juvenile individuals from various taxa show greater evidence of social learning than adults (Australian skinks *Eulamprus quoyii* (Noble *et al.* 2014), chacma baboons (Carter *et al.* 2014), meerkats *Suricata suricatta* (Thornton and Malapert 2009)). Despite the importance of immature animals' social connections for a group's ability to disseminate information (Mesoudi *et al.* 2016), few studies have characterized changes in immatures' social bonds through time, in the wild, and in both sexes.

In this study, we draw on previous knowledge of non-human primate (hereafter primate) social development to analyse immatures' social networks in a wild population of a female-philopatric primate species, the chacma baboon. Primates offer wider opportunities to explore immatures' social connections compared to other taxa because they experience a relatively long period of juvenescence (Jones 2011). Because taxa that have a later age at first reproduction have been linked with higher social learning abilities (Whiten and van de Waal 2017, Penndorf and Aplin 2020), studying primate immatures' social networks may set the bases for future studies on how these connections enhance or constrain social information transmission. Baboons are ideal models for this study because they live in large social groups (Cheney and Seyfarth 2007), readily learn socially (Carter, Torrents Ticó, *et al.* 2016), and information transmission is predicted by both the proximity and grooming social networks (Carter, Torrents Ticó, *et al.* 2016). Chacma baboons live in multimale-multifemale societies (Cheney and Seyfarth 2007). Females are philopatric and

form matrilineal (i.e., social units including a mother and her offspring) within a linear and stable hierarchy, with offspring inheriting their mother's rank (Cheney 1977, Pereira 1989). Males disperse at maturity (around eight years old) (Alberts and Altmann 1995a, 1995b). Baboons learn socially about the location of new food patches (Carter, Torrents Ticó, *et al.* 2016), and may acquire information on what to eat by observing others while foraging and/or by inspecting the same food items others are feeding upon (Alberts 2019).

Juveniles' networks may be shaped by the process of social inheritance and two individual traits: age and sex. Social inheritance suggests that offspring inherit their mother's social connections in a similar manner to how they inherit her dominance rank (vervet monkeys *Chlorocebus pygerythrus* (Jarrett *et al.* 2018), rhesus macaques (de Waal 1996), olive baboons (Owens 1975)). For example, young infant rhesus macaques who do not move independently from their mother share her network (Berman 1982a), which can last up to seven months of age. When older, infants' social networks may remain linked to that of their mother even after they start to move independently. Such social preferences may be passed passively through social learning (i.e., observation of maternal social preferences) and/or familiarity (i.e., exposure to maternal social partners) (de Waal 1996), or through active maternal intervention (i.e., encouraging relationships with certain individuals) (de Waal 1990). A modelling approach confirmed that a purely genetic explanation is not necessary (Ilany and Akçay 2016).

Social bonds could also be affected by age. Immatures tend to spend less time with their mothers and socialize with same-sex age peers as they grow older, thus expanding and differentiating their social network from the maternal one (Altmann 1980, Berman 1982a). This social exploration phase may lead to an

increase in the number of partners immatures associate with (Liao *et al.* 2018, de Lima and Ferreira 2021), which may also derive from the greater tolerance that primates show towards immatures compared to adults (Pereira 1988a, de Resende *et al.* 2004). Association with age peers (vervet monkeys (Govindarajulu *et al.* 1993), rhesus macaques (Berman 1982b), chacma baboons (Cheney 1978a)), same sex individuals (rhesus macaques (Suomi 2005), yellow baboons *P. cynocephalus* (Pereira 1988a)) or individuals who are matched by both age and sex (diademed sifakas *Propithecus diadema* (Lutz *et al.* 2019), Stuhlmann's blue monkeys *Cercopithecus mitis stuhlmanni* (Cords *et al.* 2010), olive baboons (Owens 1975)) seems to be common to social primates when immature, although some exceptions occur (e.g., a decrease in association with peers (Handen and Rodman 1980), or association with the opposite sex (Lutz *et al.* 2019)).

Finally, the development of social connections could depend on sex. In general, immature females spend more time with the mother and maternal relatives during development than males (Lonsdorf 2017, Amici, Kulik, *et al.* 2019) (but see Toda *et al.* 2021), both in female-philopatric species (geladas *Theropithecus gelada* (Barale *et al.* 2015), stump-tail macaques *M. arctoides* (Lee *et al.* 2010), yellow baboons (Pereira 1988a), vervet monkeys (Fairbanks and McGuire 1985)) and male-philopatric species (eastern chimpanzees *Pan troglodytes schweinfurthii* (Lonsdorf, Markham, *et al.* 2014), Geoffroy's spider monkeys *A. geoffroyi* (Rodrigues 2014)). Daughters' social connections may also resemble maternal ones more than sons' (rhesus macaques (Suomi 2005)). A species' social system could drive sex differences in integration in the social network, both in terms of the number and strength of social bonds and the diversity of social partners (Lonsdorf 2017, Amici, Kulik, *et al.* 2019). In female-

philopatric species, juvenile females typically dedicate more time to grooming and associate with more social partners than males (vervet monkeys (Jarrett *et al.* 2018), rhesus macaques (Kulik *et al.* 2015), Stuhlmann's blue monkeys (Cords *et al.* 2010), baboons (Young *et al.* 1982); but see Bernstein *et al.* 1993, Barale *et al.* 2015). Despite a general tendency to associate with same-sex peers with age, this becomes more marked in males than females. In fact, females tend to associate with a wider variety of partners, thus remaining more central in the group's network, while males tend to become more peripheral prior to dispersal by preferring male peers (Stuhlmann's blue monkeys (Cords *et al.* 2010), Japanese macaques *M. fuscata* (Nakamichi 1996), chacma baboons (Cheney 1978b)). Opposite tendencies were reported in male-philopatric species, in which grooming is equally common in males as in females and males have a wider social network than females (eastern chimpanzees (Lonsdorf, Anderson, *et al.* 2014), Geoffroy's spider monkeys (Rodrigues 2014)).

Although most studies agree on how social networks change with age and sex, they largely focus on cross-sectional comparisons (Nakamichi 1996, Cords *et al.* 2010), rather than following the same cohort of individuals longitudinally (but see Kulik *et al.* 2015, Jarrett *et al.* 2018). Compared to cross-sectional comparisons, longitudinal studies have the potential to identify developmental trends. In addition, many studies concern food-provisioned populations (e.g., at Cayo Santiago (Kulik *et al.* 2015)), with a few exceptions targeting wild populations (Cords *et al.* 2010, Jarrett *et al.* 2018). Wild populations may better represent the constraints faced by immatures in establishing social bonds. This is because primates trade grooming for tolerance during foraging, meaning that social bonds can be affected by competition for food (Fruteau *et al.* 2009, Marshall *et al.* 2015), which may be different in food-provisioned populations

compared to wild populations (Hill 1999). Finally, the transmission of maternal networks in female-philopatric species has been explored mainly in daughters (de Waal 1996, Jarrett *et al.* 2018) because of the stronger bond shared with the mother compared to sons (Kulik *et al.* 2016). However, males' integration in the maternal network is important to better understand possible constraints on information transmission across the group. For example, given that males tend to learn individually, while females rely more on social learning (Reader and Laland 2001, Watson *et al.* 2018), social information flow may be constrained if individuals who tend to produce information (males) have poor connections with the ones who tend to acquire it (females) (Carter *et al.* 2015). For male primates, who are generally larger than females, it may be relatively more advantageous to explore, e.g., a new, potentially higher pay-off, food patch or item because they can supplant a smaller individual, acquiring its resource, if unsuccessful (Reader and Laland 2001). Instead, females, who bear relatively higher parental investment costs (Barrett *et al.* 2006), may be less willing to forego known foraging opportunities for an uncertain reward (Carter, Torrents Ticó, *et al.* 2016).

With this study, we aimed to contribute to the understanding of how animal social networks, and thus opportunities for social learning, change with age throughout the immature period, and how they differ between the sexes. We tested two main hypotheses about the development of social connections in wild immature baboons, using social network analysis in the context of a longitudinal study. Our first hypothesis (**H1**) was that immatures would 'inherit' their mothers' social networks at birth (Ilany and Akçay 2016) and that these would differentiate during development (Berman 1982b). We had three predictions for H1. As reported in other female-philopatric primate species (Amici, Kulik, *et al.* 2019), we predicted that (**P1a**) the time spent with the mother would decrease with age and

this decrease would be greater for males than for females. We also predicted that (**P1b**), whilst mother-offspring social networks would be positively correlated (Ilany *et al.* 2021), the strength of the correlation would decrease with age as immatures become more independent from the mother (Berman 1982a). The decrease would be greater for males than for females (Lee *et al.* 2010). Finally, because the mother and maternal relatives have a special importance in matrilineal species (Silk, Alberts, *et al.* 2006, Silk, Altmann, *et al.* 2006), we predicted that (**P1c**) immatures' networks would be more correlated to the mothers' networks than to those of other individuals (Barale *et al.* 2015). This pattern would decrease with age and the decrease would be greater for males than for females (Kulik *et al.* 2015).

Our second hypothesis (**H2**) was that an individual's social network characteristics would change during development both in terms of immatures' integration in the troop's network and the type of social partners with whom immatures associate (Amici, Kulik, *et al.* 2019). We had three predictions for H2. First, we predicted that (**P2a**) the association with different social partners would increase with age as immatures widen their social network beyond the maternal network (de Lima and Ferreira 2021). As observed in other female-philopatric primate species (Amici, Kulik, *et al.* 2019), this increase would be relatively lower in males, who would also have fewer social partners than females (Jarrett *et al.* 2018). If immatures inherit their mothers' networks (P1b and P1c), we predicted that (**P2b**) their positions in the social network would remain stable throughout development for females, while males would become more peripheral with age (Nakamichi 1996). Finally, we predicted that (**P2c**) the characteristics of immatures' social partners would shift from a majority of adult partners (deriving from the maternal network) towards including more same-sex age peers or other

immature individuals. This tendency would be greater for males than for females (Cords *et al.* 2010).

2.3 METHODS

2.3.1 Study site and species

The study was carried out at the Tsaobis Baboon Project (TBP 2019), a long-term (since 2000), individual-based study located on the edge of the Namib Desert, in Namibia (22°22'S, 15°44'E). The study area includes the large ephemeral Swakop River and its tributaries, with dense patches of riparian woodland surrounded by rocky hills, where vegetation is scarce and limited to dwarf trees and small shrubs (see Cowlshaw and Davies 1997 for a full description of the area).

Adult female chacma baboons give birth to an infant approx. every two years (Dezeure, Baniel, *et al.* 2021) and infants are weaned around 12–18 months of age at Tsaobis (Huchard *et al.* 2013, Carboni *et al.* 2022). For the purposes of this study, individuals ≤ 5 years old were considered immatures. We chose this threshold because, in most classifications, males are considered juveniles until five years old, entering sub-adulthood (before reaching full adult size) around six years old; females are considered juveniles until five years old and conceive their first infant around six years old (Altmann *et al.* 1981, Alberts and Altmann 1995a, Altmann and Alberts 2003, Cheney *et al.* 2004). Immature individuals ≤ 12 months old are referred to as infants, while those ≥ 12 months old are considered juveniles (Altmann 1980).

2.3.2 Data collection

Observations were conducted on three troops (J, L, and M) during six annual field seasons between 2014 and 2019. Data collection occurred over 2–3-month periods in each field season (approx. two months in 2014, 2016, and 2017; five months in 2015; three months in 2018 and 2019). Troops J and L were followed during all years, while M, which fissioned from J troop between 2016 and 2017, was followed only in 2017 and 2019. During the study periods, baboons were usually followed daily from dawn to dusk, and data were recorded on all recognisable individuals (see below) with the application CyberTracker (Liebenberg 2022).

The study population is habituated to the presence of observers on foot and the majority of the individuals was individually recognisable, apart from the unmarked juveniles and infants (the proportions of recognizable individuals were: 0.8 in 2014 and 2017, 0.7 in 2015, 1.0 in 2016 and 2019, and 0.9 in 2018). We quantified individuals' associations based on a proximity and an interaction (i.e., grooming) rule. Networks built with different rules may provide different information (Lehmann and Ross 2011, Castles *et al.* 2014) and thus allow a more comprehensive description of baboons' social network development. In addition, both spatial and grooming networks predicted social information use in this population (Carter, Torrents Ticó, *et al.* 2016).

Proximity associations were characterized through instantaneous (scan) sampling (Altmann 1974). Because baboon troops at Tsaobis can spread over large distances with frequent mixing of individuals, it is difficult to perform surveys of the troop (the whole social group) at one point in time, as is done for some other species (Best *et al.* 2013, Carter, Seddon, *et al.* 2013). To guarantee sampling independence, we instead recorded the neighbours of 'focal'

individuals, who were chosen from a randomized list including all the baboons present in the troop. All individuals within 10 m of a focal individual were recorded as a proximity 'subgroup'. Individuals who did not have a neighbour within 10 m were recorded as alone. When a focal individual was sampled, s/he was not re-sampled within an hour if appearing again in a (new) list. Similarly, when an individual was recorded as a neighbour of a focal individual, s/he was not re-sampled as a focal individual within an hour. If group membership did not change substantially within an hour (during long resting periods, for example), observations ceased until group movement (and thus new subgroups) started again. Since very young infants are carried exclusively by their mothers, they were included in the scans only from when they were observed without the mother, indicating that they could move independently from her (Carter, Torrents Ticó, *et al.* 2016). The number of individuals sampled in proximity scans varied across the study years, ranging from 44–59 for J troop, from 41–74 for L troop, and remaining stable at 21 for M troop. In each month, each individual was sampled 4–13 times (averaged per year) in J troop (300–701 total observations per month – averaged per year), 8–18 times in L troop (423–1,037 total per month), and 13–20 times in M troop (273–427 total per month).

Grooming interactions were recorded *ad libitum* (Altmann 1974) while moving through the troops. In this way, the *ad libitum*-collected data were not biased towards the individuals who were easier to find and, as such, we did not account for individual baboon observability. We collected data on the identities of the baboons grooming and the directionality of grooming events (giver to recipient). To avoid pseudo-replication, a grooming dyad was not recorded more than once within the same half hour (Carter, Torrents Ticó, *et al.* 2016). The number of grooming individuals varied across the study years, ranging from 36–

62 for J troop, from 42–81 for L troop, and from 21–24 for M troop. In each month, each individual groomed 5–34 times (averaged per year) in J troop (129–706 total grooming events per month – averaged per year), 12–52 times in L troop (444–1,372 total per month), and 21–31 times in M troop (272–378 total per month).

Immatures' ages (in months) were determined by known and estimated dates of birth. Known dates were from births that occurred during fieldwork. If the birth occurred outside of the field season, the date of birth was estimated based on (1) possible conception dates from consortship records (i.e., mate-guarding events at the peak of a female's fertility) (Alberts and Fitzpatrick 2012) after which the female did not menstruate, and assuming a pregnancy duration of six months (Altmann *et al.* 1978); or (2), if the mother's conceptive cycle was not observed, through observation of the infant's colouration (Dezeure, Dagorrette, *et al.* 2021). The identity of an infant's mother was determined through direct behavioural observations (nursing). The mothers' numbers of offspring in the troop during each season was calculated based on long-term troop composition data.

Dominance ranks were determined for adult females through dominance interactions recorded *ad libitum*. These included displacements, supplants, threats, chases, and attacks for which a giver and recipient were identified. Only one interaction was recorded even if this involved several dominance behaviours in sequence. Female ordinal ranks were computed at the end of each season through the 'I & SI' method (de Vries 1998) using Matman 1.1.4 (Noldus Information Technology 2003). The method is appropriate for linear dominance hierarchies (de Vries 1998, Silk *et al.* 1999) and it has been applied to other studies on this population (Huchard and Cowlshaw 2011). The dominance hierarchies obtained for each season were strongly linear. We standardised absolute ranks by controlling for group size using the formula $1 - [(1 - r) / (1 - n)]$,

where r is an individual's absolute rank and n is the group size. Relative ranks range from 0 (lowest) to 1 (highest) (Huchard and Cowlshaw 2011).

2.3.3 Data analysis

Data analyses were performed with R 4.0.2 (R Core Team 2023). Following previous studies with sparse network data (Hobson *et al.* 2013, Blaszczyk 2018, Turner *et al.* 2018, Kawazoe and Sosa 2019), we used multiple static networks (i.e., describing a network sampled over a particular length of time) aggregated in approx. 30-day time periods. The periods chosen for time-aggregated networks should be appropriate for the kind of questions investigated and the available data resolution (Pinter-Wollman *et al.* 2014, Farine and Whitehead 2015). We chose these periods of time because immatures undertake rapid developmental changes during their first year of life (Altmann 1980): this 30-day resolution allowed us to capture social network transformations during infancy as well as juvenile years.

Proximity and grooming data were treated separately. The sampling periods were generated starting from the first day in which data were collected for a given field season; these dates were different for proximity and grooming data, thus generating different windows and numbers of periods overall. In J troop, this resulted in 12 and 16 30-day periods for proximity and grooming data, respectively (1–4 periods per year depending on field seasons' lengths); in L troop, there were 11 and 17 30-day periods for proximity and grooming data, respectively (1–5 periods per year); in M troop, we produced two and three 30-day periods for proximity and grooming data, respectively (1–2 per year). To have a sufficient number of observations per individual to build robust and accurate networks, we removed any period with < 95 observations. We also removed any

individual who was seen < 5 times per season (e.g., disappeared mid-season due to death or emigration). The removal of individuals for whom few data are collected is recommended because their network may not be represented accurately (Farine and Whitehead 2015).

Social networks were produced for each sampling period, within each troop. We built weighted networks in which network values indicate both the presence and strength of a connection between two individuals (Croft *et al.* 2011), and, in the case of grooming, weighted and directed networks. We did not filter associations based on edge weight because thresholding (i.e., removing the associations that have a weight lower than the threshold) eliminates weak ties, which can nevertheless be important (Brent, Heilbronner, *et al.* 2013, Sosa 2016), and may generate errors in understanding the determinants of network structure (Farine and Whitehead 2015). We used a simple ratio index (SRI) to calculate weighted connections in the proximity network. SRI is the proportion of time two individuals associated (ranging between '0' – never associated – and '1' – always associated). This index is recommended only when individuals can be detected and identified correctly (Hoppitt and Farine 2018) as is the case at Tsaobis where group membership is stable, and visibility is usually excellent due to low vegetation cover. For the grooming network, we used grooming counts or proportions depending on the model tested (see below). Network graphs were computed from association networks and matrices of grooming counts using *igraph*'s *graph_adjacency* function. The grooming network was divided into its *out* (given) and *in* (received) components, which were treated both separately and united (total). Although proximity and grooming networks were analysed separately, similar models were applied in both cases, with the response variable differing depending on the network. All analyses were run on ego-networks: the

variables tested were calculated for each immature individual in each sampling period (Hobson *et al.* 2013, Turner *et al.* 2018).

To test our predictions, we used both Linear Mixed Effects Models (LMMs) and Generalised Linear Mixed Effects Models (GLMMs) using the function *(g)lmer* from the package *lme4* (Bates *et al.* 2015). The package *lmerTest* (Kuznetsova *et al.* 2017) was required to obtain *p*-values from models' summaries. The models are summarized in Table 2.1. All models included the following fixed and random factors. The predictor variables (fixed factors) of interest were age, sex, and the interaction between age and sex. We then controlled as a fixed factor the mothers' relative dominance rank because rank is known to affect social bonds in primates (Cheney 1977, Borgeaud and Bshary 2015, Wooddell *et al.* 2020). We also controlled as a fixed factor the mothers' number of offspring in the troop because the mothers' grooming time might have to be shared among her offspring (Berman 1992). In addition, the number of maternal siblings may influence, e.g., immatures' grooming allocations in case they prefer maternal kin to other individuals (Charpentier *et al.* 2012, Kulik *et al.* 2015). In order to control for repeated measures from the same troops, we added troop as a fixed factor (because only three troops were followed in this study, it could not be included as a random factor (Harrison *et al.* 2018)). Because our data have repeated measures from the same individuals through time, in each model we included as a random factor the individuals' identity (immature and mother) (Błaszczuk 2018, Turner *et al.* 2018, Kawazoe and Sosa 2019). We nested immatures' identities within their mothers' identities because maternal behaviour could affect the offspring's sociality (Maestripieri 2018). Finally, we added year as a random factor to consider between-years variation in environmental factors. We did not control for season in our analyses because

most observations were made in the austral winter and baboons have no distinct breeding and mating seasons (Cheney *et al.* 2004, Dezeure, Baniel, *et al.* 2021) like, e.g., macaques (Brent, Heilbronner, *et al.* 2013).

The models (described in further detail below) were presented as ‘full models’: the models did not undergo any simplification procedure after the *a priori* variable selection based on the current literature (see above and Table 2.1) (Chowdhury and Turin 2020, Tredennick *et al.* 2021). We obtained R^2 values (coefficient of determination) from the package *MuMIn* (Bartoń 2022) and the function *r.squaredGLMM*. Before running the models, we checked for independent variables’ linear correlations by computing their Pearson’s correlation coefficients (r) and did not find any collinearity issue ($r < 0.7$) (Dormann *et al.* 2013). In addition, we checked for multicollinearity after running the models using variance inflation factors (VIFs) with the package *car* (Fox *et al.* 2023) and the function *vif*. For LMMs, we checked residuals’ homoscedasticity. For GLMMs, we verified overdispersion with the package *DHARMa* (Hartig 2022) and the function *testDispersion*. In all cases, VIF values were ≤ 3 , indicating low collinearity (Stanton and Mann 2012, Lehmann *et al.* 2016); LMM models’ residuals were normally distributed and GLMMs’ under/ overdispersion, when significant, was within the range of 0.7–2, indicating a normal degree of variation for a binomial distribution (Thomas *et al.* 2015). We also checked the overall model fit plotting *DHARMa*’s simulated residuals through the function *simulateResiduals*. When we obtained singular fits, we first identified the problematic random factors with *lme4*’s *rePCA* and then confirmed the results by re-running the models without those random factors (Burrow and Maerz 2021, Oberpriller *et al.* 2022). For binomial models, we obtained the (1) odds ratios (OR) by exponentiating the variables’ estimates and (2) 97.5% confidence intervals

through *lme4*'s *confint.merMod* (*method* = 'Wald'). We then calculated the percentage change in odds per each unit variation in an independent variable as $(OR - 1) \times 100$ (Szumilas 2010). We expressed differences in odds ratio changes from one age stage (t_0) to the next (t_1) as increase/ decrease percentages, computed through the formula: $[(OR_{t_1} - OR_{t_0}) / OR_{t_0}] \times 100$. For LMMs, estimates were described as increase/ decrease percentages over a dependent variable's range. In the presence of an interaction, the main effects were interpreted as conditional effects (Bauer and Curran 2005, Brambor *et al.* 2006). To compute age changes in effect sizes, we chose two specific periods based on the literature: (1) one year old, when immatures are generally weaned but still spend most of the time with the mother (Altmann 1980); (2) four years old, when immatures should have established their own social relationships, mostly independently from maternal presence (Kulik *et al.* 2015). To obtain differences in effect sizes between sexes, we calculated the effect of sex at 30 months of age (the middle of the immatures' age range). Finally, to compare the effects of different predictors (within a model) we derived standardised (i.e., all the predictors on the same scale) estimates (see Appendix 1, §1.6). In all cases, p -values ≤ 0.05 were considered significant (Farine 2017, Chowdhury and Turin 2020).

Social network data are non-independent because the data are relational. Data permutations serve to solve the issue of data non-independence when performing hypothesis testing with network data (Croft *et al.* 2011, Farine and Whitehead 2015). The permuted data are used to re-run the model to obtain a 'null' effect size against which the observed effect size can be compared. For the proximity data, in most cases we permuted the datastream using the *network_swap* function from the *asnipe* package; however, node-based

permutations (see below) were used for three of the models (as described further on). Datastream permutations randomise subgroup membership by swapping observations between individuals in the $N \times K$ matrices (i.e., N individuals per K observations) (Farine 2013) and are recommended for group membership data (Farine 2017). The original datastream was used to make the first permutation, swapping 20 observations in each 30-day period. For each successive permutation, the previous permuted matrix was re-permuted. In this way, matrices become more and more randomised compared to the original datastream. For this reason, a set of initial permutations were discarded. We made 300 permutations per period, discarded the first 200 permuted matrices, retaining 100 randomised networks/ period to be used in the ‘randomised’ models. These permuted matrices represent the null hypothesis of random associations among individuals (Farine 2017). For the grooming data and three models from proximity data (P2c models, see details below), we applied node-based permutations, which are commonly used for grooming networks (Lehmann *et al.* 2016, Liao *et al.* 2018), with the function *rmperm* from the package *sna* (Butts 2020). Node-based permutations re-distribute the nodes (individuals) while leaving the same number of associations (Farine and Whitehead 2015). As for the proximity data, we made 300 permutations per sampling period and selected the last 100 for each period. To determine the statistical significance of the estimated social network effect, we re-ran each model (see below) using the 100 permuted matrices. For each model and each network variable, the two-tailed p -value was calculated as the number of times that the observed effect size was larger or smaller than the distribution of effect sizes from the permuted data (resulting either as p -value = 0.05 or not significant) (Farine 2017).

Table 2.1: Summary of the models used to test hypotheses' H1 and H2 predictions, including the type of test used, the dependent variables, the models' fixed factors (predictors and controls) and random factors, and the network involved. Under 'Model', '**' means that a permutation test was performed. The last column indicates whether each prediction was supported and, if not or only partially, how.

Hypothesis	Prediction	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Network	Support
H1: Immatures would inherit their mothers' social networks at birth, and these would differentiate throughout development.	P1a: Time spent with the mother will decrease with age and this decrease will be greater for males than for females.	MP1a	GLMM binomial (link 'logit')	Proportion of time with mother	Immatures' age, sex, age:sex interaction.	Mothers' number of offspring and relative rank; troop.	Year, immatures' identities nested within their mothers' identities	Proximity	Yes
								Grooming	Total: Yes
	P1b: Whilst mother-offspring networks will be positively correlated, the strength of the correlation will decrease with age. This decrease will be greater for males than for females.	MP1b*	LMM	Mother-offspring network correlation				Proximity	Yes
								Grooming	Given: Partial (↑ with immatures' age in females) Received: Partial (immatures' age:sex not significant) Total: Yes
	P1c: Immatures' networks will be more correlated to the mothers' networks than to those of other individuals. This pattern will decrease with age and the decrease will be greater for males than for females.	MP1c.1*	GLMM binomial (link 'logit')	0-1 score: '1' = correlation with mother's network > correlation with random individual's network; '0' = vice versa				Proximity	No (immatures' age and age:sex not significant)
		MP1c.2*		0-1 score: '1' = correlation with mother's network				Grooming	Given: No (↑ with immatures' age, age:sex not significant) Received: No (immatures' age and age:sex not significant) Total: No (immatures' age and age:sex not significant)
								Proximity	No (↑ with immatures' age, age:sex not significant)

Hypothesis	Prediction	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Network	Support
				> mean correlation with other individuals; '0' = vice versa				Grooming	Given: No (↑ with immatures' age, age:sex not significant) Received: No (immatures' age and age:sex not significant) Total: No (↑ with immatures' age, age:sex not significant)
H2: Social network characteristics would change throughout development, both in terms of the position in the network and the type of social partners with whom immatures associate.	P2a: The associations with different social partners will increase with age as immatures widen their social network. This increase will be relatively lower in males, who will also have fewer social partners than females.	MP2a*	LMM	Immatures' strength		Mothers' number of offspring, relative rank, and network strength; troop.		Proximity	No (↓ with immatures' age, sex, and age:sex not significant)
								Grooming	Given: Yes Received: Partial (immatures' sex and age:sex not significant) Total: Partial (immatures' sex not significant)
	P2b: Immatures' positions in the social network will remain stable throughout development for females, while males will become more peripheral with age.	MP2b.1*	LMM	Immatures' eigenvector centrality		Mothers' number of offspring, relative rank, and network centrality; troop.		Proximity	No (↓ with immatures' age for females and age:sex not significant)
								Grooming	Total: No (↑ with immatures' age for both sexes and age:sex not significant)
								MP2b.2*	LMM
Grooming	Total: No (↑ with immatures' age for both sexes)								

Hypothesis	Prediction	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Network	Support			
	P2c: The characteristics of immatures' social partners will shift from a majority of adult partners to a majority of same-sex age peers or other immature individuals. This tendency will be greater for males than for females.	MP2c.1*	GLMM binomial (link 'logit')	Proportion of immature (≤ 5 years old) partners		Mothers' number of offspring and relative rank; troop.		Proximity	Partial (immatures' age not significant)			
				MP2c.2*				Proportion of peer (± 6 months) partners	Grooming	Given: Partial (immatures' age:sex not significant) Received: Partial (immatures' age:sex not significant) Total: Partial (immatures' age:sex not significant)		
		Proximity								No (immatures' age and age:sex not significant)		
		MP2c.3*								Proportion of same-sex partners	Grooming	Given: Partial (immatures' age:sex not significant) Received: Partial (immatures' age:sex not significant) Total: Partial (immatures' age:sex not significant)
												Proximity
		Grooming		Given: Partial (immatures' age:sex not significant) Received: Yes Total: Yes								

2.3.4 Testing H1: Inheritance of maternal social networks

From the base model, we tested our hypotheses and predictions using the following specific models (Table 2.1). For H1, we ran a total of four sets (applied to the different networks) of models across our three predictions. First, we quantified changes in the time immatures spend with the mother (P1a), using binomial GLMMs with a 'logit' link (Douma and Weedon 2019) in which the dependent variable was the proportion of time spent with the mother (MP1a). For proximity, we used the proportion of observations in which each immature individual was observed with the mother (within 10 m) in each observation period; for grooming, we used the proportion of observations in which each immature individual groomed with the mother, considering only the total grooming. Permutations were not run for this model because the dependent variable (i.e., proportion of observations with the mother) is not a social network value or metric.

We next tested whether there was a positive correlation between mothers' and immatures' social networks and how this changed through time (P1b). To this end, we calculated two measures of similarity between the mothers' and immatures' ego-networks for each period (i.e., the vectors that correspond to the square matrix rows of each immature focal individual and her/his mother). The two measures were (1) the test statistic from a Pearson's correlation (bounded between -1 and 1) of the mother's and offspring's vectors (Ilany *et al.* 2021); and (2) the cosine similarity between the mother's and immature's vectors (Jarrett *et al.* 2018). Because these two network similarity measures were positively correlated and the results of the models using either one of these response variables were qualitatively similar, we report here only the results for models using the Pearson's correlation (MP1b) (see Appendix 1, §1.1 for results using

the cosine similarity). For this analysis, we used the proportion matrix for grooming because we were interested in similarities between networks, and proportions better represent the distribution of grooming to/from different partners, independent of the total number of events. Immatures' grooming networks may be constrained by partner availability if they tend to be in proximity to the mother and could thus choose only amongst her social partners. Controlling for the time spent in the mother's proximity would potentially solve this issue (Albery *et al.* 2021). However, there was no significant effect of the proportion of time spent in proximity with the mother (see Appendix 1, §1.2). Because including this variable reduced our dataset (since proximity data were not available for every grooming period) it was not included in the final models.

We next tested whether immatures' ego-networks were more similar to their mothers' ego-networks than to those of other group mates and how this changed with age (P1c). Because there is no agreed method to test this, we adopted three different approaches, all of which compared the Pearson's correlation coefficient (r) of the mother-immature dyad with combinations of other dyads from the proximity networks or grooming proportions networks. We present two of these approaches here and discuss the third one in Appendix 1, §1.5. In the first approach, for each immature individual, we selected a random non-mother individual from the troop and created a new variable, assigning a score of '1' when the mother-immature's r was higher than the random-immature's r , and '0' when the reverse was true. We ran a binomial GLMM with the 1/0 score as the dependent variable (MP1c.1). In the second approach, we applied the same 1/0 scoring method and a binomial GLMM, using the mean r for all the non-mother individuals instead of a random individual (MP1c.2).

2.3.5 Testing H2: Changes in social network characteristics throughout development

For H2, we ran a further six sets of models. Predictions P2a and P2b predicted changes in individuals' node-level social network metrics that reflect the level of integration in the troop's network. We chose to calculate individuals' strength (MP2a), eigenvector centrality (MP2b.1), and betweenness centrality (MP2b.2). Strength is the sum of the edge weights connected to a node, representing the relative association rate within a sampling period and thus an individual's opportunities to collect social information. Eigenvector centrality (hereafter centrality) is the sum of the centralities of an individual's social partners. An individual can have high centrality either by having a large number of partners or associating with individuals who have numerous connections (or both) (Farine and Whitehead 2015, Sosa *et al.* 2021). This metric also describes an individual's relative opportunities to acquire and propagate social information in a network (Carter, Torrents Ticó, *et al.* 2016). Betweenness centrality (hereafter betweenness) is the number of shortest paths that cross a node. This measures an individual's importance in connecting otherwise unconnected individuals (Farine and Whitehead 2015). For both proximity SRI and grooming count data, we calculated the metrics using *igraph* (Csardi and Nepusz 2006) (functions *strength*, *eigen_centrality*, *betweenness*). Grooming given, received, and total were computed for strength, while given/ received components cannot be separated for centrality and betweenness. We analysed these five metrics using LMMs. Proximity betweenness and grooming strength given were log-transformed (*log1p* function) to make them normally distributed; grooming centrality and betweenness were square-root transformed (*sqrt* function). In these models, we additionally included the corresponding metric of the mother as

a control. This is because, if immatures inherit their mothers' networks, the mother's social network position may affect that of her offspring (Jarrett *et al.* 2018). To make metrics comparable across networks of different sizes, metrics were standardised within each sampling period by mean-centring them around zero with a standard deviation of one through the function *scale* (Wey *et al.* 2008).

To test P2c, that immatures will shift from associating with adults to similarly aged individuals as they age, we counted the number of immature, peer, and same-sex partners each immature associated with. An individual's number of social partners is their degree (Farine and Whitehead 2015). A peer was defined as an individual whose age was ± 6 months of a focal individual's age. We distinguished between immatures and peers to understand whether immatures were generally attracted to other non-adult individuals (≤ 5 years old) or if they specifically targeted partners of their same age. To test the tendency to associate with different partner categories with age, we ran binomial GLMMs with the proportion of immature (MP2c.1), peer (MP2c.2) and same-sex (MP2c.3) partners as dependent variables. Using the proportion of partners belonging to a certain category over the total number of partners of that category in the troop, we could control for partner availability (Kulik *et al.* 2015). For the P2c models, we ran node-based permutations for the proximity network. These were chosen over datastream permutations because, as mentioned, they keep the number of associations constant (Farine and Whitehead 2015) and were thus appropriate to test whether there was a shift in partner preferences based on their phenotype rather than number.

2.4 RESULTS

We collected a total of 12,592 proximity records (J: 5,862; L: 6,030; M: 700) and 19,597 grooming records (J: 6,277; L: 12,398; M: 922). The number of immature individuals followed (i.e., sample size) were 109 to 116 for the proximity network and 93 to 142 for the grooming network, born from 32 to 43 mothers (see Appendix 1, §1.3 for the number of observations and the sample size of each model) (Roatti *et al.* 2023b, 2023a).

In the following sections, we present the results (following each prediction) on our main variables of interest: age, sex, and their interaction (Tables 2.2 and 2.3; Figures 2.1–2.6). Full tables are reported in Appendix 1, §1.5 (together with the results of the third approach used to test P1c; see §2.3). Comparisons among models' variables through standardised estimates are shown in Appendix 1, §1.6.

2.4.1 Results H1: Inheritance of maternal social networks

To address hypothesis H1, we tested how the time spent with the mother (P1a) and the correlation between the offspring's and mothers' social networks (P1b and P1c) changed through time. Our first prediction for H1, P1a, was confirmed both for the proximity and grooming total networks (Table 2.2 and Figure 2.1): immatures spent significantly less time with their mothers as they grew older, and this decrease was significantly greater in males than in females. Between 1–4 years old, the odds of being in proximity with the mother decreased by 33.27% and 58.89% in females and males, respectively; the odds of grooming (total) with the mother decreased by 56.63% and 76.74% in females and males, respectively. However, males groomed significantly more with their mothers than

females (not predicted): at 30 months old, the odds of grooming (total) with the mother were 62.46% higher in males compared to females.

Our second prediction for H1, P1b, was partially confirmed, depending on the network (Table 2.2 and Figure 2.2). The mean correlation values between the mothers' and offspring's networks were positive for both the proximity and grooming networks (see Appendix 1, §1.4). As predicted for the proximity network, the immatures' networks became significantly less similar to their mothers' with age, and this decrease was significantly greater in males compared to females. Between 1–4 years old, the mother-offspring proximity network correlation decreased by 7.2% and 12.6% in females and males, respectively. For the grooming network, the support to P1b was less clear compared to the proximity network. According to our prediction for grooming received and total (as for the proximity network), the immatures' networks became significantly less similar to their mothers' with age. This pattern was significantly more marked in males than in females only for grooming total. Between 1–4 years old, the mother-offspring grooming network correlation decreased by 12.24% and 2.88% (received and total, respectively) in females, and by 11.52% and 6.84% (received and total, respectively) in males. Instead, contrary to our prediction for females, age had significant opposite effects in the two sexes for grooming given: between 1–4 years old, the mother-offspring network correlation increased by 6.84% in females and decreased by 1.08% in males.

Our third prediction for H1, P1c, had contrasting support depending on the network and the model (Table 2.2 and Figure 2.3). The observations in which the immatures' proximity and grooming networks were more similar to those of their mothers (compared to the networks of other individuals) were higher than the observations in which the opposite was true (less similar to their mothers'

networks) in nine (of 16) models (see Appendix 1, §1.4). Contrary to our prediction for the proximity network, we found evidence that immatures' networks became significantly more similar to their mothers' compared to those of other individuals with age in MP1c.2. This pattern was less marked in males than in females, but the age-sex interaction was not significant. Between 1–4 years old, the odds of having a proximity network relatively more similar to the mother's one increased by 119.79% and 20.07% in females and males, respectively. Age and the age-sex interaction were not significant in MP1c.1. For the grooming network, the models' support on age changes was less clear compared to the proximity network. Among the six models tested for the grooming network, age and the age-sex interaction were significant in three models (not significant in MP1c.1 and MP1c.2 given, and in MP1c.1 total). In contrast to our prediction (as for the proximity network), the immatures' grooming given (MP1c.1 and MP1c.2) and total (MP1c.2) networks became significantly more similar to their mothers' compared to other individuals. This pattern was less marked in males, although the age-sex interaction was not significant. Between 1–4 years old, the odds of having a network relatively more similar to the mother's one increased between (hereafter range of values) 78.44–104.32% (MP1c.2 given and MP1c.2 total, respectively) in females and between 9.89–63.67% (MP1c.1 and MP1c.2 given, respectively) in males. Finally, in MP1c.2, males' grooming given networks matched those of their mothers significantly less than the ones of other individuals compared to females (not predicted): at 30 months of age, the odds of having a network relatively more similar to the mother's one were 65.07% lower in males than in females.

Table 2.2: Results on immatures' age, sex, and their interaction (':') for hypothesis' **H1 models**, for the proximity and grooming (Groom.) networks. The values reported for sex refer to males. The estimate, standard (Std.) error, *p*-value ('NS' = not significant), and conditional (delta) *R*² are reported for each variable/ model. Significant (*p*-value ≤ 0.05) variables are highlighted (grey).

Model	Variable	Estimate	Std. Error	<i>p</i> -value	<i>R</i> ²
P1a Proximity	Age immature	-0.0112	0.0051	< 0.05	0.27
	Sex immature	0.2702	0.2529	NS	
	Age:Sex	-0.0135	0.0067	< 0.05	
P1a Groom. Total	Age immature	-0.0232	0.0035	< 0.001	0.84
	Sex immature	1.0043	0.2027	< 0.001	
	Age:Sex	-0.0173	0.0038	< 0.001	
P1b Proximity	Age immature	-0.0029	0.0013	0.05	0.20
	Sex immature	-0.0007	0.0670	NS	
	Age:Sex	-0.0021	0.0018	0.05	
P1b Groom. Given	Age immature	0.0022	0.0010	0.05	0.25
	Sex immature	-0.0227	0.0607	NS	
	Age:Sex	-0.0027	0.0015	0.05	
P1b Groom. Received	Age immature	-0.0042	0.0013	0.05	0.44
	Sex immature	-0.0222	0.0575	NS	
	Age:Sex	0.0003	0.0016	NS	
P1b Groom. Total	Age immature	-0.0010	0.0010	0.05	0.28
	Sex immature	-0.0147	0.0449	NS	
	Age:Sex	-0.0014	0.0012	0.05	
P1c.1 Proximity	Age immature	0.0053	0.0090	NS	0.03
	Sex immature	-0.3070	0.4550	NS	
	Age:Sex	0.0017	0.0120	NS	
P1c.1 Groom. Given	Age immature	0.0198	0.0091	0.05	0.08
	Sex immature	-0.1326	0.4849	NS	
	Age:Sex	-0.0172	0.0126	NS	
P1c.1 Groom. Received	Age immature	-0.0088	0.0092	NS	0.13
	Sex immature	-0.4860	0.3657	NS	
	Age:Sex	0.0108	0.0115	NS	
P1c.1 Groom. Total	Age immature	0.0096	0.0072	NS	0.17
	Sex immature	-0.3061	0.3116	NS	
	Age:Sex	-0.0022	0.0092	NS	
P1c.2 Proximity	Age immature	0.0219	0.0097	0.05	0.08
	Sex immature	0.3355	0.4720	NS	
	Age:Sex	-0.0168	0.0128	NS	
P1c.2 Groom. Given	Age immature	0.0161	0.0100	0.05	0.19
	Sex immature	-0.9799	0.5681	0.05	
	Age:Sex	-0.0024	0.0143	NS	
P1c.2 Groom. Received	Age immature	-0.0112	0.0114	NS	0.25
	Sex immature	-0.1466	0.4497	NS	
	Age:Sex	0.0021	0.0141	NS	
P1c.2 Groom. Total	Age immature	0.0198	0.0079	0.05	0.24
	Sex immature	-0.0312	0.3522	NS	
	Age:Sex	-0.0134	0.0101	NS	

Figure 2.1: Changes in the immatures' odds of being with the mother (left: model-predicted values, **MP1a**) and proportion of time spent with the mother (right: **raw data**) with age in the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (*y*-axis variable) to occur. Ribbons represent 97.5% confidence intervals.

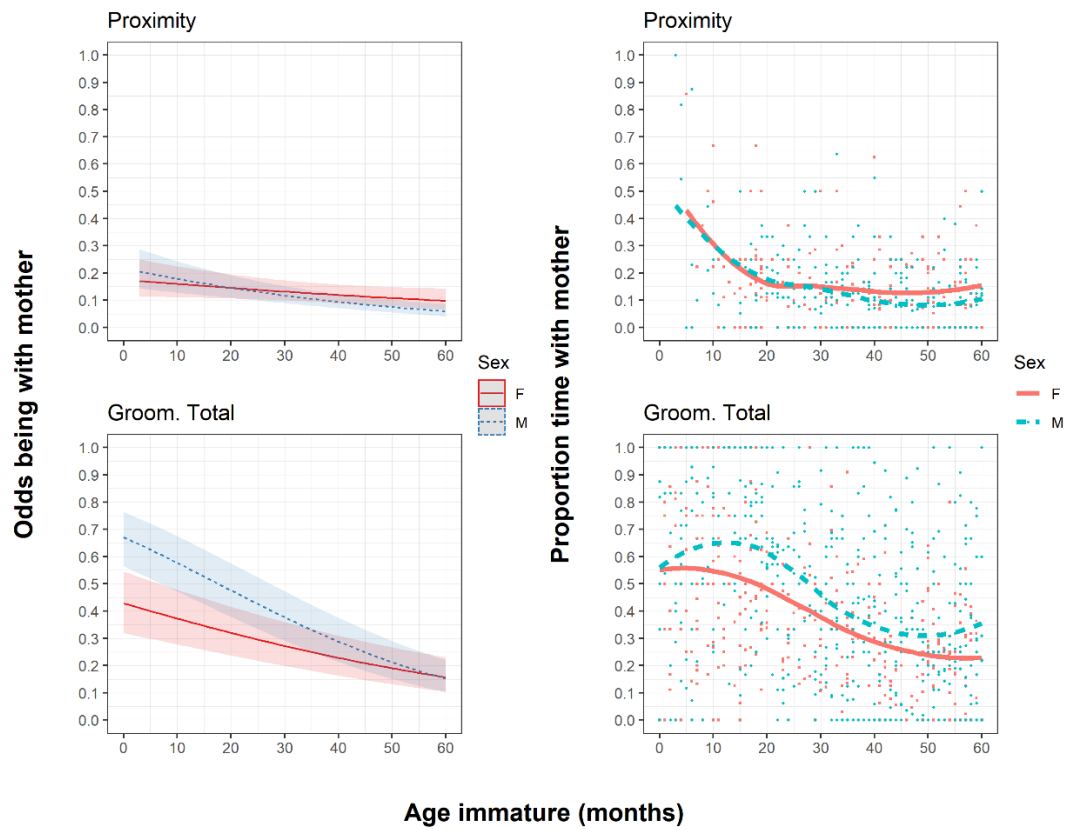


Figure 2.2: Changes in the mother-offspring social network correlation with age in the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks (**MP1b**). Ribbons represent 97.5% confidence intervals.

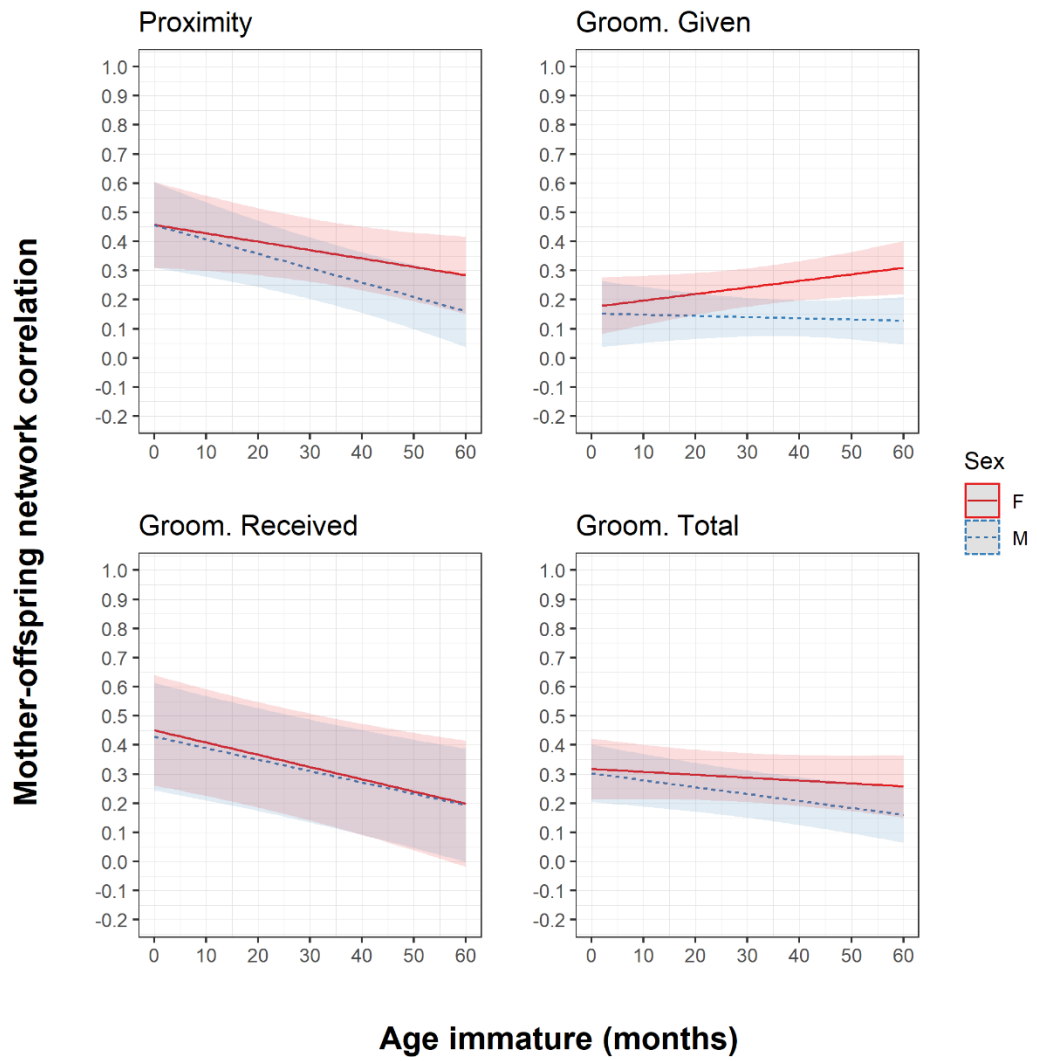
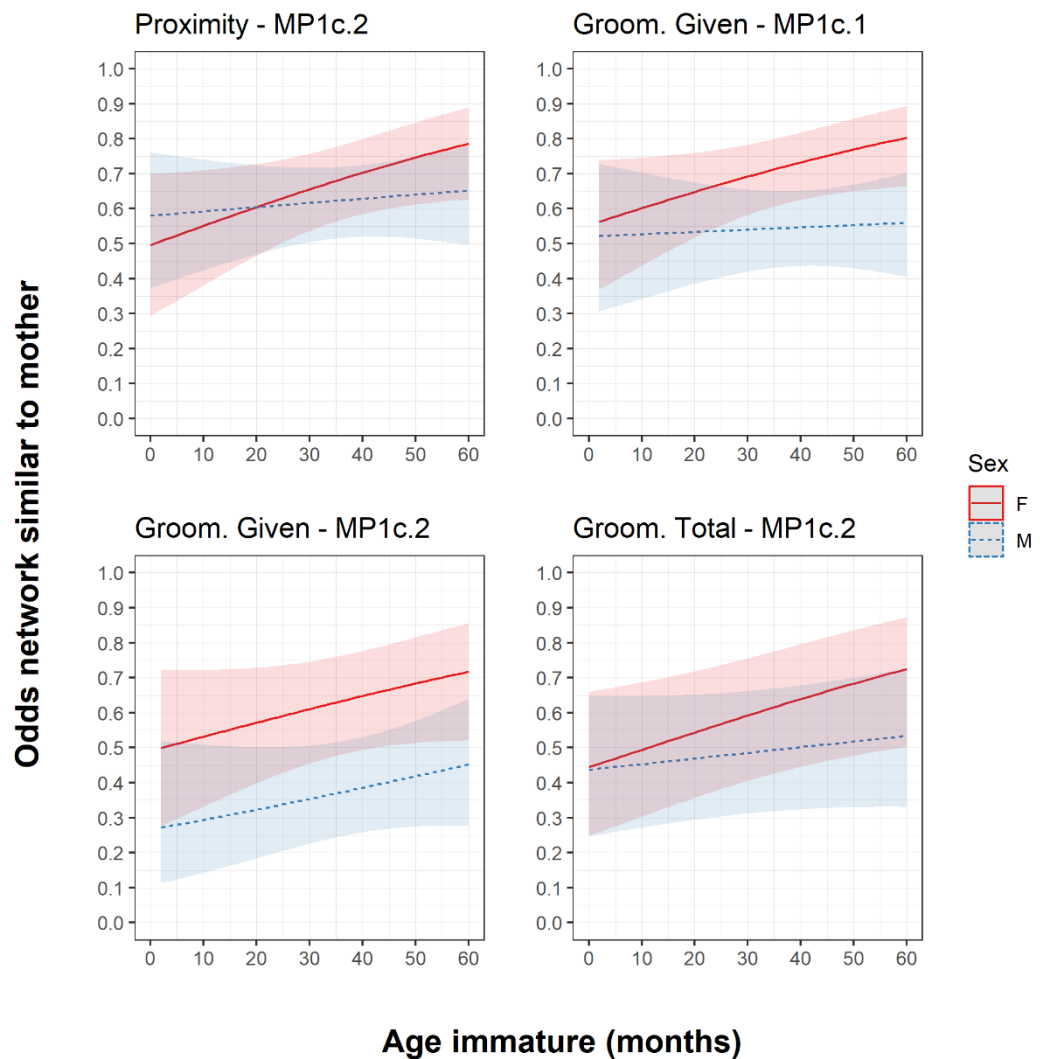


Figure 2.3: Changes in the odds that the correlation with the mother's network was higher than the correlation with a random individual's network (**MP1c.1**) and the mean correlation with other individuals' networks (**MP1c.2**). These changes are related to age and divided between the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.



2.4.2 Results H2: Changes in social network characteristics throughout development

To address hypothesis H2, we explored how immatures' integration in the troop's network changed during development (relative association rates with different social partners – P2a – and overall network position – P2b) and modelled shifts in social partner preferences (P2c). Our first and second predictions for H2, P2a and P2b, were partially confirmed, depending on the network and the metric involved (Table 2.3; Figures 2.4 and 2.5). Contrary to what we predicted for the proximity network, both strength and centrality significantly decreased as immatures grew older and this pattern was more marked in females, although the age-sex interaction was not significant. Between 1–4 years old, proximity strength and centrality decreased by 14.4% and 12.96% (strength and centrality, respectively) in females, and by 9.72% and 10.08% (strength and centrality, respectively) in males. Finally, proximity strength was not significantly predicted by sex, and betweenness was not significantly predicted by age and the age-sex interaction. Instead, for the grooming network, immatures' strength (all components, as predicted), centrality and betweenness (total, contrary to our prediction) significantly increased with age. According to our prediction, the increases in grooming strength (all components), centrality and betweenness (total) were less marked in males. However, the age-sex interaction was not significant for strength received and centrality total. Between 1–4 years old, grooming strength increased by 37.44% and 5.76% (given and received, respectively) in females, and by 20.88% and 3.96% (given and received, respectively) in males. At the same time, grooming centrality and betweenness (total) increased by 5.76% and 30.24% (centrality and betweenness, respectively) in females, and by 1.8% and 19.44% (centrality and betweenness,

respectively) in males. Finally, as predicted, males had a lower grooming given strength than females, while sex was not significant for grooming received and total: at 30 months old, males' strength given was 6.83% lower than females'.

Our third prediction for H2, P2c, was partially confirmed, depending on the network (Table 2.3 and Figure 2.6). As predicted for the proximity network, immatures shifted their social preferences towards immature (MP2c.1) and same-sex (MP2c.3) partners while growing older. This age change was significant only for MP2c.3, while the pattern was significantly more marked in males than in females in both models. Between 1–4 years old, the odds of being in proximity with an immature and a same-sex partner increased, respectively, by 2.43% and 3.51% in females, and by 10.57% and 16.28% in males. Instead, the change in preference for peer partners (MP2c.2) with age was not significant for the proximity network. As predicted for the grooming network, immatures developed a significant preference for grooming immature and peer partners with age (all components). This pattern was relatively more marked in males, but the age-sex interaction was not significant. Between 1–4 years old, the odds of grooming with an immature and a peer partner increased between 53.57–247.3% (MP2c.1 received and given, respectively) in females and between 66.93–387.93% in males (MP2c.1 received and MP2c.2 given, respectively). Moreover, as predicted, immatures groomed significantly more with partners of the same sex as they aged (all components). This pattern was more marked in males than in females, although the age-sex interaction was significant only for grooming received and total. Between 1–4 years old, the odds of grooming with a partner of the same sex increased between 33.52–270.69% (received and given, respectively) in females and between 184.75–391.22% (received and given, respectively) in males. Finally, sex had a significant effect in all MP2c models but

in MP2c.2 proximity, and in MP2c.1 and MP2c.2 grooming received (not predicted). Males were less in proximity and groomed less with partners of similar age and of the same sex than females. At 30 months of age, the odds of being in proximity with an immature and a same-sex partner were, respectively, 2.80% and 5.43% lower in males than in females; the odds of grooming with an immature, a peer, or a same-sex partner were lower in males than in females between 24.04–74.64% (MP2c.2 and MP2c.3 total, respectively).

Table 2.3: Results on immatures' age, sex, and their interaction (':') for hypothesis' **H2 models**, for the proximity and grooming (Groom.) networks. The values reported for sex refer to males. The estimate, standard (Std.) error, *p*-value ('NS' = not significant), and conditional (delta) *R*² are reported for each variable/ model. Significant (*p*-value ≤ 0.05) variables are highlighted (grey).

Model	Variable	Estimate	Std. Error	<i>p</i> -value	<i>R</i> ²
P2a Proximity	Age immature	-0.0211	0.0039	0.05	0.41
	Sex immature	-0.3603	0.1936	NS	
	Age:Sex	0.0069	0.0050	NS	
P2a Groom. Given	Age immature	0.0455	0.0019	0.05	0.72
	Sex immature	-0.2985	0.0893	0.05	
	Age:Sex	-0.0199	0.0025	0.05	
P2a Groom. Received	Age immature	0.0069	0.0020	0.05	0.40
	Sex immature	-0.0613	0.0922	NS	
	Age:Sex	-0.0022	0.0025	NS	
P2a Groom. Total	Age immature	0.0341	0.0019	0.05	0.64
	Sex immature	-0.0125	0.0863	NS	
	Age:Sex	-0.0235	0.0023	0.05	
P2b.1 Proximity	Age immature	-0.0211	0.0036	0.05	0.49
	Sex immature	-0.2964	0.1831	NS	
	Age:Sex	0.0047	0.0047	NS	
P2b.1 Groom. Total	Age immature	0.0097	0.0022	0.05	0.49
	Sex immature	-0.0195	0.1005	NS	
	Age:Sex	-0.0068	0.0028	NS	
P2b.2 Proximity	Age immature	0.0054	0.0042	NS	0.07
	Sex immature	0.1166	0.2167	NS	
	Age:Sex	-0.0055	0.0057	NS	
P2b.2 Groom. Total	Age immature	0.0355	0.0023	0.05	0.52
	Sex immature	-0.2042	0.1020	NS	
	Age:Sex	-0.0126	0.0029	0.05	
P2c.1 Proximity	Age immature	0.0007	0.0013	NS	0.14
	Sex immature	-0.0922	0.0641	0.05	
	Age:Sex	0.0021	0.0017	0.05	
P2c.1 Groom. Given	Age immature	0.0346	0.0032	0.05	0.64
	Sex immature	-1.1815	0.1887	0.05	
	Age:Sex	0.0060	0.0044	NS	
P2c.1 Groom. Received	Age immature	0.0119	0.0027	0.05	0.36
	Sex immature	-0.1137	0.1339	NS	
	Age:Sex	0.0023	0.0036	NS	
P2c.1 Groom. Total	Age immature	0.0227	0.0022	0.05	0.56
	Sex immature	-0.4327	0.1195	0.05	
	Age:Sex	-0.0010	0.0030	NS	
P2c.2 Proximity	Age immature	-0.0001	0.0026	NS	0.01
	Sex immature	-0.0362	0.1412	NS	
	Age:Sex	0.0018	0.0036	NS	
P2c.2 Groom. Given	Age immature	0.0303	0.0051	0.05	0.31
	Sex immature	-1.1021	0.3042	0.05	
	Age:Sex	0.0137	0.0073	NS	
P2c.2	Age immature	0.0261	0.0054	0.05	0.23

Model	Variable	Estimate	Std. Error	<i>p</i> -value	R ²
Groom. Received	Sex immature	-0.0887	0.2828	NS	
	Age:Sex	0.0067	0.0070	NS	
P2c.2 Groom. Total	Age immature	0.0275	0.0042	0.05	0.33
	Sex immature	-0.5450	0.2297	0.05	
	Age:Sex	0.0090	0.0057	NS	
P2c.3 Proximity	Age immature	0.0010	0.0012	0.05	0.18
	Sex immature	-0.1528	0.0627	0.05	
	Age:Sex	0.0032	0.0016	0.05	
P2c.3 Groom. Given	Age immature	0.0364	0.0029	0.05	0.70
	Sex immature	-1.5735	0.1916	0.05	
	Age:Sex	0.0078	0.0044	NS	
P2c.3 Groom. Received	Age immature	0.0080	0.0023	0.05	0.57
	Sex immature	-1.9513	0.1537	0.05	
	Age:Sex	0.0210	0.0038	0.05	
P2c.3 Groom. Total	Age immature	0.0197	0.0020	0.05	0.72
	Sex immature	-1.8453	0.1327	0.05	
	Age:Sex	0.0158	0.0032	0.05	

Figure 2.4: Changes in immatures' social network strength with age in the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks (**MP2a**). Ribbons represent 97.5% confidence intervals.

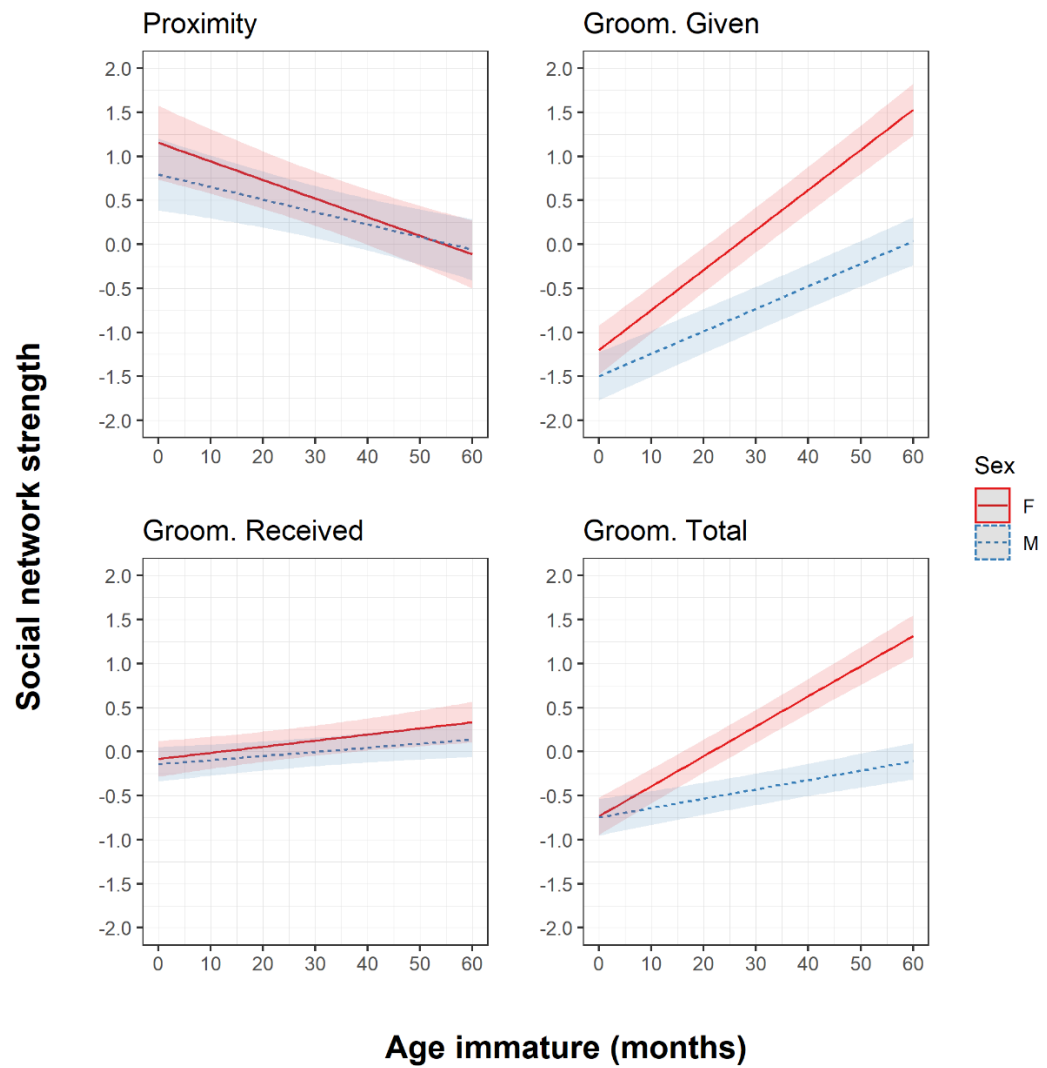


Figure 2.5: Changes in immatures' social network centrality (**MP2b.1**) and betweenness (**MP2b.2**) with age in the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks. Ribbons represent 97.5% confidence intervals.

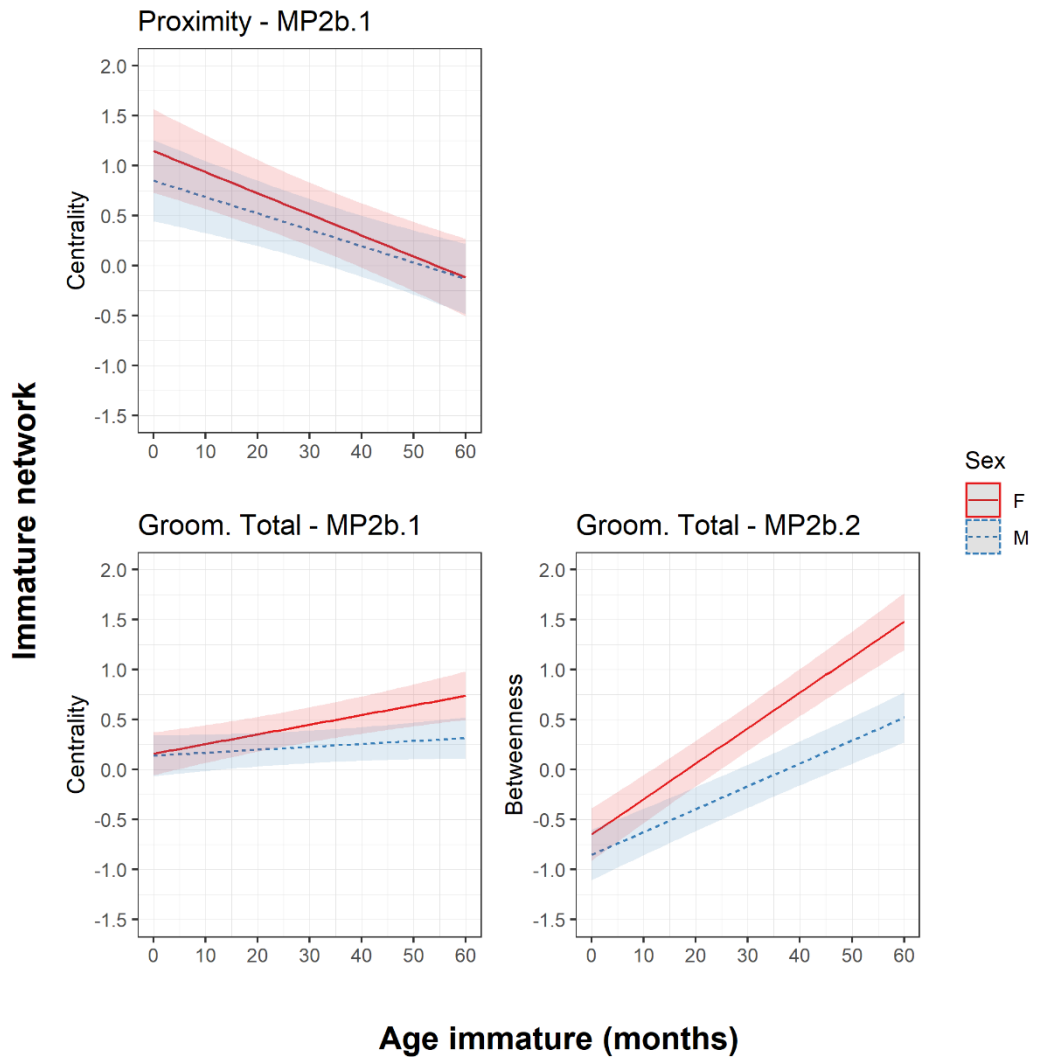
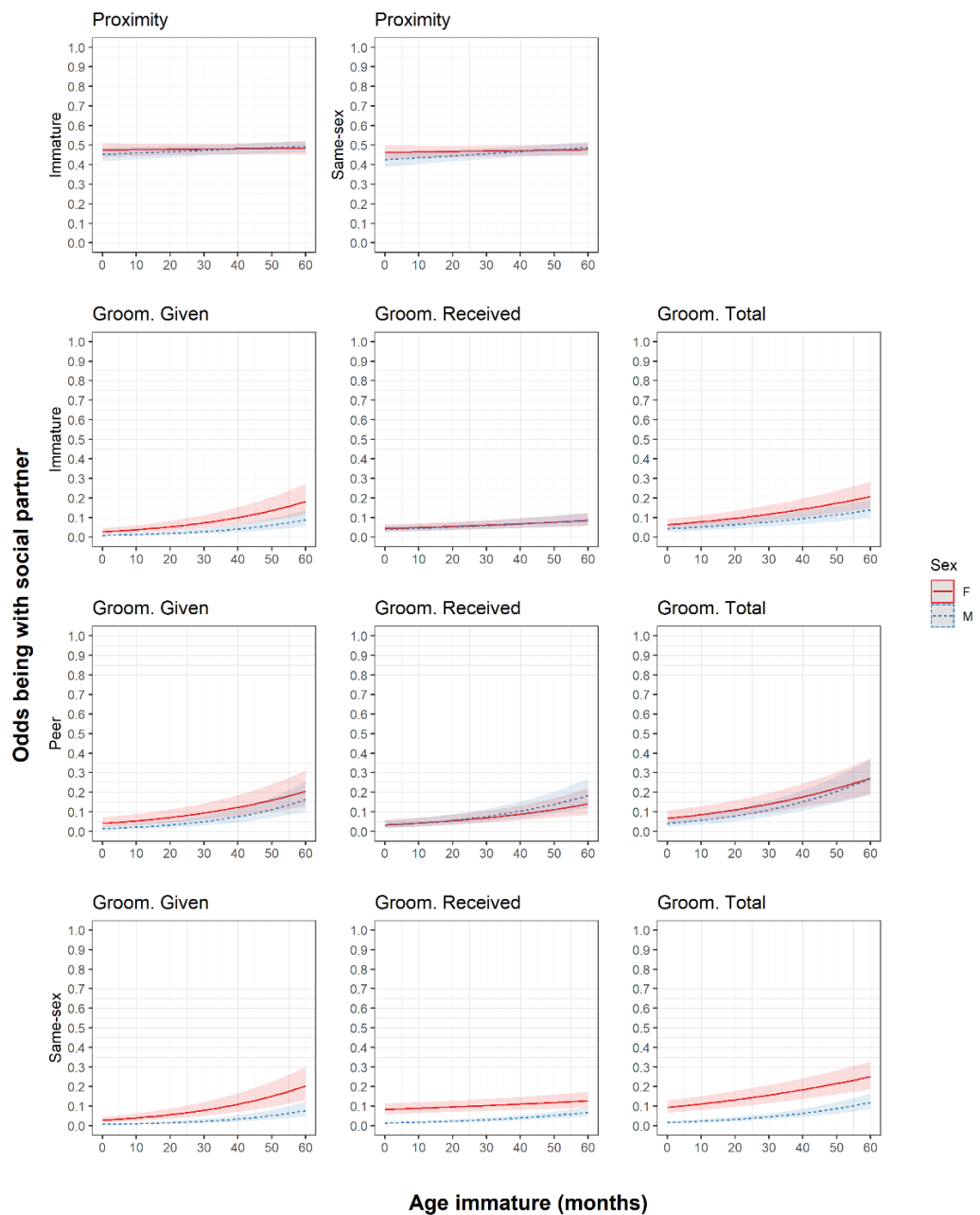


Figure 2.6: Changes in immatures' odds of being with a particular social partner (another immature, **MP2c.1**; a peer, **MP2c.2**; a same-sex individual, **MP2c.3**) with age in the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.



2.5 DISCUSSION

In this study, we explored how wild chacma baboon social networks are shaped throughout the immature period, focusing on age changes and sex differences. Here, we first discuss the effects of age and sex (and their interaction) on the inheritance of maternal networks (hypothesis H1) and on the changes in the immatures' social network integration and social partners' characteristics (hypothesis H2). We then comment on the potential implications of these developmental changes and sex differences in network patterns for social information transmission at the group level.

2.5.1 The inheritance of maternal networks

Immature baboons inherited their mothers' social connections. As they aged, they reduced the strength of their relationship with the mother and maternal social partners, but a mother's bonds continued to influence her offspring's throughout their development. The gradual acquisition of ecological competence (e.g., knowing what to eat) may decrease immatures' reliance on maternal care (van Noordwijk and van Schaik 2005, Alberts 2019) and, consequently, the time spent with the mother, as it is common among post-weaning mammals (Bateson 1994, Tsai and Mann 2013). We found that this was the case, as immature baboons spent less time with their mothers with age. Perhaps as a result, immatures' networks tended to diverge from those of their mothers with age. Nevertheless, mother-offspring proximity and grooming networks were positively correlated and immatures' networks generally became more similar to their mothers' compared to those of other individuals with age, thus supporting a social inheritance explanation (de Waal 1996, Ilany *et al.* 2021). Although the mean mother-

offspring network correlations were relatively low (< 0.5 ; see Appendix 1, §1.4), these values may be normal given that (1) immatures' grooming integration increased with age (see §2.4.2), being thus initially lower than that of their mothers, and (2) in wild populations social networks are affected by demographic changes (Borgeaud *et al.* 2017, Shizuka and Johnson 2020). Our mean cosine similarity values for immature females' grooming networks were qualitatively similar to those reported for juvenile female vervet monkeys (Jarrett *et al.* 2018) (see Appendix 1, §1.1). The relatively low cosine similarity values in vervet monkeys were hypothesised to derive from the changes in the mothers' own grooming networks, which constituted a moving target for their daughters (Jarrett *et al.* 2018). The same process may contribute to explain our results, given that the mothers' grooming networks changed between the study years (see Appendix 1, §1.7).

2.5.2 Developmental changes in network structure

Although immature baboons inherited their mothers' social networks, our results showed that their social network integration and social partner preferences changed throughout development. Age was an important determinant of this process (see Appendix 1, §1.6). Given that the mother's presence constrains the number and kind of partners with whom immatures can associate (Förster and Cords 2005, Gibson and Mann 2008a), age, which determines the extent of an immature's dependence on the mother (Altmann 1980), could be an important predictor of these network changes. In particular, as they aged, immatures had lower associations in their proximity network but were more active in grooming. First, the decrease in proximity network integration may be due to both external factors and immatures' partner choices. External

factors could include primates' attraction towards infants (Altmann 1980, Berman 1982b) and the greater tolerance that adults have towards younger versus older immatures (Whiten and van de Waal 2018). The infant network may shrink as older infants lose their attractiveness (Silk 1999, Dunayer and Berman 2018). In addition, younger immature primates are generally granted relatively higher proximity tolerance (Whiten and van de Waal 2018), which could aid their survival through the acquisition of ecological knowledge (de Resende *et al.* 2004, Rapaport and Brown 2008) and protection (Cheney 1977, Maestripieri 2018). On the other hand, older immatures may need relatively less support and be willing to associate with fewer partners (Pereira 1988a, 1989). Alternatively (or concurrently), immatures' proximity integration may decrease because they become more 'socially selective'. Social selectivity has been reported in mammals during senescence and may result from several factors, such as reduced energetic and cognitive capacities (Siracusa *et al.* 2022). For example, older eastern chimpanzees (Rosati *et al.* 2020) and killer whales (Weiss *et al.* 2021) associate with fewer partners than younger adults. It is possible that a similar process, although for different reasons, happens during development, when immatures narrow their association preferences from a variety of adult and immature partners to individuals of similar age and the same sex (see below). Second, the increase in immatures' grooming integration with age (contrary to the proximity network) may have two possible explanations. As they age, immatures could dedicate more time to grooming and less to play (capuchins *Sapajus* spp. (de Lima and Ferreira 2021), Japanese macaques (Shimada and Sueur 2017)), allowing them to groom more frequently or a wider network of troop members. Concurrently, they may become more proficient groomers, thus becoming more desirable grooming partners (Dunbar 2010).

We then analysed the changes in partner preferences with age, which confirmed other studies' findings (Nakamichi 1989, Kulik *et al.* 2015). Immatures groomed more with partners of similar age (both other immatures – ≤ 5 years old – and peers – ± 6 months age difference) while growing older. In addition, they both spent more time in proximity and groomed more with partners of the same sex as they aged, indicating strong social selectivity with age. Immatures could favour similar age and same-sex partners over other group members because of their increasing independence from adult social partners and the benefit of forming (potentially) long-lasting bonds. In the first case, while adults are important sources of knowledge on what to eat (Whiten and van de Waal 2018), baboons are generally weaned and thus able to forage independently within the first year of life (Altmann 1980, Alberts 2019), which could allow greater social selectivity. In addition, while young immatures could benefit from the proximity of adult kin to receive agonistic support, this may become less important with age as older immatures have established their social rank (Maestripieri 2018). Finally, juveniles may need less foraging time compared to adults (due to a relatively smaller body size), having thus more time to socialise with other immatures (killer whales (Weiss *et al.* 2021), bottlenose dolphins (Gibson and Mann 2008a)). In the second case, long-lasting bonds are important because they can enhance fitness (Silk *et al.* 2010b, Archie *et al.* 2014). Bonding with individuals of similar age (e.g., paternal kin (Altmann 1979)) and the same sex could translate into stable social bonds (Smith *et al.* 2003, Silk *et al.* 2010a, Stanton *et al.* 2011). Philopatric females could share a large part of their lives with similarly-aged females (Silk *et al.* 2010a), while males could disperse together at maturity (Jack *et al.* 2009) (see below).

2.5.3 Sex differences in network formation

Age changes in immature baboon social networks differed by sex, which had generally a strong effect in our models compared to the other variables (see Appendix 1, §1.6). The results of our study are consistent with males' gradual social peripheralization prior to dispersal in female-philopatric species (Lonsdorf 2017, Amici, Kulik, *et al.* 2019). In our first analyses (H1), we found that males formed relatively weaker bonds with their mothers and with maternal partners. First, the decrease in time spent with the mother was more pronounced for males than for females. Male primates' physical distancing from their mothers could arise, from the mothers directing more agonism towards sons than daughters (Kulik *et al.* 2016) or males being more physically precocious than females (e.g., in play (Lonsdorf, Markham, *et al.* 2014)). These patterns may lead males to spend time farther from the mother earlier than females. Nevertheless, males groomed proportionally more with their mothers than females. This pattern may derive from males' lower grooming integration, leading mothers to be important grooming partners for their sons. Rates for grooming given were qualitatively higher in females than in males, but both sexes received similar amounts of grooming (see Appendix 1, §1.8). If females receive grooming from more partners than males (Nakamichi 1989) (see below), they may have less time to dedicate to the mother. Second, males' proximity and grooming networks resembled their mothers' less closely compared to females. In female-philopatric species, maternal kin form close bonds with each other (as in baboons (Silk, Alberts, *et al.* 2006, Silk, Altmann, *et al.* 2006)). These are more important for females compared to males for two reasons: maternal kin bonds will help females inherit and maintain their social rank (Holekamp and Smale 1991) (through agonistic support (Silk *et al.* 2004)), and they will last throughout their lives, potentially

leading to fitness benefits (Silk, Alberts, *et al.* 2003, Silk *et al.* 2010b). Instead, when males reach a body size greater than that of adult females (at approx. six years old), they attain their social rank through agonistic interactions, without the support of their matriline (Kitchen *et al.* 2005). Males also disperse at adulthood, leaving behind the social bonds formed in their natal troop (Cheney and Seyfarth 2007), and thus can 'afford' to invest less in them during juvenescence.

Our second analyses (H2) showed that males became relatively less integrated in the grooming network as they aged. Males' relatively lower grooming network integration could derive both from their lower tendency to groom and their higher sexual segregation compared to females. In female-philopatric primate species, immature males groom less than females, but spend more time playing (Amici, Kulik, *et al.* 2019). Play has been hypothesized to be important to acquire fighting skills for immature males, who will compete for dominance (Förster and Cords 2005). Focusing on same-sex grooming partners, males' integration may diminish also because of lower availability of potential partners, while females share grooming more evenly with both sexes. Juvenile males may prefer to groom with each other because male bonding could lead them to emigrate together, increasing their probability of survival during dispersal and integration in a new group (Jack *et al.* 2009, Widdig *et al.* 2016). Despite males' gradual peripheralization, immatures' grooming integration increased with age in both sexes. This is partly explained by the fact that infants of both sexes dedicate very little time to grooming, given that it is a behaviour learnt with time (Dunbar 2010, Shimada and Sueur 2017). In addition, the increase in males' grooming activity may be explained by a similar increase in their sexual activity during development (Gunst *et al.* 2013): older juveniles may copulate with adult females at the early or late stages of their cycle (when fertility is low and females are not

monopolised by a dominant male (Huchard, Courtiol, *et al.* 2009)) and exchange grooming with them (snub-nosed monkeys *Rhinopithecus roxellana* (Yu *et al.* 2013), long-tailed macaques *M. fascicularis* (Gumert 2007)).

2.5.4 Implications for social information transmission

The age and sex differences in network structure highlighted by our results may have important implications for social learning, and thus the formation of culture (i.e., behaviours shared by most members of a group and maintained through time (Laland and Janik 2006, Allen 2019)). In particular, we suggest that the emergence of culture, according to its most common definition (i.e., at the group level; but see Schuppli and van Schaik 2019), in female-philopatric societies may be limited by age- and sex-driven social clustering (van de Waal *et al.* 2012). Matrilineal centres could be pivotal centres of information transmission for young immatures (vervet monkeys (van de Waal *et al.* 2012, 2014), Japanese macaques (Tanaka 1995, 1998)). However, the presence of social clusters around matrilineal centres, as our results show, could diminish social information transmission across a group and instead cause it to cluster in matrilineal 'subgroups'. This is because the individuals who tend to acquire information are socially separated from those who are more likely to produce it (Carter *et al.* 2015): (1) immatures, who rely more on social learning, and adults, who have a greater ability to produce information (Whiten and van de Waal 2018); (2) females, who learn more socially, and males, who learn more individually (Reader and Laland 2001). Although these considerations remain speculative, this theoretical framework could help future studies to investigate the constraints leading to the formation of matrilineal 'cultures' as opposed to group cultures (van

de Waal *et al.* 2012), ultimately questioning culture as a group-level behaviour (Schuppli and van Schaik 2019).

3 CHAPTER 3: MATERNAL INFLUENCES ON SOCIALITY IN WILD BABOONS

3.1 ABSTRACT

Immatures' social development may be important to understand which factors affect social information transmission, potentially producing variation in fitness, in wild populations. Our aim was to determine how maternal social features shape the offspring's social network inheritance and differentiation (social integration and social partners' characteristics) in wild immature baboons, group-living primates that readily learn socially. We adopted a longitudinal approach testing the independent effects of three maternal features: a mother's number of offspring in the group (matriline size), her dominance rank, and her social network integration. Our results show that the inheritance of maternal networks was enhanced both by matriline size and dominance rank. Social network integration was positively correlated with matriline size and a mother's own network integration, while dominance rank had a negative effect on immatures' ability to connect different social clusters. Finally, both matriline size and dominance rank increased immatures' association with partners of similar age and the same sex. We suggest that, in female-philopatric societies, social clustering within matriline and same-sex immature subgroups may limit information transmission at the group level. Our results may thus stimulate further studies aimed at testing this hypothetical framework.

3.2 INTRODUCTION

Social connections are known to enhance individuals' fitness (Ellis et al. 2019, Snyder-Mackler et al. 2020) (but see Evans et al. 2020, Menz et al. 2020). For example, strong social bonds in wild baboons (*Papio* spp.) (Silk et al. 2009, Archie et al. 2014, Cheney et al. 2016), bottlenose dolphins (*Tursiops* sp.) (Stanton and Mann 2012), killer whales (*Orcinus orca*) (Ellis et al. 2017), and spotted hyenas (*Crocuta crocuta*) (Ilany et al. 2021, Turner et al. 2021) can increase the survival of individuals and/or their offspring. The mechanisms linking sociality to fitness are not well known, but they may include reduced stress levels (rhesus macaques *Macaca mulatta* (Brent, Semple, et al. 2011), chacma baboons *P. ursinus* (Crockford et al. 2008)), thermal benefits (Barbary macaques *M. sylvanus* (Campbell et al. 2018), vervet monkeys *Chlorocebus pygerythrus* (McFarland et al. 2015)), and lower risks of injury (rhesus macaques (Pavez-Fox et al. 2022)). Another biological process that could affect fitness and is intrinsically related to social connections may be social learning (i.e., learning from others) (Laland 2004, Rendell et al. 2010, van Schaik and Burkart 2011). Social learning may be adaptive, e.g., by allowing individuals to spare the time and energy needed for individual exploration (Laland 2004). In some cases, group-level social knowledge maintained through time (i.e., local culture (Laland and Janik 2006, Allen 2019)) is positively related to between-group variation in fitness (sperm whales *Physeter macrocephalus* (Marcoux et al. 2007), African elephants *Loxodonta africana* (McComb et al. 2001)).

Because immature age classes tend to learn from others more than adults (Australian skinks *Eulamprus quoyii* (Noble et al. 2014), chacma baboons (Carter et al. 2014), meerkats *Suricata suricatta* (Thornton and Malapert 2009)), they

could have a fundamental role in social information spread at the group level (Mesoudi *et al.* 2016, Whiten and van de Waal 2018), with potential implications on wild social groups' fitness (Whiten 2017). Inexperienced immatures may have proportionally higher costs than adults in collecting information personally rather than socially (Laland 2004). Social learning can entail costs, such as acquiring unreliable (e.g., on patch quality) or outdated (e.g., a patch that has already been depleted) information (Giraldeau *et al.* 2002, Carter, Marshall, *et al.* 2013). However, immatures need to learn basic survival skills from others, such as avoidance of predators (Siberian jays *Perisoreus infaustus* (Griesser and Suzuki 2017), black-tailed prairie dogs *Cynomys ludovicianus* (Shier and Owings 2007)) or noxious foods (great tits *Parus major* (Landová *et al.* 2017), squirrel monkeys *Saimiri oerstedii* (Boinski and Fragaszy 1989)), that would be risky to acquire through direct experience (Thornton and Clutton-Brock 2011).

Social connections may influence social learning by setting an upper limit to an individual's social learning opportunities (Cantor and Whitehead 2013, Kulahci and Quinn 2019, van Boekholt *et al.* 2021). Indeed, socially central chacma baboons (Carter, Torrents Ticó, *et al.* 2016) and ravens (*Corvus corax*) (Kulahci *et al.* 2016) were faster in discovering experimental food patches because they were bonded to relatively more individuals who could provide that information. Social connections can be quantified through social network analysis (Croft *et al.* 2011, Pinter-Wollman *et al.* 2014). Social networks represent the direct and indirect bonds among the individuals in a social group, and can be assessed through proximity (i.e., individuals are associating if they share similar spatial positions) and interactions (i.e., individuals are associating if they are observed interacting) (Croft *et al.* 2008). The two resulting networks may be differentiated (Castles *et al.* 2014), and they may both predict social information transmission

(Carter, Torrents Ticó, *et al.* 2016). For example, individuals may learn from others who are most often in visual proximity (e.g., during foraging; threespine sticklebacks *Gasterosteus aculeatus* (Atton *et al.* 2012), sympatric tits – *Paridae* Family (Aplin *et al.* 2012)). In other cases, individuals may prefer to learn from those with whom they share positive interactions, such as grooming (Dunbar 1991) in non-human primates (hereafter primates) (ring-tailed lemurs *Lemur catta* (Kulahci *et al.* 2018a), tufted capuchins *Sapajus apella* (Coelho *et al.* 2015)).

Previous studies characterised how immatures' social networks change with age and differ by sex (chacma baboons (Roatti *et al.* 2023a), vervet monkeys (Jarrett *et al.* 2018, Vilette *et al.* 2022), spotted hyenas (Turner *et al.* 2018, Ilany *et al.* 2021), rhesus macaques (Berman 1982a, de Waal 1996, Kulik *et al.* 2015)). In general, immatures inherit the social networks of their mothers through exposure to the same social partners during the dependency period (de Waal 1996, Jarrett *et al.* 2018, Ilany *et al.* 2021). Immatures' networks then differentiate from the maternal ones when infants become independent from maternal care (Berman 1982a, 1982b, Roatti *et al.* 2023a). As they age, immatures spend more time alone (Turner *et al.* 2018), being in proximity to a relatively smaller circle of partners of similar age and the same sex (Kulik *et al.* 2015, Vilette *et al.* 2022, Roatti *et al.* 2023a), while they may become more integrated into the adults' affiliative network (e.g., grooming) (Jarrett *et al.* 2018, Vilette *et al.* 2022, Roatti *et al.* 2023a). On top of these developmental changes, maternal social features may affect different aspects of immatures' social networks throughout their development (Wolf and Wade 2009, Maestriperi 2018).

Mothers may have strong influences on their offspring's phenotype through a variety of mechanisms (e.g., genetic, hormonal, phenotypical) (Wolf and Wade 2009, Maestriperi 2018). Three phenotypical maternal features could be

important in shaping immatures' social bonds: a mother's number of offspring in the group (i.e., matriline size), her dominance rank, and her social network integration. A mother's matriline size may affect her offspring's social network inheritance, their network integration, and their choice of social partners. First, immatures with more siblings may interact (e.g., groom) proportionally less with their mothers (Lee 1987a), but they may inherit relatively more their mothers' networks (Silk, Alberts, *et al.* 2006, Silk, Altmann, *et al.* 2006). Mothers and offspring may maintain a strong relationship throughout the immature period (killer whales (Weiss *et al.* 2023), western chimpanzees *Pan troglodytes verus* (Samuni *et al.* 2020), spotted hyenas (Watts *et al.* 2009)) and siblings may compete for access to the mother (chacma baboons (Delaunay *et al.* 2023), bonobos *P. paniscus* (Behringer *et al.* 2022), Japanese macaques *M. fuscata* (Schino and Troisi 2001)). Therefore, each sibling may exchange proportionally less grooming with the mother in larger compared to smaller matriline. However, because matriline members preferentially associate with each other (chacma baboons (Silk *et al.* 2010a), African elephants (Archie *et al.* 2006), spotted hyenas (Holekamp *et al.* 1997)), immatures belonging to larger matriline may spend a relatively higher proportion of time with close maternal kin. This may increase immatures' fidelity to their mothers' networks because their common attraction towards close kin (Silk 2009, Smith 2014) adds to the effect of being raised around their mothers' social partners (de Waal 1996, Ilany and Akçay 2016). On the other hand, immatures from smaller matriline may need to seek social connections outside their maternal cluster, reducing the extent to which they inherit their mothers' networks (Koyama 2003, Silk *et al.* 2012).

Matriline size could have two alternative effects on immatures' social network integration and partners' choice. On the one hand, immatures with more siblings

may both be relatively more integrated in the group's network and have a stronger preference for partners of similar age and the same sex. Individuals' network integration may be enhanced through the indirect connections with the partners of their social partners ('friends of friends' bonds; e.g., spotted hyenas (Ilany *et al.* 2015)), which can potentially turn into direct bonds. Siblings may thus give a 'head start' to immatures' network formation (Brent 2015, Sosa *et al.* 2021). Owing to their numerous social connections, immatures with more siblings may have a relatively better access to partners with whom they could form long lasting bonds (Farine and Whitehead 2015, Sosa *et al.* 2021). Because strong and durable social bonds have fitness benefits (Silk *et al.* 2009, 2010a), individuals may prefer social partners of similar age (e.g., paternal siblings (Altmann 1979)) and the same sex (Roatti *et al.* 2023a). Peer bonds with partners of the same sex may last for life for the philopatric sex (rhesus macaques (Schülke *et al.* 2013), chacma (Silk *et al.* 2010a) and yellow *P. cynocephalus* (Smith *et al.* 2003) baboons) and they may be valuable for the dispersing sex as well (Assamese *M. assamensis* (De Moor *et al.* 2020) and rhesus (Widdig *et al.* 2016) macaques). Indeed, bonded dispersing sub/adults may leave the natal group together, which could facilitate their survival and integration into a new group (Jack *et al.* 2009). On the other hand, if matriline members tend to form tight clusters with few outward connections, immatures with more siblings may be relatively less integrated in the group's network and, consequently, be less able to bond with same-sex peers compared to more socially central immatures (Koyama 2003, Pasquaretta *et al.* 2014).

Second, a mother's dominance rank (inherited by the offspring (Holekamp and Smale 1991)) may enhance all aspects of immatures' social network structure. Because dominant matrilines are more cohesive (Japanese macaques

(Koyama 2003), chacma baboons (Silk *et al.* 1999), spotted hyenas (Holekamp *et al.* 1997)), higher-ranking immatures may both spend more time with their mothers and inherit their mothers' networks more than lower-ranking immatures (spotted hyenas (Ilany *et al.* 2021)). Higher-ranking immatures may have relatively greater advantages from associating with close maternal kin because they could receive more agonistic support (Pereira 1989, East *et al.* 2009) and they could access better foraging opportunities (Mills 1985, Coelho *et al.* 2015). On the other hand, lower-ranking individuals may benefit relatively more from bonding with dominant group mates outside their matriline in order to gain social tolerance (Sick *et al.* 2014, Marshall *et al.* 2015). Due to this attraction for higher-ranking partners and the social opportunities granted by their dominant mothers' greater social integration (Barrett *et al.* 1999, Smith *et al.* 2007), higher-ranking immatures tend to be more socially central than lower-ranking ones (Tibetan *M. thibetana* (Liu *et al.* 2022) and rhesus (Wooddell *et al.* 2020) macaques). Both their higher social integration and greater competitive abilities (see above) may allow dominant immatures to bond with same-sex peers more than subordinate ones (Range 2006).

Third, immatures' social network integration may be influenced by their mothers' own network integration. Mothers' social integration could depend on others associating with them (Farine and Whitehead 2015, Sosa *et al.* 2021) and/or their tendency to form and maintain social relationships (sociability) (Krause *et al.* 2010, Wilson *et al.* 2013). Both these factors could affect the offspring's social connections by providing bonding opportunities during development and/or shaping immatures' sociability (Brent 2015, Maestriperi 2018). Because infants share their mothers' networks at birth and maternal social connections continue to influence their offspring's throughout development (de

Waal 1996, Roatti *et al.* 2023a), a mother's social integration may determine her offspring's exposure to potential social partners (Brent 2015). Immatures could bond with their mothers' partners (eastern chimpanzees *P. t. schweinfurthii* (Murray *et al.* 2014), bottlenose dolphins (Gibson and Mann 2008b)) and with the offspring of the females associated with their mothers (rhesus macaques (Wooddell *et al.* 2020), Stuhlmann's blue monkeys *Cercopithecus mitis stuhlmanni* (Förster and Cords 2005), olive baboons *P. anubis* (Owens 1975)). Independently from social inheritance, social exposure during early life may affect immatures' sociability (Stuhlmann's blue monkeys (Thompson and Cords 2020), rhesus macaques (Wooddell *et al.* 2020), chimpanzees (Hemelrijk and De Kogel 1989)) and a mother's own sociability could be transmitted genetically (yellow and yellow-olive *P. cynocephalus-anubis* baboons (Lange *et al.* 2023), rhesus macaques (Brent, Heilbronner, *et al.* 2013), barn swallows *Hirundo rustica* (Møller 2002)).

With this study, we aimed to contribute to the understanding of how immatures' social connections, and thus their opportunities for social learning (van Boekholt *et al.* 2021), are shaped by maternal social features in a wild primate, the chacma baboon. Primates offer wide opportunities to study the development of social networks because they experience a longer period of juvenescence compared to other taxa, which has been linked to higher social learning abilities (Jones 2011, Street *et al.* 2017, Whiten and van de Waal 2017). In addition, mothers are the primary caring figures in most species of primates (Maestriperi 2018). Baboons are an ideal taxon for this study because they live in large multi-male-multi-female social groups (Cheney and Seyfarth 2007) and experiments linked social information transmission to both their proximity and grooming networks (Carter, Torrents Ticó, *et al.* 2016). Baboons' social groups

are organised into matrilineal societies where females are philopatric (Silk *et al.* 1999, Cheney and Seyfarth 2007), while males disperse at maturity (around eight years old) (Alberts and Altmann 1995a, 1995b). Females' dominance hierarchy is linear and stable, with offspring inheriting their mothers' ranks (Cheney 1977, Pereira 1989) and maternally-related adult females supporting each other in agonistic interactions (Silk *et al.* 2004, Wittig, Crockford, Seyfarth, *et al.* 2007). Males' rank, on the other hand, is determined through agonistic competition with other males when they reach subadult-hood (from approx. six years old) (Pereira 1988b, 1989).

We used social network analysis in the context of a longitudinal study to assess the simultaneous effects of three maternal characteristics on immatures' social development. A mother's number of offspring in the group, her dominance rank, and her social network integration may be particularly important in despotic female-philopatric species, where socially central females form close bonds with maternal kin within a stable dominance hierarchy (spotted hyenas (Ilany *et al.* 2021), chacma baboons (Silk *et al.* 2010a)). However, these maternal features may play a role also in relatively more egalitarian matrilineal societies (Stuhlmann's blue monkeys (Thompson and Cords 2020), white-faced capuchins *Cebus capuchinus* (Perry *et al.* 2008)) and male-philopatric species (eastern chimpanzees (Murray *et al.* 2014), bonobos (Surbeck *et al.* 2011)). While previous studies analysed the influence of single maternal phenotypes (Wooddell *et al.* 2020) or focused on how maternal effects during infancy affected the offspring's behaviours later in life (Thompson and Cords 2020), our approach addressed the relative importance of different maternal features throughout immatures' network formation. Filling this gap in the literature may pave the way to future studies on how immatures' social connections enhance or constrain

social information transmission (Carter, Torrents Ticó, *et al.* 2016, Mesoudi *et al.* 2016), which may, in turn, help to unravel the adaptive value of sociality (Silk 2007a, 2007b).

We tested two main hypotheses about maternal influences on sociality in wild immature baboons. Our first hypothesis (**H1**) was that the time immatures spent with their mothers (**P1a**) and the inheritance of maternal social networks (**P1b** and **P1c**) would depend on a mother's number of offspring and her dominance rank. We had three sets of predictions for this hypothesis (see Table 3.1 and §3.3). First, because matriline members preferentially associate together (Silk *et al.* 2010a), we predicted that (**P1a.1**) immatures with more siblings would spend more time in proximity with their matriline, including their mothers. However, because mothers distribute their grooming time among their offspring (Lee 1987a), we predicted that immatures with more siblings would groom relatively less with their mothers compared to immatures with fewer siblings. In addition, because higher-ranking matriline members are more cohesive (Koyama 2003) and immatures may gain advantages from the proximity of dominant kin (Pereira 1989, Huchard *et al.* 2013), we predicted that (**P1a.2**) both the time spent in proximity and grooming with the mother would increase with the mother's dominance rank. Because of the same reasons that may lead immatures to spend more time with their mothers (see above), we also predicted that: the strength of the mother-offspring social network correlation would increase with a mother's number of offspring (**P1b.1**) and her dominance rank (**P1b.2**); and that the fact that immatures' networks are more correlated to their mothers' networks than to those of other individuals (Roatti *et al.* 2023a) would increase with a mother's number of offspring (**P1c.1**) and her dominance rank (**P1c.2**).

Our second hypothesis (**H2**) was that immatures' social network integration – measured through the association with different social partners (**P2a**) and the positions in the social network (**P2b**) – and the type of social partners with whom they associate (**P2c**) would depend on a mother's number of offspring, her dominance rank, and her own network integration. We had three sets of predictions for this hypothesis. For matriline size, we foresaw two mutually exclusive alternatives: first, because of the indirect social connections with their close kin's social partners (Brent 2015), we predicted that immatures' network integration would increase with a mother's number of offspring (**P2a.1** and **P2b.1**); alternatively, we predicted that matrilineal social clustering would constrain immatures' social integration in larger matrilineal lines (Pasquaretta *et al.* 2014) (alternative **P2a.1** and **P2b.1**). In addition, because of the enhanced social centrality of dominant individuals (Smith *et al.* 2007), we predicted that immatures' social network integration would increase with a mother's dominance rank (**P2a.2** and **P2b.2**). We also predicted that, because of the wider bonding opportunities provided by socially integrated mothers, and/or the effects of a mother's sociability on her offspring's sociability (Brent 2015), immatures' social network integration would increase with a mother's own network integration (**P2a.3** and **P2b.3**). Finally, owing to their better competitive abilities (Pereira 1989) and/or social integration (Brent 2015, Liu *et al.* 2022), we predicted that the association with partners with whom to form long-lasting bonds (i.e., of similar age and the same sex) (Silk *et al.* 2010b) would be relatively stronger for immatures with more siblings (**P2c.1**) and a higher rank (**P2c.2**).

3.3 METHODS

3.3.1 Study site and species

The study was carried out at the Tsaobis Baboon Project (TBP 2019), a long-term, individual-based study of wild baboons in central Namibia (22°22'S, 15°44'E). The study area is characterised by the presence of the ephemeral Swakop River, hosting dense patches of riparian woodland and surrounded by rocky hills with scarce vegetation (see Cowlshaw and Davies 1997 for a full description of the area). The methods for this study are described in more detail in Chapter 2, §2.3 (Roatti *et al.* 2023a).

For the purposes of this study, individuals ≤ 5 years old were considered immatures. Adult female chacma baboons give birth to an infant approx. every two years (Dezeure, Baniel, *et al.* 2021) and infants are weaned around 12–18 months of age at Tsaobis (Huchard *et al.* 2013, Carboni *et al.* 2022). Males typically enter sub-adulthood (before reaching full adult size) around six years old; females start menstruating around five years old and conceive their first infant around six years old (Altmann *et al.* 1981, Alberts and Altmann 1995a).

3.3.2 Data collection

Observations were conducted on up to three troops (J, L, and M) during six annual field seasons (each of about three months) between 2014 and 2019. M troop was a fission of J troop from 2017 – 2019. During the study periods, baboons were usually followed daily from dawn to dusk, and data were recorded on all recognisable individuals with the application CyberTracker (Liebenberg 2022). The study population is habituated to the presence of observers on foot

and the majority of the individuals was individually recognisable (proportion of recognizable individuals: 0.9 on average).

We quantified individuals' associations based on a proximity and an interaction (i.e., grooming) rule. Proximity associations were characterized through instantaneous (scan) sampling. To guarantee sampling independence, we recorded the neighbours within 10 m of 'focal' individuals, who were chosen from a randomized list including all the baboons present in the troop. When a focal individual was sampled, s/he was not re-sampled within an hour if appearing again in a (new) list. Similarly, when an individual was recorded as a neighbour of a focal individual, s/he was not re-sampled as a focal individual within an hour (see Carter, Torrents Ticó, *et al.* 2016 for more details). Grooming interactions were recorded *ad libitum* while moving through the troops. In this way, the *ad libitum*-collected data were not biased towards the individuals who were easier to find and, as such, we did not account for individual baboon observability. To avoid pseudo-replication, a grooming dyad was not recorded more than once within the same half hour (Carter, Torrents Ticó, *et al.* 2016).

Immature individuals' ages (in months) were determined by known (occurred during fieldwork) and estimated dates of birth. Dates of birth were estimated based on (1) possible conception dates, assuming a pregnancy duration of six months (Altmann *et al.* 1978, Alberts and Fitzpatrick 2012); and/or (2) through observation of the infant's colouration (Dezeure, Dagorrette, *et al.* 2021). The identity of an infant's mother was determined through direct behavioural observations (nursing). The mothers' numbers of offspring in the troop during each season was calculated based on long-term troop composition data. Matriline size was strongly correlated (Pearson's $r = 0.79$) with maternal age (in years) but not with her dominance rank (calculated as below) (Pearson's $r < 0.5$).

Dominance ranks were assessed for adult females through dominance interactions recorded *ad libitum*. To increase data independence, only one behaviour of a sequence of agonistic actions (e.g., threat, chase, attack) was included in the rank calculation. Female ordinal ranks were computed at the end of each season through the 'I & SI' method for linear dominance hierarchies (de Vries 1998) using Matman 1.1.4 (Noldus Information Technology 2003). Absolute ranks were standardised by controlling for group size (see Huchard and Cowlshaw 2011 for more details), thus obtaining relative ranks (ranging from '0' – lowest – to '1' – highest).

3.3.3 Data analyses

Data analyses were performed with R 4.0.2 (R Core Team 2023). Following previous studies with sparse network data (Turner *et al.* 2018, Kawazoe and Sosa 2019), we used multiple static networks (i.e., network sampled over a particular length of time) aggregated in approx. 30-day time periods (Pinter-Wollman *et al.* 2014). This 30-day resolution allowed us to capture social network transformations during infancy as well as juvenile years (Altmann 1980). Proximity and grooming data were treated separately. To have a sufficient number of observations per individual to build robust and accurate networks, we removed any time period with < 95 observations. We also removed any individual who was seen < 5 times per season (disappeared due to death or emigration), whose network may not be represented accurately (Farine and Whitehead 2015).

Social networks were produced for each sampling period, within each troop (for more details, see Chapter 2, §2.3 (Roatti *et al.* 2023a)). We built weighted networks (i.e., values indicate both the presence and strength of a connection) (Croft *et al.* 2011), and, in the case of grooming, weighted and directed networks

(Farine and Whitehead 2015). We used a simple ratio index (SRI), i.e., the proportion of time two individuals associated, to calculate weighted connections in the proximity network (Hoppitt and Farine 2018). For the grooming network, we used grooming counts or proportions depending on the model tested (see below). The grooming network was divided into its *out* (given) and *in* (received) components, which were treated both separately and united (total). Although proximity and grooming networks were analysed separately, similar models were applied in both cases, with the response variable differing depending on the network. All analyses were run on ego-networks: the variables tested were calculated for each immature individual in each sampling period (Hobson *et al.* 2013) (for more details, see Chapter 2, §2.3 (Roatti *et al.* 2023a)).

To test our predictions, we used both Linear Mixed Effects Models (LMMs) and Generalised Linear Mixed Effects Models (GLMMs) with a binomial family (*link* = '*logit*') (for more details, see Chapter 2, §2.3 (Roatti *et al.* 2023a)). All models, summarized in Table 3.1, included the following fixed and random factors. The predictor variables (fixed factors) of interest were three maternal social features: a mother's number of offspring in the troop, her relative dominance rank, and (for the P2a and P2b models – see below) her social network integration. We then controlled as fixed factors for immatures' age, sex, and the interaction between age and sex (discussed in Chapter 2 (Roatti *et al.* 2023a)), which are known to affect immatures' social development (Turner *et al.* 2018, Amici, Kulik, *et al.* 2019, Vilette *et al.* 2022). To control for repeated measures from the same troops, we added troop as a fixed factor (< 5 levels) (Harrison *et al.* 2018). Because our data have repeated measures from the same individuals through time, in each model we included as a random factor the individuals' identities (immature and mother) (Turner *et al.* 2018, Kawazoe and

Sosa 2019). We nested immatures' identities within the mothers' identities to account for other maternal influences on the offspring's sociality (e.g., maternal style) (Maestriperi 2018). Finally, we added year as a random factor to control for between-year variation in environmental factors. We did not control for season because most observations were made in the austral winter and baboons have no distinct breeding and mating seasons (Cheney *et al.* 2004, Dezeure, Baniel, *et al.* 2021).

The models (described in further detail below) were presented as 'full models' (i.e., they did not undergo any simplification procedure after the *a priori* variable selection) (Tredennick *et al.* 2021). We checked for multicollinearity, general model fit, and under/ overdispersion. For binomial GLMMs, we obtained odds ratios (OR) and 97.5% confidence intervals (for more details, see Chapter 2, §2.3 (Roatti *et al.* 2023a)). We then calculated the percentage change in odds per each unit variation in an independent variable as $(OR - 1) \times 100$ (Szumilas Magdalena 2010). For LMMs, estimates were described as increase/ decrease percentages over a dependent variable's range. In all cases, p -values ≤ 0.05 were considered significant (Chowdhury and Turin 2020).

Social network data are non-independent because the data are relational. Permuted data can be used to re-run a model to obtain a 'null' effect size against which the observed effect size (derived from the actual data) can be compared (Farine and Whitehead 2015). For the proximity data, in most cases, we permuted the datastream (Farine 2017). For the grooming data and the three P2c models from proximity data (see below), we applied node-based permutations (Lehmann *et al.* 2016) (for more details, see Chapter 2, §2.3 (Roatti *et al.* 2023a)). To determine the statistical significance of the estimated social network effect, we re-ran each model on the permuted matrices. For each model and each network

variable, the two-tailed p -value was calculated as the number of times that the observed effect size was larger or smaller than the distribution of effect sizes from the permuted data (resulting either as p -value = 0.05 or not significant) (Farine 2017).

3.3.4 Testing H1: Inheritance of maternal social networks

For hypothesis H1, we ran a total of four sets (applied to the different networks) of models across our three predictions. First, we quantified changes in the time immatures spend with the mother (P1a), using binomial GLMMs (Douma and Weedon 2019) in which the dependent variable was the proportion of time spent with the mother (MP1a). For proximity, we used the proportion of observations in which each immature was observed with the mother (within 10 m) in each observation period; for grooming, we used the proportion of observations in which each immature groomed with the mother, considering only the total grooming. Permutations were not run for these models because the dependent variables are not a social network value or metric.

We next tested whether there was a positive correlation between mothers' and immatures' social networks and how this changed depending on maternal features (P1b). To this end, we calculated the Pearson's correlation of the mothers' and offspring's ego-networks (i.e., the vectors that correspond to the square matrix rows of each immature individual and her/his mother) for each period (Ilany *et al.* 2021). We obtained qualitatively similar results using an alternative measure, the cosine similarity between the mothers' and immatures' vectors (Jarrett *et al.* 2018) (see Appendix 2, §2.1). For this analysis, we used the proportion matrix for grooming, representing the distribution of grooming to/from different partners, independent of the total number of events. Grooming partners'

availability may be constrained if immatures tend to spend time with their mothers (Albery *et al.* 2021). However, because the proportion of time spent in proximity to the mother had no significant effect and its addition reduced our dataset (see Appendix 1, §1.2), it was not included in the final models.

We next tested whether the fact that immatures' ego-networks are more similar to their mothers' ego-networks than to those of other group mates (as previously found in Chapter 2 (Roatti *et al.* 2023a)) changed depending on maternal features (P1c). We adopted three different approaches, all of which compared the Pearson's correlation coefficient (r) of the mother-immature dyad with combinations of other dyads from the proximity networks or grooming proportions networks. Two approaches are discussed here while the third one is presented in Appendix 2, §2.2. In the first approach, for each immature individual, we selected a random non-mother individual from the troop and created a new variable, assigning a score of '1' when the mother-immature's r was higher than the random-immature's r , and '0' when the reverse was true. We ran a binomial GLMM with the 1/0 score as the dependent variable (MP1c.1). In the second approach, we applied the same 1/0 scoring method and a binomial GLMM, using the mean r for all the non-mother individuals (MP1c.2).

3.3.5 Testing H2: Changes in social network characteristics

For hypothesis H2, we ran a further six sets of LMM models. Predictions P2a and P2b predicted changes in immatures' social integration measured through the troop-level network measures: strength (MP2a), eigenvector centrality (hereafter centrality) (MP2b.1), and betweenness centrality (hereafter betweenness) (MP2b.2). Strength represents an individual's relative association rate within a sampling period. Centrality characterises an individual's overall

social connectedness, with higher centrality indicating an individual with either a large number of partners or associating with individuals who have large numbers of partners (or both). Betweenness measures an individual's importance in connecting otherwise unconnected individuals (Farine and Whitehead 2015, Sosa *et al.* 2021). In these models, we included the corresponding network metric of the mother as a predictor. Grooming given, received, and total were computed for strength, while centrality and betweenness have only the total component. To make social network metrics comparable across networks of different sizes, the metrics were standardised within each sampling period by mean-centring them around zero with a standard deviation of one through the function *scale* (Wey *et al.* 2008).

To test P2c, that immatures' association with different partners changes depending on maternal features, we counted the number of immature, peer and same-sex partners each immature associated with (degree) (Farine and Whitehead 2015). A peer was defined as an individual whose age was ± 6 months of a focal individual's age. Association with peers reflects the preference for partners of similar age rather than a general attraction for immatures (≤ 5 years old). We ran binomial GLMMs with the proportion of immature (MP2c.1), peer (MP2c.2), and same-sex (MP2c.3) partners as dependent variables (Kulik *et al.* 2015). To test for a shift in social preferences based on the partners' phenotype (and not number), we ran node-based permutations for the proximity network, which keep the number of associations constant (Farine and Whitehead 2015).

Table 3.1: Summary of the models used to test the hypotheses' H1 and H2 predictions, including the type of test used, the dependent variable, the models' fixed factors (predictors and controls) and random factors, and the network involved. Under 'Model', '**' means that a permutation test was performed. The last column indicates whether each prediction was supported and, if not or only partially, how.

Hypothesis	Prediction	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Network	Support
H1: Immatures' inheritance of maternal social networks would depend on a mother's number of offspring and her dominance rank.	P1a: Immatures with more siblings will spend relatively more time in proximity but groom relatively less with their mothers.	MP1a	GLMM binomial (link 'logit').	Proportion of time with mother.	Mothers' nb. offspring and relative rank.	Immatures' age, sex, and age:sex interaction; troop.	Year, immatures' identities nested within their mothers' identities.	Proximity	Partial (mothers' nb. offspring not significant).
								Grooming	Total: Partial (mothers' relative rank not significant).
								Proximity	Yes
	P1b: The strength of the mother-offspring network correlation will increase both with a mother's number of offspring and her dominance rank.	MP1b*	LMM	Mother-offspring network correlation.				Grooming	Given: No (mothers' nb. offspring and relative rank not significant); Received: Yes; Total: Partial (mothers' relative rank not significant).
								Proximity	No (mothers' nb. offspring and relative rank not significant).
								Grooming	Given: No (mothers' nb. offspring and relative rank not significant); Received: Yes; Total: Partial (mothers' relative rank not significant).
	P1c: The fact that immatures' networks are more correlated to their mothers' networks than to those of other individuals will increase both with a mother's number of offspring and her dominance rank.	MP1c.1*	GLMM binomial (link 'logit')	0-1 score: '1' = correlation with mother's network > correlation with random individual's network; '0' = vice versa.				Proximity	No (mothers' nb. offspring and relative rank not significant).
								Grooming	Given: No (mothers' nb. offspring and relative rank not significant); Received: Yes; Total: Partial (mothers' relative rank not significant).
		MP1c.2*		0-1 score: '1' = correlation with mother's network > mean correlation with other individuals; '0' = vice versa.				Proximity	No (mothers' nb. offspring and relative rank not significant).
Grooming	Given: No (mothers' nb. offspring and relative rank not significant); Received: Yes; Total: Partial (mothers' relative rank not significant).								
H2: Immatures' social network	P2a: Immatures' associations with	MP2a*	LMM	Immatures' strength	Mothers' nb. offspring,		Proximity	Partial (mothers' relative rank not significant).	

Hypothesis	Prediction	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Network	Support
integration and the type of social partners with whom they associate would depend on a mother's number of offspring, her dominance rank, and her own network integration.	different social partners will increase or decrease with a mother's number of offspring; and increase with a mother's dominance rank and her own network integration.				relative rank, and network strength.			Grooming	Given: Partial (mothers' nb. offspring and relative rank not significant); Received: No (mothers' nb. offspring, relative rank, and strength not significant); Total: Partial (mothers' nb. offspring and relative rank not significant).
	P2b: Immatures' positions in the social network will increase or decrease with a mother's number of offspring; and increase with a mother's dominance rank and her own network integration.	MP2b.1*	LMM	Immatures' eigenvector centrality	Mothers' nb. offspring, relative rank, and network centrality.			Proximity	Partial (mothers' relative rank not significant).
		MP2b.2*	LMM	Immatures' betweenness centrality	Mothers' nb. offspring, relative rank, and network betweenness.			Grooming	Total: Partial (mothers' nb. offspring and relative rank not significant).
								Proximity	No (↓ with mothers' relative rank; mothers' nb. offspring and betweenness not significant).
		MP2c.1*	GLMM binomial (link 'logit').	Proportion of immature (≤ 5 years old) partners.	Mothers' nb. offspring and relative rank.			Grooming	Total: Partial (mothers' relative rank and betweenness not significant).
	Proximity							Partial (mothers' nb. offspring not significant).	
	MP2c.2*	Proportion of peer (± 6		Grooming				Given: No (mothers' nb. offspring and relative rank not significant); Received: Partial (mothers' relative rank not significant); Total: No (mothers' nb. offspring and relative rank not significant).	
								Proximity	No (mothers' nb. offspring and relative rank not significant).

Hypothesis	Prediction	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Network	Support
				months) partners.				Grooming	Given: No (mothers' nb. offspring and relative rank not significant); Received: No (mothers' nb. offspring and relative rank not significant); Total: No (mothers' nb. offspring and relative rank not significant).
								Proximity	Partial (mothers' nb. offspring not significant).
		MP2c.3*		Proportion of same-sex partners.				Grooming	Given: No (mothers' nb. offspring and relative rank not significant); Received: Partial (mothers' relative rank not significant); Total: Partial (mothers' relative rank not significant).

3.4 RESULTS

We collected a total of 12,592 proximity records and 19,597 grooming records. The number of immature individuals followed (i.e., sample size) were 109 to 116 for the proximity network and 93 to 142 for the grooming network, born from 32 to 43 mothers (Roatti *et al.* 2023b) (for more details, see Chapter 2, §2.4 (Roatti *et al.* 2023a)). In the following sections, we present the results (following each prediction) on our main variables of interest: a mother's number of offspring in the troop, her relative dominance rank, and (for MP2a and MP2b) her social network integration (Tables 3.2 and 3.3; Figures 3.1–3.7). The number of observations and the sample size of each model, the full results' tables (including all independent variables), and the within-models variables' comparison through standardised estimates are reported in Appendix 1.

3.4.1 Results H1: Inheritance of maternal social networks

To address hypothesis H1, we tested how the time spent with the mother (P1a) and the correlation between the offspring's and mothers' social networks (P1b and P1c) changed depending on maternal features. Our P1a prediction – that immatures with more siblings will spend more time in proximity but less grooming with their mothers and that higher-ranking immatures will spend more time both in proximity and grooming with their mothers – was partially supported (Table 3.1). In general, maternal features positively affected the immatures' odds of being in proximity to their mothers, while they had a negative effect on the odds of grooming (total) with them. For the proximity network, only a mother's relative rank was significant: a rise in one position in relative rank caused an increase of 59.48% in the odds of being in proximity with the mother. For the grooming

network, only a mother's number of offspring was significant: the addition of one sibling produced a decrease of 19.56% in the odds of grooming with the mother (Table 3.2 and Figure 3.1).

Our P1b prediction – that the strength of the mother-offspring network correlation will increase both with a mother's number of offspring and her dominance rank – had variable support (Table 3.1). In general, immatures who had more siblings and a higher rank had networks relatively more similar to those of their mothers. For the proximity network, both a mother's number of offspring and her relative rank were significant. The addition of one sibling and the increase in one rank position produced, respectively, an increase of 1.26% and 13.46% in the mother-offspring network correlation. For the grooming network, the number of offspring had a significant effect on grooming received and total: the addition of one sibling produced an increase of 4.53% and 1.64% in the mother-offspring network correlation (received and total, respectively). Relative rank had a significant effect only on grooming received: a rise in one position of relative rank caused an increase of 9.36% in the mother-offspring network correlation (Table 3.2 and Figure 3.2). Maternal features had no significant effects on the mother-offspring network correlation for grooming given.

Our P1c prediction – that the fact that immatures' networks are more correlated to their mothers' networks than to those of other individuals will increase both with a mother's number of offspring and her dominance rank – had variable support (Table 3.1). In general, immatures who had more siblings and a higher rank resembled relatively more their mothers' networks than those of other individuals. Maternal features had no significant effect in MP1c.1 and MP1c.2 for the proximity network. For the grooming network, the number of offspring had a significant effect on grooming received and total: the addition of one sibling

caused an increase between (hereafter range of values) 31.49–64.71% (MP1c.2 total and received, respectively) in the odds that the immatures' networks were relatively more correlated to their mothers'. Relative rank had a significant effect only on grooming received: an increase in one position of relative rank produced an increase of 138.48% (MP1c.1) and 90.01% (MP1c.2) in the odds that the immatures' networks were relatively more correlated to their mothers' (Table 3.2, Figures 3.3 and 3.4). Maternal features had no significant effect in MP1c.1 and MP1c.2 for grooming given.

Table 3.2: Results on a mother's number (Nb.) of offspring and relative rank for the hypothesis **H1 models** (see Appendix 1, §5 for tables with all the independent variables), for the proximity and grooming (Groom.) networks. The estimate, standard (Std.) error, *p*-value ('NS' = not significant), and conditional (delta) R² are reported for each variable/ model. The significant (*p*-value ≤ 0.05) models/ variables are highlighted (grey).

Model	Variable	Estimate	Std. Error	<i>p</i> -value	R ²
P1a Proximity	Nb. offspring	0.03	0.0498	NS	0.27
	Relative rank	0.4667	0.2129	< 0.05	
P1a Groom. Total	Nb. offspring	-0.2177	0.0452	< 0.001	0.84
	Relative rank	-0.0057	0.2284	NS	
P1b Proximity	Nb. offspring	0.0179	0.0121	0.05	0.20
	Relative rank	0.1911	0.0476	0.05	
P1b Groom. Given	Nb. offspring	0.0025	0.0112	NS	0.25
	Relative rank	-0.0337	0.0466	NS	
P1b Groom. Received	Nb. offspring	0.0557	0.0172	0.05	0.44
	Relative rank	0.1151	0.0786	0.05	
P1b Groom. Total	Nb. offspring	0.0207	0.0121	0.05	0.28
	Relative rank	0.0225	0.0554	NS	
P1c.1 Proximity	Nb. offspring	-0.0427	0.0791	NS	0.03
	Relative rank	0.7873	0.3135	NS	
P1c.1 Groom. Given	Nb. offspring	0.0664	0.0781	NS	0.08
	Relative rank	0.2714	0.2952	NS	
P1c.1 Groom. Received	Nb. offspring	0.3278	0.1035	0.05	0.13
	Relative rank	0.8691	0.4383	0.05	
P1c.1 Groom. Total	Nb. offspring	0.3399	0.0842	0.05	0.17
	Relative rank	0.0217	0.3497	NS	
P1c.2 Proximity	Nb. offspring	0.1617	0.085	NS	0.08
	Relative rank	1.1377	0.341	NS	
P1c.2 Groom. Given	Nb. offspring	0.1519	0.1016	NS	0.19
	Relative rank	0.5948	0.409	NS	
P1c.2 Groom. Received	Nb. offspring	0.499	0.1434	0.05	0.25
	Relative rank	0.6419	0.5136	0.05	
P1c.2 Groom. Total	Nb. offspring	0.2737	0.0901	0.05	0.24
	Relative rank	0.3147	0.3604	NS	

Figure 3.1: Changes in the immatures' odds of being with the mother (**MP1a**) with a mother's relative rank (proximity) and number (Nb.) of offspring (grooming – Groom. – total). Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.

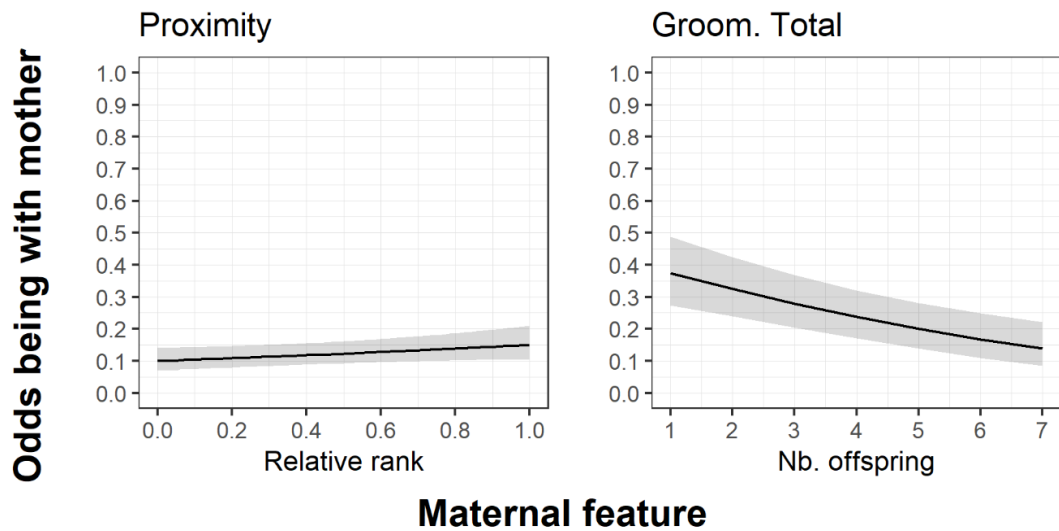


Figure 3.2: Changes in the mother-offspring social network correlation (**MP1b**) with a mother's number (Nb.) of offspring (1st row) and relative rank (2nd row) for the proximity and grooming (Groom.) networks. Ribbons represent 97.5% confidence intervals.

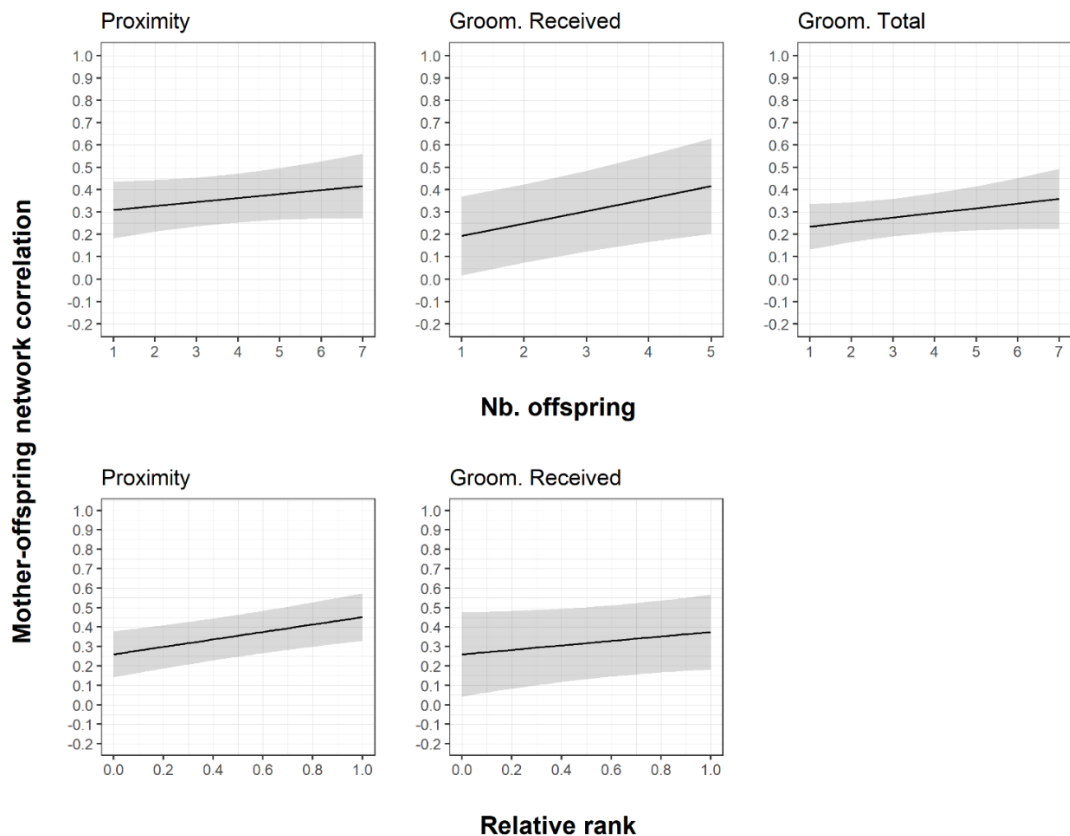


Figure 3.3: Changes in the odds that the mother-offspring social network correlation was higher than the correlation with a random individual's network (**MP1c.1**) and the mean correlation with other individuals' networks (**MP1c.2**). These changes are related to a mother's number (Nb.) of offspring for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.

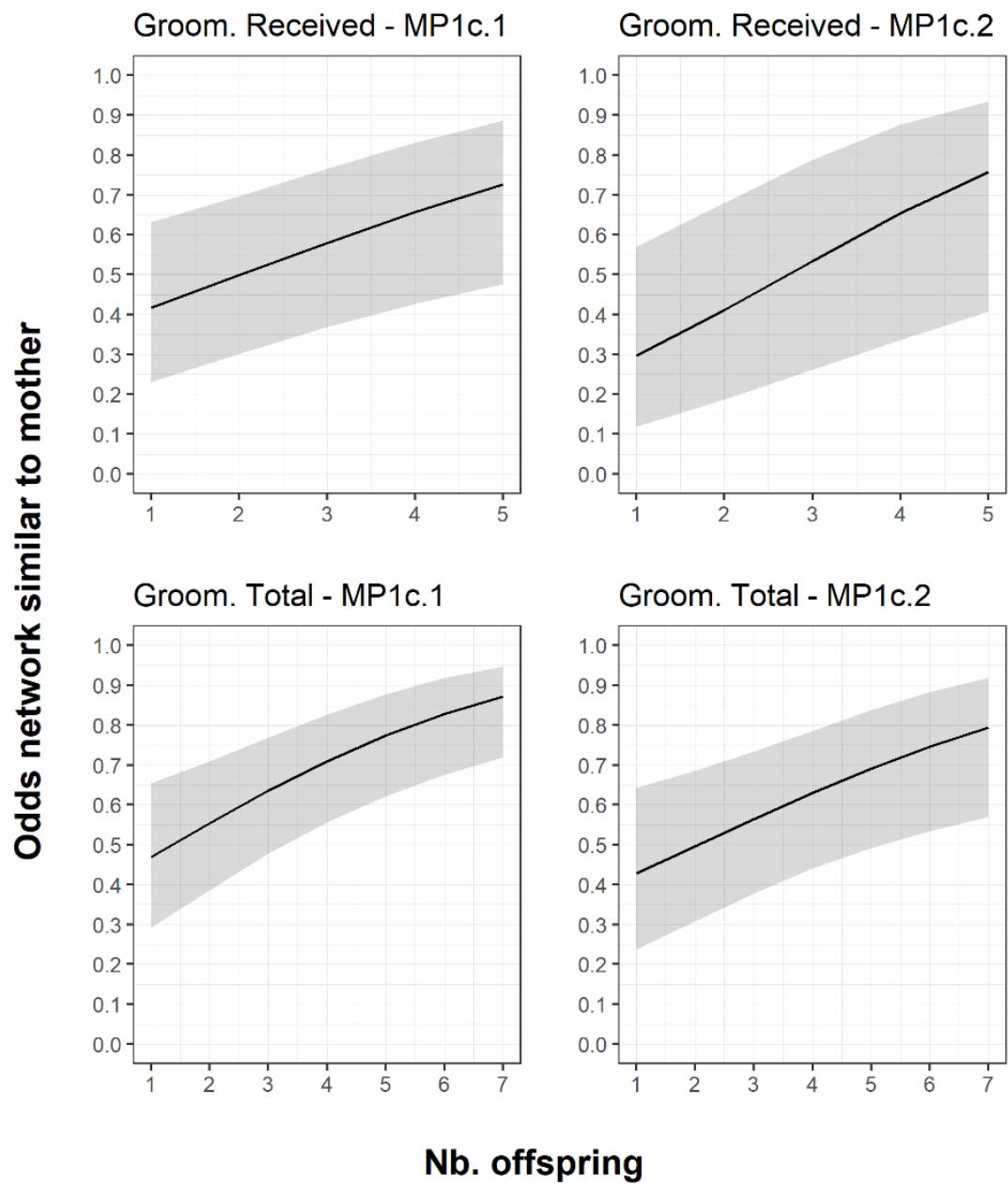
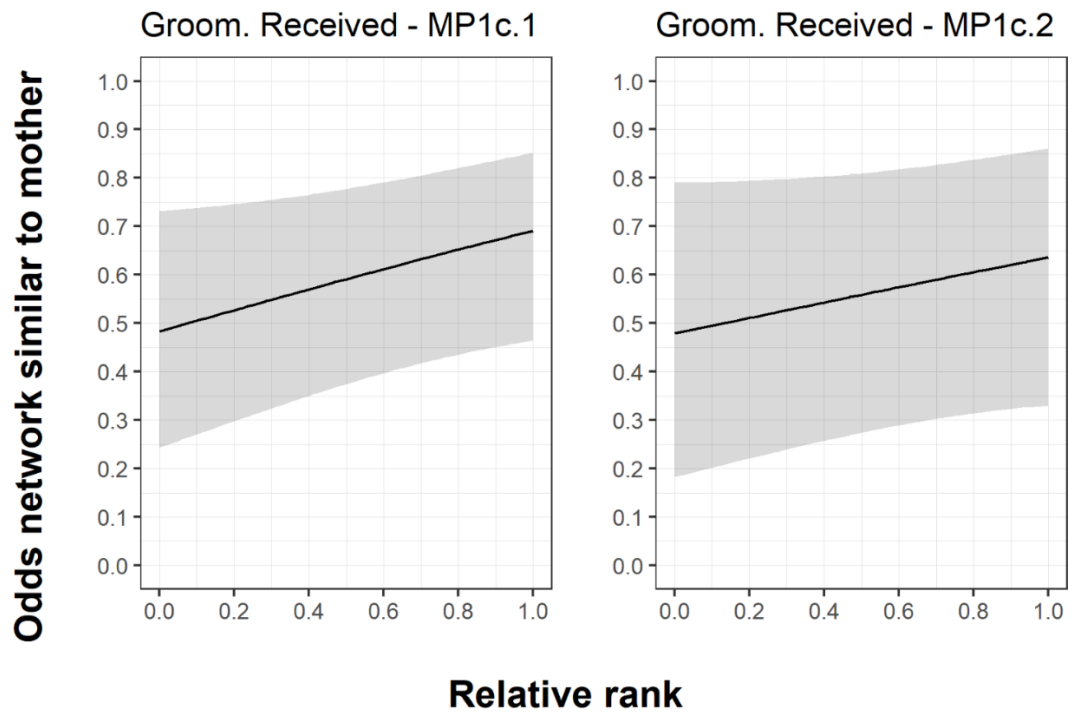


Figure 3.4: Changes in the odds that the mother-offspring social network correlation was higher than the correlation with a random individual's network (**MP1c.1**) and the mean correlation with other individuals' networks (**MP1c.2**). These changes are related to a mother's relative rank for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y -axis variable) to occur. Ribbons represent 97.5% confidence intervals.



3.4.2 Results H2: Changes in social network characteristics

To address our second hypothesis, we explored how immatures' integration in the troop's network (relative association rates with different social partners – P2a – and overall network position – P2b) changed depending on maternal features and modelled shifts in social partner preferences (P2c). Our P2a and P2b predictions – that immatures' network integration will increase or decrease with a mother's number of siblings, and it will increase with a mother's dominance rank and her own network integration – received mixed support (Table 3.1). In general, immatures who had more siblings and whose mothers were more integrated in the network had a relatively higher social network strength (MP2a), centrality (MP2b.1), and betweenness (MP2b.2). However, there was no support for the predicted (positive) effect of a mother's relative rank, while rank had a significant negative effect in one case. For the proximity network, a mother's number of offspring, and her social network strength and centrality were significant. The addition of one sibling caused an increase in immatures' strength and centrality of 1.19% and 0.83%, respectively; an increase of one unit in a mother's proximity strength and centrality brought an increase of 3.60% and 5.26%, respectively, in the immatures' correspondent metrics. On the other hand, a rise in one position of relative rank produced a decrease of 2.49% in proximity betweenness. Maternal features had no significant effects on immatures' proximity betweenness. For the grooming network, the number of offspring was significant only in one case: the addition of one sibling caused an increase in betweenness (total) of 1.56%. The effect of a mother's grooming network integration was significant in most models (five out of eight): the increase in one unit of a mother's network metric produced an increase between 1.13–6.91% (strength given and centrality total, respectively) in the immatures' correspondent

network metrics (Table 3.3, Figures 3.5 and 3.6). Maternal features had no significant effects on immatures' strength for grooming received.

Our P2c prediction – that the association with other immature (MP2c.1), peer (MP2c.2) and same-sex (MP2c.3) partners will increase or decrease with a mother's number of offspring, and it will increase with a mother's dominance rank – had partial support (Table 3.1). In general, immatures who had more siblings and a higher rank associated relatively more with partners of similar age and the same sex. For the proximity network, a mother's relative rank had a significant effect on immatures' association with other immature and same-sex partners: a rise in one position of relative rank caused an increase of 8.79% and 9.12% in the odds of being in proximity to an immature and a same-sex partner, respectively. For the grooming network, a mother's number of offspring had a significant effect in the same cases: the addition of one sibling produced an increase between 4.50–6.70% (MP2c.3 total and received, respectively) in the odds of grooming with an immature or a same-sex partner (Table 3.3 and Figure 3.7). Maternal features had no significant effects on immatures' odds of being in proximity and grooming (all components) with peer partners, with immature partners for grooming given and total, and with same-sex partners for grooming given.

Table 3.3: Results on a mother's number (Nb.) of offspring, relative rank, and social network integration (measured through strength, centrality, and betweenness) for the hypothesis **H2 models** (see Appendix 1, §5 for tables with all the independent variables), for the proximity and grooming (Groom.) networks. The estimate, standard (Std.) error, *p*-value ('NS' = not significant), and conditional (delta) R^2 are reported for each variable/ model. The significant (*p*-value ≤ 0.05) models/ variables are marked in bold.

Model	Variable	Estimate	Std. Error	<i>p</i> -value	R^2
P2a Proximity	Nb. offspring	0.0627	0.0385	0.05	0.41
	Relative rank	0.3433	0.161	NS	
	Strength mother	0.189	0.0387	0.05	
P2a Groom. Given	Nb. offspring	0.0464	0.0224	NS	0.72
	Relative rank	0.0634	0.0909	NS	
	Strength mother	0.0494	0.0472	0.05	
P2a Groom. Received	Nb. offspring	0.0136	0.0244	NS	0.4
	Relative rank	0.0804	0.106	NS	
	Strength mother	-0.0369	0.0211	NS	
P2a Groom. Total	Nb. offspring	0.0504	0.0228	NS	0.64
	Relative rank	-0.0383	0.0987	NS	
	Strength mother	0.1142	0.0238	0.05	
P2b.1 Proximity	Nb. offspring	0.0481	0.0365	0.05	0.49
	Relative rank	0.2511	0.1529	NS	
	Centrality mother	0.3044	0.0346	0.05	
P2b.1 Groom. Total	Nb. offspring	0.0301	0.025	NS	0.49
	Relative rank	0.1654	0.1064	NS	
	Centrality mother	0.4283	0.0262	0.05	
P2b.2 Proximity	Nb. offspring	-0.0198	0.0406	NS	0.07
	Relative rank	-0.136	0.1694	0.05	
	Betweenness mother	0.1262	0.0468	NS	
P2b.2 Groom. Total	Nb. offspring	0.0656	0.0251	0.05	0.52
	Relative rank	0.121	0.0959	NS	
	Betweenness mother	-0.0228	0.0354	NS	
P2c.1 Proximity	Nb. offspring	0.0025	0.0115	NS	0.14
	Relative rank	0.0843	0.0443	0.05	
P2c.1 Groom. Given	Nb. offspring	0.008	0.0407	NS	0.64
	Relative rank	0.1236	0.1643	NS	
P2c.1 Groom. Received	Nb. offspring	0.0547	0.0339	0.05	0.36
	Relative rank	0.0607	0.141	NS	
P2c.1 Groom. Total	Nb. offspring	0.0243	0.0287	NS	0.56
	Relative rank	0.0726	0.1182	NS	
P2c.2 Proximity	Nb. offspring	-0.0059	0.0221	NS	0.01
	Relative rank	0.0531	0.0886	NS	
P2c.2 Groom. Given	Nb. offspring	-0.0315	0.0571	NS	0.31
	Relative rank	0.0897	0.2273	NS	
P2c.2 Groom. Received	Nb. offspring	0.0357	0.0551	NS	0.23
	Relative rank	0.0478	0.2121	NS	
P2c.2 Groom. Total	Nb. offspring	0.0142	0.0447	NS	0.33
	Relative rank	0.0507	0.1748	NS	
P2c.3 Proximity	Nb. offspring	0.0022	0.0109	NS	0.18
	Relative rank	0.0872	0.0422	0.05	

Model	Variable	Estimate	Std. Error	p-value	R ²
P2c.3 Groom. Given	Nb. offspring	0.0291	0.0407	NS	0.7
	Relative rank	0.1874	0.1697	NS	
P2c.3 Groom. Received	Nb. offspring	0.0649	0.0303	0.05	0.57
	Relative rank	0.1066	0.1174	NS	
P2c.3 Groom. Total	Nb. offspring	0.044	0.0271	0.05	0.72
	Relative rank	0.1433	0.1068	NS	

Figure 3.5: Changes in immatures' social network strength (**MP2a**), centrality (**MP2b.1**), and betweenness (**MP2b.2**) with a mother's number (Nb.) of offspring (1st row) and relative rank (2nd row) for the proximity and grooming (Groom.) network. Ribbons represent 97.5% confidence intervals.

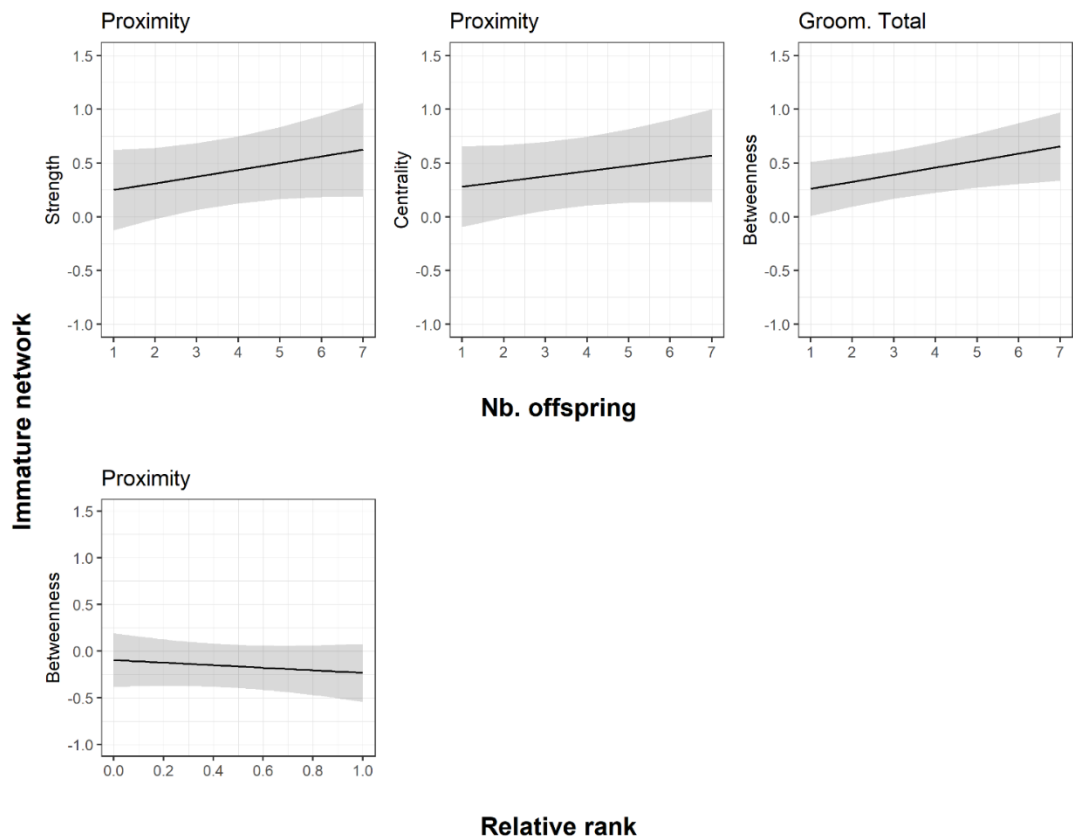


Figure 3.6: Changes in immatures' social network strength (**MP2a**) and centrality (**MP2b.1**) with a mother's own network strength (1st row) and centrality (2nd row) for the proximity and grooming (Groom.) network. Ribbons represent 97.5% confidence intervals.

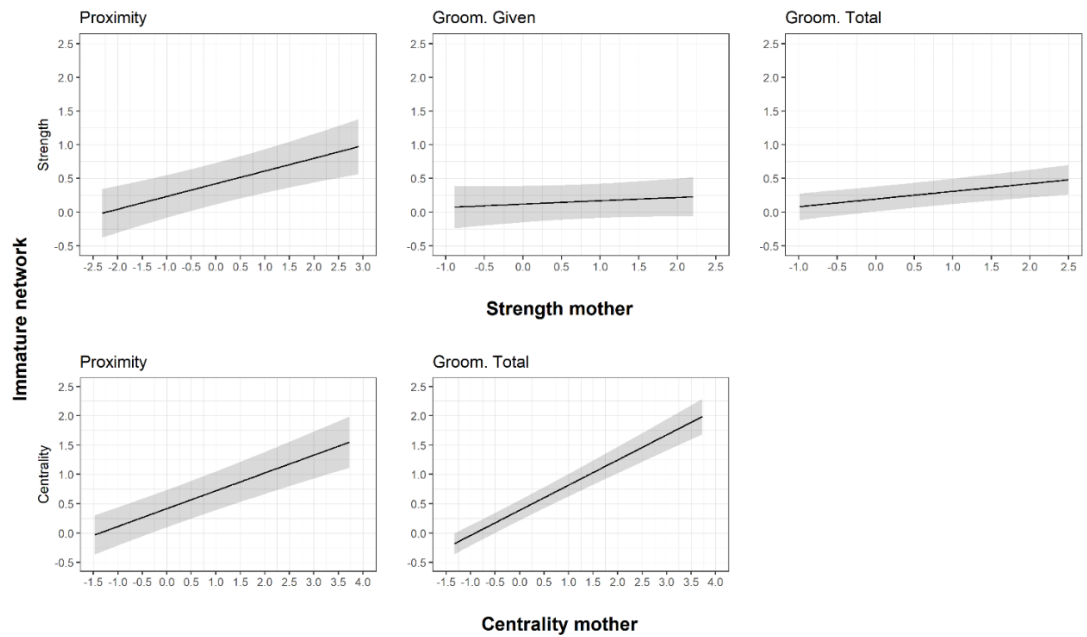
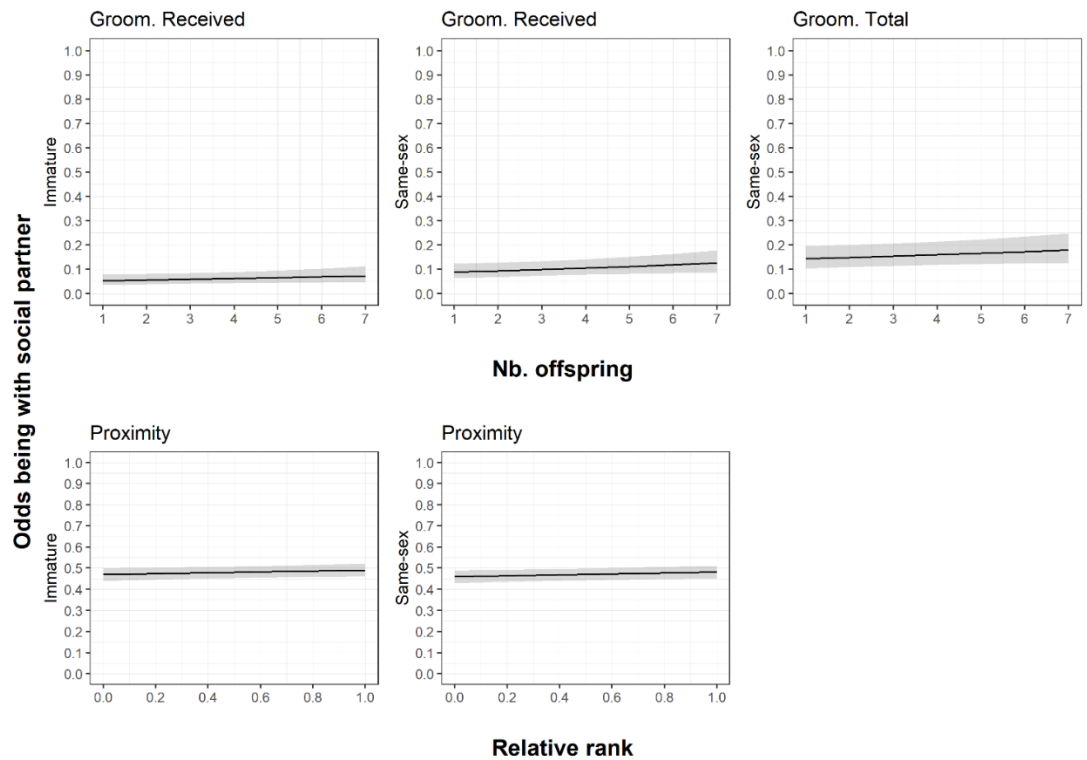


Figure 3.7: Changes in the immatures' odds of being with a particular social partner (another immature, **MP2c.1**; a same-sex individual, **MP2c.3**) with a mother's number (Nb.) of offspring (1st row) and relative rank (2nd row) for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.



3.5 DISCUSSION

In this chapter, we explored how the development of wild chacma baboon social networks during the immature period is influenced by maternal social features. We focused on the effects of a mother's number of offspring in the group, her dominance rank, and her social network integration. Here, we first discuss the effects of maternal features on the inheritance of maternal networks (hypothesis H1) and on the changes in the immatures' network integration and social partners' characteristics (hypothesis H2). We then highlight the potential implications of maternal influences on sociality for social information transmission at the group level.

3.5.1 Matriline size

A mother's number of offspring in the group had generally larger effects than her dominance rank, and the immatures' age and sex on the inheritance of maternal grooming networks (see Appendix 1, §1.6). As predicted, immatures with more siblings inherited their mothers' proximity and grooming networks more than those with fewer siblings. Because of the attraction towards close maternal kin (Silk 2009) (also found in our population (Paisley *et al.* In preparation)), the more matriline members are available in a group, the more they tend to associate together. In addition, they may form indirect connections with each other's non-maternal kin partners (see below). Close maternal kin tend to spend time with each other in matrilineal Cercopithecine monkeys (chacma (Silk *et al.* 2010a) and yellow baboons (Silk, Alberts, *et al.* 2006, Silk, Altmann, *et al.* 2006), Japanese (Nakamichi and Shizawa 2003) and rhesus (Kapsalis and Berman 1996a) macaques), African elephants (Archie *et al.* 2006), and spotted hyenas

(Holekamp *et al.* 1997). Relatedness through both maternal and paternal kin also predicts the fission-fusion dynamics of female-calf groups in Indo-Pacific bottlenose dolphins (*T. aduncus*) (Möller *et al.* 2006) and sperm whales (Gero *et al.* 2008). In some cases, individuals specifically prefer maternal kin over paternal kin (mandrills *Mandrillus sphinx* (Charpentier *et al.* 2012), white-faced capuchins (Perry *et al.* 2008), rhesus macaques (Widdig *et al.* 2001)). Individuals may also bond with maternal relatives when the species' dispersal patterns constrain their availability (hamadryas baboons *P. hamadryas* (Städele *et al.* 2016), eastern chimpanzees (Langergraber *et al.* 2009)).

The association among close maternal kin may be explained by nepotism independently from the attraction between individuals of similar dominance rank (Kapsalis and Berman 1996b, Silk *et al.* 1999). Nepotistic cooperation generally occurs among closely related individuals (i.e., mother-offspring and siblings dyads) and may be advantageous because of kin selection (i.e., an individual indirectly increases her/his fitness by helping another individual sharing the same genes), kin-biased mutualism (i.e., selfish mutual interactions), and kin-biased reciprocal altruism (i.e., altruistic reciprocal interactions) (Chapais 2001, Silk 2009, Holekamp and Sawdy 2019). Cooperation among maternal kin can occur in different contexts. Maternal relatives may form coalitions during dominance interactions with non-kin (spotted hyenas (Holekamp *et al.* 2007), chacma (Wittig, Crockford, Seyfarth, *et al.* 2007) and yellow (Silk *et al.* 2004) baboons, Japanese macaques (Chapais *et al.* 1997)). This may be particularly important for immature individuals, who inherit their mothers' ranks through kin support in agonistic encounters (spotted hyenas (East *et al.* 2009), yellow (Pereira 1989) and chacma (Cheney 1977) baboons, Japanese macaques (Kutsukake 2000)). In addition, maternal kin may benefit from the communal defence of food resources and/or

mutual tolerance during foraging (Japanese macaques (Chapais and Belisle 2001), spotted hyenas (Mills 1985)), and allomaternal care (sperm whales (Gero *et al.* 2013), grey mouse lemurs *Microcebus murinus* (Eberle and Kappeler 2006), vervet monkeys (Fairbanks 1990), African elephants (Lee 1987b)).

Despite matching their mothers' networks more closely, immatures with more siblings groomed relatively less with their mothers. Within a matriline, siblings may compete for maternal care and attention (Bateson 1994). Even in species that generally give birth to one infant at a time (Trillmich 1990, Jones 2011), young offspring may need to share maternal care with a sibling (Altmann 1980, Trillmich and Wolf 2008). In primates, this may include competing for grooming with the mother since grooming has an important social bonding function (Dunbar 1991) and the mother-offspring bond enhances the offspring's health and survival beyond weaning (Nakamura *et al.* 2014, Stanton *et al.* 2020). The birth of a younger sibling may increase the stress levels of the older offspring (chacma baboons (Delaunay *et al.* 2023), bonobos (Behringer *et al.* 2022)) and drive down the relative time spent with their mothers (Japanese (Schino and Troisi 2001) and rhesus (Devinney *et al.* 2001) macaques). Mothers may reduce care towards her older offspring passively and/or actively directing aggression towards them (Galápagos fur seals *Arctocephalus galapagoensis* and sea lions *Zalophus wolfebaeki* (Trillmich and Wolf 2008), Japanese (Kutsukake 2000) and rhesus (Devinney *et al.* 2001) macaques). Alternatively, or concurrently, siblings may compete with each other through agonistic interactions (Galápagos fur seals and sea lions (Trillmich and Wolf 2008), vervet monkeys (Lee 1987a)) and/or interference of each other's grooming with the mother (as reported in mandrills (Schino and Lasio 2018) and in our population (Delaunay *et al.* In preparation)).

We further found that immatures with more siblings had a relatively higher proximity and grooming network integration and a stronger preference to groom with same-sex immature partners. The first results confirm one of our two alternative predictions. Because matriline members in our population reached a maximum of six with a mean of three (see Appendix 2, §2.3), the degree of matrilineal social clustering may be relatively low. Instead, indirect bonds with their siblings' partners enhanced immatures' own social connections. Indirect connections are at the base of many social processes in wild groups (Brent 2015). For example, individuals' knowledge of simultaneous third-party rank and kin relationships (i.e., an individual recognizes the relationship existing between two others) allows them to form alliances (chacma baboons (Wittig, Crockford, Seyfarth, *et al.* 2007), spotted hyenas (Holekamp *et al.* 2007)) and reconcile with their friends' opponents (western chimpanzees (Wittig and Boesch 2010), chacma baboons (Wittig, Crockford, Wikberg, *et al.* 2007)). Second, because social centrality may provide more social bonding opportunities (Farine and Whitehead 2015, Sosa *et al.* 2021), immatures with more siblings may bond with partners of similar age and the same sex relatively more easily, which may be advantageous both for females (i.e., forming potentially life-long bonds (Silk *et al.* 2010b)) and males (e.g., dispersing together (Widdig *et al.* 2016)). For instance, adult female chacma baboon prefer to associate with similarly aged females independently from their relatedness (Silk *et al.* 2010a).

3.5.2 Maternal dominance rank

A mother's dominance rank (inherited by both female and male offspring (Holekamp and Smale 1991); see Appendix 2, §2.4) had generally stronger effects than immatures' age and sex on the inheritance of maternal networks, and

overall larger effects than a mother's number of offspring on the proximity networks (see Appendix 1, §1.6). As predicted, higher-ranking immatures spent more time in proximity with their mothers (confirming previous results on this population (Delaunay *et al.* 2023)) and they inherited their mothers' proximity and grooming networks more than lower-ranking immatures. This may derive from dominant immatures' relatively greater advantages of associating with close maternal kin. Although higher-ranking matriline are not larger than lower-ranking ones (Cheney *et al.* 2004) (see Appendix 2, §2.3), they may be relatively more cohesive (as in Japanese macaques (Koyama 2003)). Dominant kin's ability to recruit agonistic support from matriline ranking in-between the two opponents (Pereira 1989, Holekamp *et al.* 1997) ensures the maintenance of the hierarchical order (Hausfater *et al.* 1982, Samuels *et al.* 1987) and thus the benefits associated with having a high rank (Majolo *et al.* 2012). Higher-ranking immatures may thus benefit relatively more from the vicinity of dominant kin who can effectively protect them when their rank is not yet well established (Holekamp and Smale 1991). In addition, the presence of high ranking maternal kin may allow immatures to access better food resources (capuchins (Coelho *et al.* 2015), spotted hyenas (Mills 1985)), providing at the same time foraging and social learning (e.g., about food type and processing) opportunities (Ottoni and Izar 2008, Whiten and van de Waal 2018). Lower-ranking baboons may instead need to bond with maternally unrelated dominant individuals to gain the same advantages (Sick *et al.* 2014, Marshall *et al.* 2015): juveniles associating with an adult male receive agonistic support (Buchan *et al.* 2003, Moscovice *et al.* 2009) and forage in relatively higher quality patches (Huchard *et al.* 2013) independently from their maternal rank.

We then found that, contrary to our prediction, higher-ranking immatures had a relatively lower proximity network integration in one model, while the other positive rank effects were not significant: higher-ranking immatures were relatively less able to connect different social clusters. These patterns may result from age differences in network structure. Dominant adult baboons in our population have a higher network integration (King, Clark, *et al.* 2011), perhaps because subordinates affiliate with them in order to gain tolerance benefits (Sick *et al.* 2014, Marshall *et al.* 2015). However, because immatures' relative association with different social partners and social network position change throughout development, the strong effect of age may overcome that of dominance rank in determining network integration (Roatti *et al.* 2023a) (see Appendix 1, §1.6). Because, as mentioned, higher-ranking females are relatively more socially central (vervet monkeys (Canteloup, Puga-Gonzalez, *et al.* 2021), spotted hyenas (Smith *et al.* 2007), chacma baboons (Barrett *et al.* 1999)) and adults' affiliation network integration (e.g., grooming) is higher than immatures' (chacma baboons (Roatti *et al.* 2023a); see below), a dominant mother's betweenness will diminish her offspring's own betweenness if she is preferred as a social partner over her offspring. For example, because immatures dedicate more time to play and less to grooming than adults (capuchins (de Lima and Ferreira 2021), Japanese macaques (Shimada and Sueur 2017), eastern chimpanzees (Shimada and Sueur 2014)) and individuals tend to choose partners who reciprocate grooming equitably (Silk *et al.* 2010a, 2010b), immatures may both give and receive less grooming than adults (Roatti *et al.* 2023a). Given that mothers and offspring partly share the same social bonds (de Waal 1996, Roatti *et al.* 2023a), and that only one connection is necessary to bridge over two poorly connected groups (Sosa *et al.* 2021), the more a dominant

mother connects different groups, the fewer opportunities may be left to her offspring to do the same.

As predicted, we also found that higher-ranking immatures had a relatively stronger preference to be in proximity to same-sex immature partners. Greater social integration and competitive abilities may facilitate bonding with partners of similar age and the same sex, with whom to form long-lasting bonds (Silk *et al.* 2010b) (see above). Although dominant immatures were not more integrated than subordinate ones in the proximity and grooming networks (see above), they could be relatively more central in the play network (Tibetan (Liu *et al.* 2022) and rhesus (Wooddell *et al.* 2020) macaques), where partners generally match each other in age and sex (chacma (Cheney 1978a) and olive (Owens 1975) baboons). In addition, dominant individuals can monopolize resources, such as food and social partners (Majolo *et al.* 2012). In this population, dominant adult baboons lead group foraging decisions (King *et al.* 2008), are more central in foraging networks (King, Clark, *et al.* 2011), feed in higher-quality foraging patches (Huchard *et al.* 2013), and exploit ephemeral high-quality foods (Marshall *et al.* 2015, Carter, Torrents Ticó, *et al.* 2016) more than subordinate ones. Dominance rank also positively affects adult female competition for male ‘friends’, who can provide protection and care to their offspring (Huchard and Cowlshaw 2011, Baniel *et al.* 2018a, 2018b). Similarly, higher-ranking immature individuals may be more likely to win a between-peers competition (eastern chimpanzees (Markham *et al.* 2015), Japanese macaques (Chapais 1988)) for the same partners, perhaps because they receive more agonistic support (Pereira 1989) (see above) and less threats (Barbary macaques (Prud’Homme and Chapais 1993), vervet monkeys (Horrocks and Hunte 1983)) than lower-ranking peers.

3.5.3 Maternal social integration

A mother's social network integration had often the strongest influence on her offspring's integration (see Appendix 1, §1.6) independently from her matriline size and dominance rank. As predicted, immatures born from mothers with a higher social integration were relatively more socially central themselves. Young immatures' social environment may be shaped by temporary changes in mothers' integration and differ depending on between-mother variations in sociability. First, because primates tend to be attracted to others' infants (Dunayer and Berman 2018), the social centrality of new mothers may increase owing to others' attempts to interact with their infants (olive (Frank and Silk 2009) and chacma (Silk, Rendall, *et al.* 2003) baboons, Bonnet macaques *M. radiata* (Silk 1999)). Mothers may also form 'friendships' with the putative father of their infants, which can last throughout lactation and ensure paternal care for their offspring (chacma (Baniel *et al.* 2016) and yellow (Nguyen *et al.* 2009) baboons). These female-male bonds may connect mothers with offspring of similar age independently from females' relatedness (baboons (Altmann 1980, Silk *et al.* 2017)). Second, a mother's social integration may reflect her personality (Krause *et al.* 2010), i.e., consistent and repeatable individual-level behaviour (Sih *et al.* 2004). Within-individual network positions tend to be stable through time and different contexts (common bottlenose dolphins *T. truncatus* (Díaz López 2020), vervet monkeys (Blaszczyk 2018), great tits (Aplin, Farine, *et al.* 2013)), indicating that individuals' sociability determines their social connectedness relative to between-individual variations in network structure due to, e.g., demographic processes (Shizuka and Johnson 2020) (see Appendix 1, §1.7).

Mothers may affect their offspring's social integration by providing social bonding opportunities, which could affect the offspring's long-term sociability,

and/or transmitting their social tendencies genetically (Brent 2015, Maestriperi 2018). Social exposure due to maternal social connections may affect infants in particular, who spend more time with their mothers than juveniles (chacma (Roatti *et al.* 2023a) and yellow (Altmann 1980) baboons). For example, infants may form long-lasting bonds with the similarly aged offspring of their mothers' partners (Altmann 1980) (see above). Early social experiences may have long-lasting effects. For instance, the amount of time a mother Stuhlmann's blue monkey spent grooming with other females during her offspring's infancy determined the same offspring's propensity to play with peers during juvenescence (Thompson and Cords 2020). Finally, social tendencies may be heritable: in yellow and yellow-olive baboons the age at first grooming is predicted by heritable genetic variation in both sexes (Lange *et al.* 2023). These effects could partially depend on mothers and offspring sharing social bonds (Ilany *et al.* 2021, Roatti *et al.* 2023a). However, the fact that both a mother's proximity and grooming networks integration positively influenced their offspring's respective network integrations suggests that offspring's social connectedness is not just a by-product of being close to the mother (Albery *et al.* 2021). Indeed, grooming partner choice may be independent from their proximity (Lehmann and Ross 2011, Castles *et al.* 2014) and the time spent in proximity to the mother did not affect the inheritance of grooming networks in this population (see Appendix 1, §1.2).

3.5.4 Implications for social information transmission

Maternal influences on sociality may have important implications for group-level social information transmission, and thus the emergence of culture and between-groups fitness differences (Marcoux *et al.* 2007, Whiten 2017). In particular, supporting our previous considerations on the effects of immatures'

age and sex (Roatti *et al.* 2023a), we suggest that, in female-philopatric societies, social clustering within matrilineal and same-sex immature subgroups may constrain information flow (van de Waal *et al.* 2012, Pasquaretta *et al.* 2014). In matrilineal societies, immatures may acquire information more from within their matrilineal than outside them (vervet monkeys (van de Waal *et al.* 2012), Japanese macaques (Tanaka 1995, 1998)). This can lead to the formation of matrilineal 'cultures' (van de Waal *et al.* 2012) as opposed to group cultures (Laland and Janik 2006). In addition, same-sex immature social clusters may separate the individuals who tend to acquire information – immatures and females (Carter *et al.* 2014, Canteloup, Cera, *et al.* 2021) – from those who tend to produce it – adults and males (Reader and Laland 2001, Amici, Widdig, *et al.* 2019), potentially limiting social information spread within a group (Carter *et al.* 2015).

Matriline size may constrain information transmission because immatures from larger matrilineal groups tended to groom relatively more with close maternal kin and with same-sex immature partners. However, these aspects may not strongly limit information flow because members of larger matrilineal groups were relatively more socially central and thus could benefit from greater opportunities to learn socially (Carter, Torrents Ticó, *et al.* 2016, van Boekholt *et al.* 2021). In addition, dominance rank may affect information transmission because members of higher-ranking matrilineal groups tended to associate relatively more with close maternal kin and other same-sex immatures. These matriline size and dominance rank influences could be modulated by a mother's social integration, which had a strong independent influence on immatures' social connectedness. Although these considerations remain speculative, they may inform future studies investigating from whom immatures acquire information and ultimately testing

how social connections and learning preferences affect behaviours' transmission in wild groups (Pasquaretta *et al.* 2014, Whiten and van de Waal 2018).

4 CHAPTER 4: THE DEVELOPMENT OF SOCIAL LEARNING IN WILD IMMATURE BABOONS

4.1 ABSTRACT

Immature individuals may have an important role in group-level information transmission because they learn socially more than adults. However, little is known about social learning during development, particularly in non-tool using species. Our aim was to determine how immatures' social learning behaviours changed with age and differed between the sexes, and to whom immatures directed more learning behaviours. We collected longitudinal and cross-sectional behavioural data on 53 immature wild chacma baboons (*Papio ursinus*) across two years, recording in focal observations all behaviours associated with social learning. We found that immatures concentrated social learning behaviours before and around the weaning period, but there were no sex differences. Immatures tended to learn from individuals in proximity when they were young, while they looked for specific demonstrators when older. In general, immatures preferred to learn from grooming affiliates and younger over older individuals, who could be part of their play network. Immature males directed fewer learning behaviours to grooming partners compared to female peers. Finally, higher-ranking immatures directed more learning behaviours and to a wider variety of individuals compared to lower-ranking peers. Our results suggest that the information acquired from others helps immatures to reach an adult-level foraging competence before being weaned. Tolerance, through shared grooming and proximity, seems important in determining immatures' choice of demonstrators.

Because baboons live in a matrilineal society with a high degree of nepotism, immatures' learning from tolerant individuals may translate into a higher within-matriline versus across-matriline information transmission, which could limit the formation of group-level cultures.

4.2 INTRODUCTION

Social learning, i.e., acquiring information from other individuals or their artefacts, is widespread in the animal kingdom (Allen 2019). Gaining information from others is advantageous because it can require less energy than acquiring it personally (Laland 2004). Social information transmission has been a major research focus in animal behaviour because of its role on the formation of culture, i.e., socially learnt behaviours shared by most members of a group and maintained through time (Castro and Toro 2004, Laland and Janik 2006). For example, moss-sponging, a novel tool-use behaviour transmitted socially in a group of wild eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Hobaiter *et al.* 2014), persisted three years after its initial emergence, and spread to individuals beyond the social partners of the original innovator (Lamon *et al.* 2017). Understanding constraints on social information transmission may be important because cultural differences can produce variation in fitness (McComb *et al.* 2001, Marcoux *et al.* 2007); in this way, cultural transmission may contribute to species' evolution in addition to genetic inheritance (Whiten 2017). Importantly, knowing how information flows in a group may inform conservation practices aimed at reducing anthropogenic disturbance on social learning processes (Brakes *et al.* 2021).

Immature age classes could have a fundamental role in group-level information transmission because they tend to learn socially more than adults (Reader and Laland 2001, Whiten and van de Waal 2018). Experiments both in captivity and in the wild showed that juveniles learn socially more than adults in various animal taxa (smooth-coated otters *Lutrogale perspicillata* (Ladds *et al.* 2017), Australian skinks *Eulamprus quoyii* (Noble *et al.* 2014), chacma baboons (Carter *et al.* 2014), caracaras chimangos *Milvago chimango* (Biondi *et al.* 2010), meerkats *Suricata suricatta* (Thornton and Malapert 2009), brown rats *Rattus norvegicus* (Galef *et al.* 2001)). This may be because of immatures' inexperience with the environment, leading them to have a different costs-benefits balance of asocial versus social learning compared to adults. Despite the benefits of gathering social information (e.g., sparing the energy needed for individual learning), there may be also costs because such information (e.g., about the quality of a food patch) may be unreliable or outdated (Giraldeau *et al.* 2002). However, the costs of individual learning could be relatively higher for inexperienced immatures, increasing their benefits of learning from more experienced individuals compared to adults (Laland 2004).

Our knowledge of social learning during development derives mainly from studies on non-human primates (hereafter primates) (Whiten and van de Waal 2018), who have a relatively longer period of juvenescence compared to other similarly-sized mammals (Jones 2011). Because juveniles are well tolerated by other group members, young primates have wide opportunities to learn socially (Ottoni and Izar 2008). Most studies focus on the acquisition of foraging skills, since the first challenges faced by immatures are learning where to find food, what food they can eat, and how to process it (Rapaport and Brown 2008, Alberts 2019). In addition to foraging skills, immatures may learn in other domains, such

as nest-building (Bornean *Pongo pygmaeus* and Sumatran *P. abelii* orangutans (Schuppli, Meulman, *et al.* 2016)), grooming (eastern chimpanzees (Wrangham *et al.* 2016), Japanese macaques *Macaca fuscata* (Tanaka 1995, 1998)), vocal communication (Geoffroy's spider monkeys *Ateles geoffroyi* (Briseno-Jaramillo *et al.* 2018), meerkats (Hollén and Manser 2006)), defensive responses to predators (Siberian jays *Perisoreus infaustus* (Griesser and Suzuki 2017), black-tailed prairie dogs *Cynomys ludovicianus* (Shier and Owings 2007)) and parasites (deer mice *Peromyscus maniculatus* (Kavaliers *et al.* 2005)), and migratory routes (whooping cranes *Grus americana* (Mueller *et al.* 2013)).

Knowledge and skill acquisition may involve both individual and social learning and be affected by physical maturation (e.g., motor development and dental eruption) (Gunst *et al.* 2008, Bray *et al.* 2018). Although many studies in the wild are observational, and thus cannot quantify the role of social versus individual learning, they report behaviours that may be indicative of social information acquisition (e.g., proportional to foraging competence and increasing individual exploration (Schuppli, Meulman, *et al.* 2016); affecting foraging choices (Troisi *et al.* 2021)). These behaviours include observing others; obtaining food, materials, and/or olfactory information from others; and co-feeding on the same food (Rapaport and Brown 2008). While, in this study, we did not link these behaviours to immatures' foraging proficiency and/or choices as indicators of social learning, based on the previous literature and for simplicity, we refer to them as 'social learning from a given demonstrator'. Despite the increase in studies on immature age classes (Whiten and van de Waal 2018), our knowledge on how immatures learn socially throughout development is limited, especially in non-tool-using species (Schuppli and van Schaik 2019).

Social learning behaviours in immatures could vary according to three factors: the learner's age, the learner's sex, and the characteristics of the demonstrator (i.e., the individual to whom they pay attention). In most cases, immatures need to be nutritionally self-sufficient by weaning because post-weaning provisioning is rare (Carvajal and Schuppli 2022), except in cooperatively-breeding species (Snowdon 1996). For omnivorous species, the dietary knowledge to be learnt may be vast (Whiten and van de Waal 2018): for instance, yellow baboons (*P. cynocephalus*) can consume more than 250 types of food (Alberts 2019). Nevertheless, adult-level dietary breadth and efficiency for most foods is reached by weaning (Schuppli, Forss, *et al.* 2016, Bray *et al.* 2018). Accordingly, social learning of foraging skills is more common in infants than in juveniles (orangutans (Mikeliban *et al.* 2021), tufted capuchins *Sapajus apella* (Gunst, Boinski, *et al.* 2010), meerkats (Thornton and Hodge 2009), western chimpanzees *P. t. verus* (Biro *et al.* 2003)). During juvenescence, learning from others may continue at relatively high levels up to sexual maturity to include rare foods in the diet and refine foraging skills that are not fundamental for post-weaning survival (Bray *et al.* 2018). In fact, immatures may encounter seasonal or uncommon foods for the first time after weaning (orangutans (Schuppli, Forss, *et al.* 2016)). In addition, juveniles could be less efficient than adults in assessing patch quality, and thus rely relatively more on others to choose suitable patches (meerkats (Thornton and Hodge 2009), chacma baboons (Johnson and Bock 2004)). Finally, relatively complex techniques, such as predation (many mammalian predators (Thornton and Clutton-Brock 2011), black capuchins *S. nigritus* (Agostini and Visalberghi 2005)) or extractive foraging (Javan slow lorises *Nycticebus javanicus* (Maynard *et al.* 2021), banded mongooses *Mungos mungo* (Müller and Cant 2010)), potentially involving tools (long-tailed macaques *M.*

fascicularis (Tan *et al.* 2018), common bottlenose dolphins *Tursiops truncatus* (Sargeant and Mann 2009)), could require a long learning period, including the gradual addition of social information to individual practice (de Resende *et al.* 2008, Musgrave *et al.* 2021).

The balance between social and individual learning may also differ in the two sexes (Reader and Laland 2001). This has been reported in social groups including a majority of adults: for example, adult female primates learn socially more than males (vervet monkeys (Canteloup *et al.* 2020), chimpanzees (Watson *et al.* 2018)). However, opposite patterns have been reported for immature male and female primates, matching species-specific sex differences in tool use (Gruber *et al.* 2010, Falótico and Ottoni 2014): juvenile female eastern chimpanzees (Lonsdorf *et al.* 2004) and male bearded capuchins (*S. libidinosus*) (Falótico *et al.* 2021) pay more attention to others and learn faster than peers of the opposite sex, despite equal learning opportunities. Second, when females are better integrated in the group's social network compared to males (killer whales *Orcinus orca* (Weiss *et al.* 2021), female-philopatric primates (Lonsdorf 2017, Amici, Kulik, *et al.* 2019)), they may have greater social learning opportunities (Carter, Torrents Ticó, *et al.* 2016, Kulahci *et al.* 2016), which can translate to enhanced learning (meerkats (Hollén and Manser 2006)). Males and females may also acquire information from different group mates, who can vary with age (Lonsdorf and Bonnie 2010, Whiten and van de Waal 2018).

The demonstrators from whom immatures learn may differ based on their spatial associations within their social group or other characteristics. In the first case, young immatures could be constrained in their choice of demonstrators by the proximity of close kin, who provide care and protection (Bateson 1994, Lehmann *et al.* 2006). Consequently, immatures tend to learn first from related

individuals who are more frequently in spatial proximity, primarily the mother, and shift toward other group members later during development (vervet monkeys *Chlorocebus pygerythrus* (Grampp *et al.* 2019), orangutans (Schuppli, Meulman, *et al.* 2016), bottlenose dolphins (Mann *et al.* 2007), western chimpanzees (Biro *et al.* 2003)), when they expand their social network beyond the maternal one (Tsai and Mann 2013, Whiten and van de Waal 2018). Paying attention to specific demonstrators independently from their spatial associations is referred to as directed social learning (van de Waal *et al.* 2010). Specific demonstrator choice may be more common among older immatures, who can search out particular individuals farther from their close spatial associates (de Resende *et al.* 2004, Grampp *et al.* 2019), but it could occur among all immature age classes if different demonstrators are available within their spatial proximity group (Sargeant and Mann 2009, Estienne *et al.* 2019). Conversely, juveniles can still learn from those most often in proximity, who may differ in the two sexes as their social connections differentiate (bottlenose dolphins (Stanton *et al.* 2011), black capuchins (Agostini and Visalberghi 2005)).

In the second case, individuals' other characteristics that could affect their suitability as a demonstrator include their age, sex, kinship, affiliation, social rank, and foraging efficiency (Lonsdorf and Bonnie 2010). Older, more experienced individuals (white-faced capuchins *Cebus capuchinus* (Barrett *et al.* 2017), Japanese macaques (Tarnaud and Yamagiwa 2008), bottlenose dolphins (Mann *et al.* 2007), western chimpanzees (Biro *et al.* 2003)) and the philopatric sex (vervet monkeys (van de Waal *et al.* 2010), common marmosets *Callithrix jacchus* (Schiel and Huber 2006)) may be chosen because of their local knowledge. However, the dispersing sex may be more flexible in their choice of demonstrators: for instance, male, but not female, vervet monkeys shifted from

adopting the same technique as a female demonstrator to copying a male demonstrator when the latter received a greater reward (Bono *et al.* 2018). In addition, when the diets of adult males and females differ, immatures may pay more attention to adults of the same sex during foraging, despite having similar social connections (bearded capuchins (Falótico *et al.* 2021), orangutans (Ehmann *et al.* 2021)). Close kin (long-tailed macaques (Tan *et al.* 2018), eastern chimpanzees (Lamon *et al.* 2017), vervet monkeys (van de Waal *et al.* 2014), bottlenose dolphins (Sargeant and Mann 2009)), social affiliates (ravens *Corvus corax* (Kulahci *et al.* 2016), chacma baboons (Marshall *et al.* 2015), tufted capuchins (Gunst, Leca, *et al.* 2010), deer mice (Kavaliers *et al.* 2005)) or lower-ranking individuals (chimpanzees (Watson *et al.* 2017), chacma baboons (King *et al.* 2009)) may be targeted because their tolerance of observers allows for close proximity and thus better learning and scrounging opportunities (Chapais and Belisle 2001). Preference for close kin could vary depending on immatures' sex, even when association patterns are similar, with females paying proportionally more attention to the mother than males (orangutans (Ehmann *et al.* 2021), white-faced capuchins (Perry 2009)). More efficient foragers may also grant higher pay-offs in scrounging (vervet monkeys (Canteloup, Cera, *et al.* 2021), long-tailed macaques (Tan *et al.* 2018), tufted capuchins (Ottoni *et al.* 2005)), which could positively reinforce learning (common marmosets (Caldwell and Whiten 2003), Florida scrub-jays *Aphelocoma coerulescens* (Midford *et al.* 2000); but see pigeons *Columba livia* (Giraldeau and Lefebvre 1987)). Similarly, higher-ranking individuals (vervet monkeys (Canteloup *et al.* 2020), chimpanzees (Kendal, Hopper, Whiten, Brosnan, Susan, *et al.* 2015), tufted capuchins (Coelho *et al.* 2015)) may be preferred as demonstrators because they can access high quality food patches (Huchard *et al.* 2013, Marshall *et al.* 2015).

In this study, we aimed to understand (1) how social learning behaviours during foraging (i.e., feeding or searching for food) change throughout development in baboons, and (2) from whom immature baboons learn while they forage. We focused on social learning during foraging because it is the most common form of social learning reported in the literature (Whiten and van de Waal 2018) and because, in our study, immatures' observation of others outside the foraging context was relatively rare (< 2% of learning records). We adopted a longitudinal approach, which allows the detection of developmental trends and selective social attention at different age stages (Lonsdorf and Bonnie 2010, Mesoudi *et al.* 2016). Baboons are ideal models to study social learning behaviour because they live in large social groups (Cheney and Seyfarth 2007), which may provide wide opportunities for social learning (van Boekholt *et al.* 2021), and their ability to learn socially has been confirmed by experimental studies (Carter *et al.* 2014, Carter, Torrents Ticó, *et al.* 2016). Baboons' multi-male multi-female social groups are organised into matriline (i.e., social units formed by a mother and her offspring) where females are philopatric and males disperse after sexual maturity (Cheney and Seyfarth 2007).

Building on the current literature, we tested two hypotheses on the development of social learning in baboons. Our first hypothesis (**H1**) was that immatures' tendency to learn socially changes with age and differs by sex. We had two predictions for H1. Because young immatures need to acquire the necessary dietary knowledge to reach foraging independence (Bray *et al.* 2018), we predicted that (**P1a**) social learning would increase during infancy and decrease during juvenile years. We also predicted that (**P1b**) this decrease would be greater in males than in females, because of their lower sociability compared to female peers (Lonsdorf 2017).

Our second hypothesis (**H2**) was that immatures would direct learning behaviours to different demonstrators depending on their own age and on the demonstrators' characteristics. We had three predictions for H2. First, we predicted that (**P2a**) learning from individuals in proximity would decrease with age because immatures may look more for specific demonstrators when older (Grampp *et al.* 2019). Then, we predicted that (**P2b**) immatures would prefer demonstrators who are knowledgeable of local resources, such as older individuals (Barrett *et al.* 2017) and the philopatric sex (females in baboons) (van de Waal *et al.* 2010). Finally, we predicted that (**P2c**) immatures would prefer tolerant demonstrators, such as close kin, grooming affiliates, and lower- or similarly ranked individuals (Lonsdorf and Bonnie 2010). Because chacma baboons live in a despotic society (King *et al.* 2008), tolerant demonstrators may offer relatively better learning opportunities (King *et al.* 2009).

4.3 METHODS

4.3.1 Study site and species

This research was carried out at the Tsaobis Baboon Project, a long-term (since 2000), individual-based study of a wild chacma baboon population (TBP 2019). Tsaobis is a semi-desertic area located on the edge of the Namib desert, in central Namibia (22°22'S, 15°44'E). The main features of the area are the ephemeral Swakop River and its tributaries, bordered by dense patches of woodland and surrounded by rocky hills with scarce vegetation (see Cowlshaw and Davies 1997 for a full description of the area).

The study population is formed of two troops (J and L) that range across Tsaobis Nature Park and the surrounding farmland. The troops are habituated to the presence of observers on foot and the majority of the individuals (see below) are recognisable through a unique combination of ear marks. Adult females give birth to an infant approx. every two years (Dezeure, Baniel, *et al.* 2021) and infants of both sexes are weaned around 12–18 months of age at Tsaobis (Huchard *et al.* 2013, Carboni *et al.* 2022). For the purposes of this study, individuals ≤ 5 years old are considered immatures and those ≤ 12 months old are considered infants (Roatti *et al.* 2023a). Females undergo menarche around five years old and have their first infant around six years old; males develop secondary sexual characteristics around six years old, reaching full adult development after approx. eight years old, when they typically emigrate (Altmann *et al.* 1981, Alberts and Altmann 1995a, Cheney *et al.* 2004).

4.3.2 Data collection

Observations were conducted on the two study troops during two field seasons in 2021 (approx. six months) and 2022 (approx. three months), totalling nine months of data collection over the two years. Baboons were followed daily from dawn to dusk while collecting observational data with the application CyberTracker (Liebenberg 2022). The troops numbered 59 and 64 individuals in J and 72 and 79 in L in 2021 and 2022, respectively (see Appendix 3, §3.1). The proportion of recognisable individuals was 1.0 in 2021 and 0.98 in 2022 (across both troops).

Our study focused on a total of 53 immature study subjects (J: 24; L: 29), born from 38 mothers. Among these, 37 immatures (J: 15; L: 22) were followed throughout the study period (in both years). In 2021, the sample included all the

individuals ≤ 4 years old at the start of the field season and those born during the field season: 34 females and 19 males, of which 23 were infants and 30 were juveniles when they entered the study. The same individuals were observed in 2022, with the exception of 16 individuals who were no longer immature (eight), died (four), or were not recognisable (unmarked) when they became independent from the mother (four). The 2022 sample comprised 23 females and 14 males, all juveniles but one infant at the start of the field season.

To test our predictions, we collected different kinds of behavioural data, both on our immature study subjects and on all the recognisable troop members. Specifically, we recorded three kinds of data (Altmann 1974): focal observations on the immature study subjects' social behaviours; *ad libitum* grooming and dominance interactions for all troop members to build grooming social networks and compute dominance ranks, respectively; and instantaneous observations (scans) of social proximity on all the recognisable troop members to build proximity networks. Social networks based on proximity and grooming interactions may provide different information (Castles *et al.* 2014) and both served to quantify associations (Croft *et al.* 2008). Finally, we used long-term demographic records and maternal relatedness.

Focal observations consisted of 20-min observations on a specific focal individual included in the immature study subject sample. Observations lasting < 5 min were discarded. If the observer lost sight of the focal individual, the observation was paused for up to 10 min until the focal individual was found again or the observation was ended. To avoid bias towards a time of the day, observations per individual were distributed evenly in four daily periods of approx. three hours each: (1) from dawn until 1000 h, (2) from 1000–1300 h, (3) from 1300–1600 h, and (4) from 1600 h until dusk. In addition, to increase data

independence, each individual was observed as a focal only up to twice per day in two different and non-consecutive time periods. Focal observations per individual were also spread evenly throughout the field season by checking the number of observations weekly (see Appendix 3, §3.2).

Focal observations served to record immatures' social learning, grooming and dominance interactions, and proximity associations, including the directionality of interactions (given or received) and the identity of the social partners. First, we collected the frequency of six behaviours indicative of social learning during foraging (Figure 4.1): 'observe feed,' defined as peering for ≥ 3 s at another individual while the latter is foraging (Biro *et al.* 2003, Schuppli, Meulman, *et al.* 2016); 'inspect food,' defined as manipulating the food accessed by another individual without eating it (Schiel and Huber 2006, Rapaport and Brown 2008); 'feed scraps,' defined as feeding on the scraps dropped by another individual (Ottoni *et al.* 2005, Tan *et al.* 2018); 'sniff mouth,' defined as smelling the mouth of another individual (Gunst, Leca, *et al.* 2010, Alberts 2019); 'steal food,' defined as grabbing a – generally difficult to gain – food item in possession of another individual (Brown *et al.* 2004, Mikeliban *et al.* 2021); 'scrounging,' defined as foraging on the same food as another individual within 1 m of the latter (in the same patch) (Ueno 2005, O'Mara and Hickey 2012). The first five behaviours (i.e., all but scrounging) were defined as directed towards one specific individual within a short distance (approx. 0–3 m). Scrounging could be directed to more than one individual because several individuals could be within 1 m of each other in a patch. We chose a relatively shorter distance threshold for scrounging to assess a (potential) learner's choice of a specific place to forage based on the demonstrator's location and not simply reflect a preference in association partners (King *et al.* 2009, Huchard *et al.* 2013). For all social learning

behaviours, the demonstrators could be present during a learning interaction, or they could have just left (within approx. 10 s, seen by the learner before leaving). Because chacma baboons live in a highly hierarchical society (King *et al.* 2008), recording these ‘delayed’ learning occurrences allowed us to account for instances in which a learner would not approach a more dominant individual or a demonstrator left because a more dominant learner approached.

Second, during focal observations, we collected the frequency of immatures’ grooming and dominance interactions, using the same protocol as for *ad libitum*-collected data (see below), and quantified their proximity associations. Focal grooming and dominance interactions, together with the *ad libitum* data, were used to build immatures’ grooming ego-networks (i.e., the vectors that correspond to the square matrix row of each immature individual (Hobson *et al.* 2013, Turner *et al.* 2018)) and calculate their dominance ranks, respectively. Immatures’ proximity associations were assessed through scan samples performed every 5 min (during the continuous observation), during which we recorded the identities of all the neighbours within 5 m of a focal individual and the activity of the focal individual (i.e., forage, groom, nurse, play, rest, travel). Focal proximity scans were used to build immatures’ proximity ego-networks. Focal observations were preferred over *ad libitum*-only interactions and troop-level proximity scan data (see below) because of their higher resolution on immature age classes.

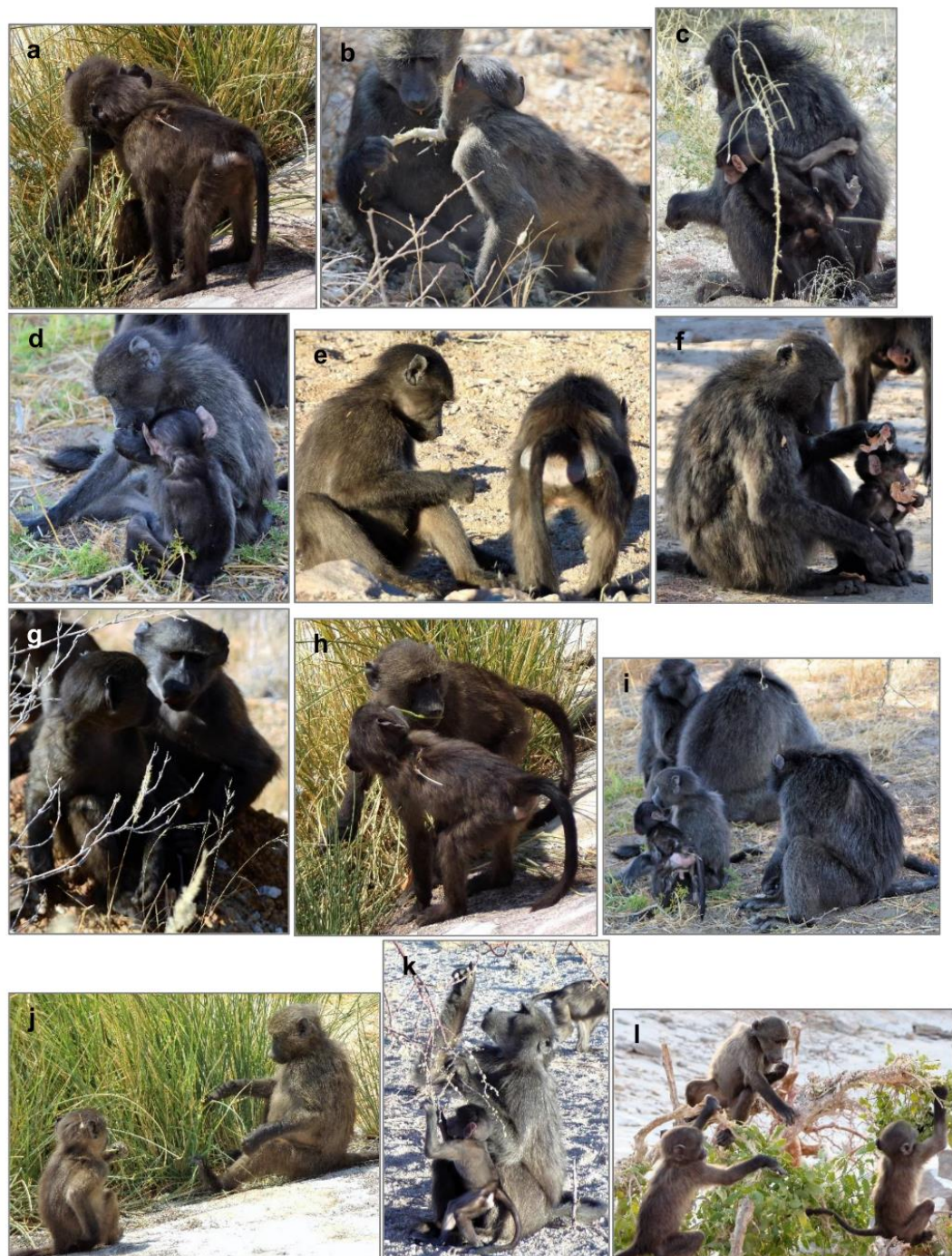
Ad libitum grooming and dominance interactions were collected on all the recognisable troop members when both a giver and a recipient could be identified. To avoid bias towards the individuals who were easier to find, these data were recorded while moving through the troops as part of other data collection protocols. In this way, we did not need to account for individual baboon

observability (Carter, Torrents Ticó, *et al.* 2016). Dominance behaviours comprised displacements, supplants, threats, chases, and attacks (Huchard and Cowlshaw 2011). To avoid pseudo-replication, a grooming dyad was not recorded more than once within the same half an hour (Carter, Torrents Ticó, *et al.* 2016) and only one dominance interaction was collected even if this involved several dominance behaviours in sequence (Huchard and Cowlshaw 2011). *Ad libitum*-only grooming interactions were used to build troop-level grooming networks, which were preferred over focal observations because they were not biased towards immature age classes (Croft *et al.* 2008). *Ad libitum* dominance interactions were used to calculate dominance rank for all individuals.

Troop-level proximity scans served to characterise proximity associations for all the recognisable troop members. These data were not biased towards a certain age group and were thus chosen over focal proximity data to build troop-level proximity networks (Croft *et al.* 2008). Because baboons at Tsaobis can spread over large distances with frequent mixing of individuals, we could not perform surveys of the whole social group at one point in time (Best *et al.* 2013, Carter, Seddon, *et al.* 2013). We instead recorded the neighbours within 10 m of 'focal' individuals chosen from a randomised list of all troop members to guarantee sampling independence. Individuals who did not have a neighbour within 10 m were recorded as alone. Focal individuals and their neighbours were not re-sampled within an hour (as focal individuals) if appearing again in a list. During long resting periods when group membership did not change, observations were ceased until the group moved (and thus individuals mixed again). Young infants were included in the focal list when they could move independently from their mothers (Carter, Torrents Ticó, *et al.* 2016) since before that point they share their mothers' networks (Berman 1982a, 1982a).

Demographic variables and maternal kinship were determined through long-term data. Sex and the identity of an infant's mother (nursing) were assigned when an infant was first identified through direct observation. Baboons' ages (in months) were determined by known and estimated dates of birth. The first case applied to births occurring during fieldwork. In the second case, when births occurred in between field seasons, dates of birth were estimated based on (1) the observation of infants' colouration (Dezeure, Dagorrette, *et al.* 2021); and/or (2) possible conception dates from consortship records (i.e., mate-guarding events at the peak of a female's fertility) (Alberts and Fitzpatrick 2012) after which a female did not menstruate, and assuming a pregnancy duration of six months (Altmann *et al.* 1978); or, (3) for individuals not observed as infants (eight), dentition (molar emergence and wear) (Huchard, Benavides, *et al.* 2009).

Figure 4.1: Social learning behaviours of wild immature chacma baboons: ‘observe feed’ (a–e), ‘inspect food’ (f), ‘sniff mouth’ (g–i), ‘scrounging’ (i–l). Photo credit (b, d, f, g, i): Elisa Fernández-Fueyo.



4.3.3 Data analyses

Data analyses were performed with R 4.0.3 (R Core Team 2023) using a longitudinal approach with repeated measures of individuals within our sample. We divided the data into three time periods of approx. three months each: two in 2021 (first and second half of the six-month field season) and one in 2022. We chose these time windows because they fit our data resolution and could capture developmental changes. Data were removed for individuals who were present for less than a month in each time period because these data may not be representative of the whole time period (Farine and Whitehead 2015). These individuals were either born towards the end of a time period (seven), died (three) or emigrated (one) at the beginning of a time period, or were no longer followed among immatures (focal data-only) because they became adult at the beginning of a time period (one). One adult male emigrated between the study troops and was present for about half of time period three in each of the two troops.

Immatures' social learning behaviours from focal data were divided into two categories based on the type of behaviour: (1) scrounging and (2) other social learning behaviours, including the other five learning behaviours (see above). We distinguished these two categories because scrounging was more frequent than all the other learning behaviours together, allowing for separate analyses. To increase data independence, we removed, in each of these two categories, observations of the same dyad within the same 30 s. To test our predictions (see below), we created a binary variable ('0' = absent; '1' = present) describing the presence of scrounging and the other learning behaviours given by each immature individual in each focal observation. In addition, in each time period, we calculated the proportion of scrounging and the other learning behaviours given to each demonstrator chosen by each immature individual. Overall, we collected

1,529 h of focal observation during the two field seasons (see Appendix 3, §3.3). Focal individuals included in a time period had > 7 h of observation in that time period.

We produced social networks for each time period within each troop, at the immatures' and at the troop's levels. Both the proximity and the grooming networks were weighted (i.e., values indicate both the presence and strength of a social connection) (Croft *et al.* 2011) and the grooming network was directed. Associations were not filtered based on edge weight because this may eliminate important ties (Brent, MacLarnon, *et al.* 2013, Sosa 2016) and generate errors in the network structure (Farine and Whitehead 2015). At the immatures' level, we computed ego-networks (Turner *et al.* 2018, Grampp *et al.* 2019). For the proximity network, to ensure data independence, one scan (see above) was randomly sampled per each focal observation. To test our predictions (see below), we built foraging ego-networks from scans when the focal individual was foraging. We used a simple ratio index (SRI; i.e., the proportion of time two individuals associated) to calculate weighted connections. This index is recommended only when individuals can be detected and identified correctly (Hoppitt and Farine 2018) as is the case at Tsaobis where group membership is stable, and visibility is usually excellent due to low vegetation cover. For the grooming network, we calculated the proportion of the total grooming given and received by a focal individual with each other troop member.

At the troop level, network graphs were created from proximity SRI and total grooming count matrices (i.e., number of interactions per dyad) using the package *igraph* (Csardi and Nepusz 2006) and the function *graph_adjacency*. From these, we calculated each individual's eigenvector centrality (hereafter centrality), i.e., the sum of the centralities of an individual's social partners. An

individual can have high centrality either by having a large number of social connections, or by associating with individuals who have themselves numerous connections (or both) (Sosa *et al.* 2021). This metric represents an individual's relative opportunities to acquire (and propagate) social information in a network (Carter, Torrents Ticó, *et al.* 2016). Centrality values were derived using *igraph*'s *eigen_centrality* function. In addition, we calculated each individual's proximity degree, i.e., the number of social partners in the proximity network (Sosa *et al.* 2021). Degree values were derived using *igraph*'s *degree* function. To make metrics comparable across networks of different sizes, values were standardised within each time period by mean-centring them around zero with a standard deviation of one through the function *scale* (Wey *et al.* 2008). During the two field seasons, we collected 2,824 and 8,770 ego-network (on immatures) proximity and grooming records, respectively. In addition, we recorded 7,985 and 14,186 proximity and grooming observations, respectively, on the whole troop (see Appendix 3, §3.3).

Dominance ranks were determined for each troop member in each time period through the 'I & SI' method (de Vries 1998, Schmid and de Vries 2013). The method is appropriate for linear dominance hierarchies (de Vries 1995, Sánchez-Tójar *et al.* 2018) and is consistent with other studies on this population (Huchard and Cowlshaw 2011). Dominance matrices were tested for triangle transitivity, a measure of linearity for large social groups, through the package *compete* (Curley 2023) and the function *ttri* (1000 permutations) (Shizuka and McDonald 2012). The resulting matrices were strongly linear. Ordinal ranks were computed through *compete*'s *isi13* (500 iterations) (Sánchez-Tójar *et al.* 2018, Vilette *et al.* 2020). Because infants ≤ 12 months old were involved in very few or no dominance interactions, they were excluded from the rank calculation and

assigned one ordinal rank below their mothers'. Absolute ranks were standardised by controlling for group size using the formula $1 - [(1 - r) / (1 - n)]$, where r is an individual's absolute rank and n is the group size. Relative ranks range from '0' (lowest) to '1' (highest) (Baniel *et al.* 2018a). Overall, we collected 8,260 dominance interactions during the two field seasons (see Appendix 3, §3.3).

For all individuals, age was calculated as the number of months at the date midpoint (median) of each time period. Maternal relatedness for each dyad was represented by a 3-levels coefficient: '0' for non-relatives, '0.5' for mother-offspring dyads, '0.25' for half siblings (Grampp *et al.* 2019). We did not consider lower levels of maternal relatedness because the grandmothers' identities were not available for a part of the individuals.

To test our predictions, we used generalized linear mixed effects models (GLMMs) with the function *glmer* from the package *lme4* (Bates *et al.* 2015). We built a total of four (see below and Table 4.1) main binomial '*logit*' models, which are recommended to fit dependent variables with ≤ 2 categories that are binary (H1) or proportions derived from counts (H2) (Douma and Weedon 2019). The package *lmerTest* (Kuznetsova *et al.* 2017) was required to obtain p -values from models' summaries. Significance was accepted at p -value ≤ 0.05 (Chowdhury and Turin 2020, Tredennick *et al.* 2021). We obtained R^2 values (coefficient of determination) from the package *MuMIn* (Bartoń 2022) and the function *r.squaredGLMM*. Before running the models, we checked for independent variables' linear correlations by computing their Pearson's correlation coefficients (r) (Thomas *et al.* 2015). We did not include in the same model variables with $r \geq 0.5$ (Suzuki *et al.* 2008, Dormann *et al.* 2013) (see below and Appendix 3, §3.4). In addition, we assessed multi-collinearity after running the models using

variance inflation factors (VIFs) with the package *car* (Fox *et al.* 2023) and the function *vif*. In all cases, VIFs were < 3 , indicating low collinearity (Dormann *et al.* 2013). We verified under/ overdispersion with the package *DHARMA* (Hartig 2022) and the function *testDispersion*. In all cases, significant dispersion values were within the range of 0.7–2, indicating a normal degree of variation for a binomial distribution (Thomas *et al.* 2015). We also checked the overall model fit plotting *DHARMA*'s simulated residuals through the function *simulateResiduals*. When we obtained singular fits, we first identified the problematic random factors with *lme4*'s *rePCA* and then confirmed the results by re-running the models without those random factors (Burrow and Maerz 2021, Oberpriller *et al.* 2022). For each model variable, we obtained both the odds ratios (OR) and the 97.5% confidence intervals (CIs) (see below). OR represent the strength of the association between an exposure (independent variable) and an outcome (dependent variable). When $OR = 1$ and/or CIs cross one, there is no relationship between the exposure and the outcome (no change); when OR are < 1 or > 1 (and CIs do not cross one), the exposure is associated with lower or higher odds of the outcome, respectively (Szumilas 2010, George *et al.* 2020). The percentage change in OR per each unit variation in an independent variable was expressed as $(OR - 1) \times 100$. In the presence of an interaction, the main effects were interpreted as conditional effects (Bauer and Curran 2005, Brambor *et al.* 2006).

In all models, we controlled for the following independent variables (Table 4.1). Because dominance rank may affect the opportunities to acquire social information (King *et al.* 2009, Marshall *et al.* 2012), we inserted as a fixed factor immatures' relative rank. To control for year and season, and differences between the two troops, we inserted as fixed factors (< 5 levels) (Harrison *et al.* 2018) the

(categorical) time period ('1' = winter 2021; '2' = summer 2021; '3' = winter 2022) and troop ('J'; 'L'). Because our data have repeated measures from the same individuals through time, we included as a random factor the immatures' identity and the identity of their mothers. We nested immatures' identities within their mothers' identities because maternal behaviour could affect the offspring's sociality (Maestripieri 2018). Finally, the mother's loss may affect immatures' personality (Botero *et al.* 2013) and, in turn, their propensity to collect social information (Carter *et al.* 2014, Grampp *et al.* 2019). Although 26% of our immature individuals were orphaned, we did not control for being orphan because it was correlated with age (see Appendix 3, §3.4). Other independent variables specific to each hypothesis were added to test the outlined predictions. Model selection varied between H1 and H2 depending on the aim of each hypothesis' test (see below).

4.3.4 Testing H1: Immatures' tendency to learn socially changes with age and differs by sex

To test our predictions for hypothesis H1 we built two models. The dependent variables were the binary outcome (0/ 1) of the presence of either scrounging (Model 1) or other social learning behaviours (Model 2) given by each immature in each focal observation (Table 4.1). Because most observations had either no social learning behaviours or one behaviour, we opted for a binary dependent variable instead of a count (see Appendix 3, §3.5). Both models had the same independent variables as fixed factors. To test for P1a – that social learning increases during infancy and decreases during juvenile years – we inserted as predictors immatures' linear age (continuous) and quadratic age (to model a non-linear relationship with learning presence) using orthogonal second degree

polynomials (Thomas *et al.* 2015). To test for P1b – that the decrease in social learning will be greater in males than in females – we added as predictors the interactions between age (linear and quadratic) and sex (the latter also added as a main factor). In addition to the control variables stated above, we controlled for observation length as a continuous fixed factor. Immatures' centrality in the proximity and grooming troop networks could affect individuals' access to social information (King *et al.* 2009, Carter, Torrents Ticó, *et al.* 2016). However, we did not control for proximity and grooming centrality because they were correlated with age and relative rank, respectively (see Appendix 3, §3.4).

For H1, we were interested in the effects of specific variables (i.e., age, sex, and their interaction) on social learning presence. We thus presented 'full models': the models did not undertake any *a posteriori* simplification procedure (Chowdhury and Turin 2020, Tredennick *et al.* 2021). We derived predicted values using the package *ggeffects* (Lüdtke 2018) and the function *ggpredict*. We expressed differences in OR from one age (t_0) to another (t_1) as increase/decrease percentages, through the formula $[(OR_{t_1} - OR_{t_0}) / OR_{t_0}] \times 100$. We chose two age periods based on the literature: (1) 1 year old, when infant baboons are weaned or almost weaned (Huchard *et al.* 2013), but still spend most of the time with the mother (Altmann 1980, Roatti *et al.* 2023a); and 4 years old, when immatures should be fully foraging competent and formed their own social relationships (Johnson and Bock 2004, Roatti *et al.* 2023a). Confidence intervals were derived through *lme4*'s *confint.merMod* function with the 'Wald' method.

4.3.5 Testing H2: Immatures' learning from different demonstrators depends on their own age and on the demonstrators' characteristics

To test our predictions for hypothesis H2 we built another two models. The dependent variables were (Model 3) the proportion of the number of scrounging events given by each immature to each demonstrator in each time period over an immature's total scrounging, and (Model 4) the proportion of the number of other social learning behaviours given by each immature to each demonstrator in each time period over an immature's total number of these learning behaviours (Table 4.1). The total counts associated with these proportions were included as weights (Thomas *et al.* 2015). Both models had the same independent variables as fixed factors. To test for P2a – that learning from individuals in proximity decreases with immatures' age – we inserted as a predictor the interaction between immatures' age and the proximity foraging ego-network value (SRI) correspondent to the immature-demonstrator dyad (also included as main continuous factors). To test P2b – that immatures prefer demonstrators who are knowledgeable on local resources, such as older individuals and the philopatric sex (females) – we inserted as predictors the demonstrators' age (continuous) and sex. To test P2c – that immatures prefer tolerant demonstrators, such as close kin, grooming affiliates, and lower- or similarly ranked individuals – we included as predictors a dyad's grooming (total) ego-network value (grooming allocation) and their relative rank difference ($\Delta RR = \text{immature's rank} - \text{demonstrator's rank}$). The latter served to check whether the rank of the demonstrator tends to be relatively lower (ΔRR positive) and for immature-demonstrator rank similarity (ΔRR close to zero). For the last prediction (P2c), we did not include maternal relatedness because it was strongly positively correlated with the proportion of grooming total ($r = 0.7$; see Appendix 3, §3.4), according to

matriline members' preference to groom together (Charpentier *et al.* 2012, Kulik *et al.* 2015). Therefore, we prioritised testing for learning from grooming affiliates, who include both maternal kin and other closely bonded individuals. However, to control for the importance of within-matriline bonds, we added the number of matriline members (i.e. mother and maternal siblings) per time period as a continuous fixed factor. In addition, we controlled for the following variables as continuous fixed factors: immatures' total amount of grooming given and received in each time period, because the overall grooming effort could influence the dyadic grooming allocation; immatures' proximity degree in each time period, because the number of individuals in proximity may affect the dyadic network association; the proportion of individuals of a certain age in each troop/ time period, to control for demonstrator availability. Finally, we added as random factor the demonstrators' identity to control for repeated learning from the same individuals. Because immatures' sex was correlated with the total amount of grooming (see Appendix 3, §3.4), we could not include it in the model. We thus run the models both with a full dataset (both sexes) and for females and males separately to check for sex differences. The sex-separated models' results were qualitatively similar to the full models' ones and are presented in Appendix 3, §3.6.

For H2, we were interested in finding the 'best model' explaining the distribution of learning allocated to different individuals. We thus adopted an information theoretic approach (Chowdhury and Turin 2020, Tredennick *et al.* 2021) based on Akaike's Information Criterion (AIC) (Anderson *et al.* 2000). In order to compare the effects of different predictors, we first standardised models' independent variables with a mean of zero and a standard deviation of 0.5 through the package *arm* (Gelman and Su 2022) and the function *standardize*.

Then, we used the package *MuMIn*'s *dredge* to calculate AICc values (corrected for small sample size) and weights (i.e., models' relative likelihood) for a set of candidate models (Symonds and Moussalli 2011, Thomas *et al.* 2015). In order to compare biologically plausible models (Burnham *et al.* 2011), we constrained the model set to include fixed variables (i.e. present in all models) and subset models that included controls for specific variables. The fixed variables were immatures' age (to control for the decrease in social learning with age), a dyad's proximity during foraging (SRI; to test for the effect of demonstrators' characteristics independently from association patterns), immatures' proximity degree (the number of partners being a control for dyads' SRI) and their number of matriline members (to control for the effect of these bonds on social learning), time period and troop. We additionally subset models that included either one of immatures' relative rank or a dyad's relative rank difference. The two variables could not be present together because correlated (see Appendix 3, §3.4), but one of the two needed to be present to control for the effect of immatures' rank on learning opportunities (Marshall *et al.* 2012). Finally, we constrained the proportion of individuals of a certain age and immatures' total grooming amount (controls) to be present together with demonstrators' age and a dyad's grooming proportion, respectively (see Appendix 3, §3.8). We then selected and averaged the best models as those with a $\Delta AICc < 7$ (including those with a sum of weights < 0.95) using *MuMIn*'s *get.models* and *model.avg*, respectively (Burnham *et al.* 2011). We interpreted the results deriving from the full average (i.e., an estimate of zero is added in models where a variable is absent) to determine which factors have the strongest effect on the proportion of social learning (Grueber *et al.* 2011). Confidence intervals were calculated with the function *confint.default*. Finally, we assessed the relative importance of each independent variable (RVI)

by summing its best models' Akaike weights. When $RVI = 1$, it means that the variable is present in all the best models and thus explains a large part of the variance in the dependent variable (Grampp *et al.* 2019).

Table 4.1: Summary of the models used to test hypotheses' H1 and H2 predictions, including the type of test used, the dependent variables, the models' fixed factors (predictors and controls) and random factors, and the network involved. Under 'Model', '*' means that a permutation test was performed. The last column indicates whether each prediction was supported and, if not or only partially, how.

Hypothesis	Predictions	Model	Type	Dependent variable	Fixed predictors	Fixed controls	Random factors	Selection	Support
H1: Immatures' tendency to learn socially changes with age and differs by sex.	P1a: Social learning increases during infancy and decreases during juvenile years; P1b: This decrease will be greater in males than in females.	1	GLMM binomial (link 'logit').	Presence/absence of immatures' scrounge given in each focal observation.	Immatures' age, age ² (P1a); age:sex, age ² :sex, sex (P1b).	Immatures' rank, time period, troop, observation length.	Immatures' identities nested in the mothers' identities.	Full models	P1a: Yes; P1b: No (immatures' age:sex not significant).
		2		Presence/absence of immatures' other learning behaviours given in each focal observation.					P1a: Partial (immatures' age ² not significant); P1b: No (immatures' age:sex not significant).
H2: Immatures' learning from different individuals depends on their own age and on the demonstrators' characteristics.	P2a: Learning from demonstrators in proximity decreases with immatures' age; P2b: Immatures prefer demonstrators knowledgeable on local resources (older individuals and philopatric females); P2c: Immatures prefer tolerant demonstrators (grooming affiliates, lower- or similarly ranked individuals).	3	GLMM binomial (link 'logit') with weights (counts).	Proportions of immatures' scrounge given to each demonstrator in each time period.	Immatures' age, immature-demonstrator dyads' proximity foraging, age:dyads' proximity foraging (P2a); demonstrators' age and sex (P2b); dyads' grooming allocation, relative rank difference (P2c).	Immatures' rank, total grooming amount, degree proximity; time period, troop, demonstrators' availability (age).	Immatures' identities nested in the mothers' identities, demonstrators' identities.	Information Theoretic (AICc), models with $\Delta AICc < 7$ averaged.	P2a: Yes; P2b: No (demonstrators' age and sex not significant); P2c: Partial (dyads' relative rank difference not included).
		4		Proportions of immatures' other learning behaviours given to each demonstrator in each time period.					P2a: Yes; P2b: No (demonstrators' age and sex not significant); P2c: Partial (dyads' relative rank difference not significant).

4.4 RESULTS

In the following sections, we present the results (following each prediction) related to our main variables of interest (predictors) for hypotheses H1 and H2 (see §4.3). We also discuss the results of immatures' relative rank (control) because of the important role that dominance rank plays in baboon society (King *et al.* 2008). The number of observations and sample size for each model are shown in Appendix 3, §3.8. Full results' tables (i.e. including all the independent variables) are reported in Appendix 3, §3.9. Comparisons among H1 models' variables through standardised (i.e., all variables on the same scale) estimates are shown in Appendix 3, §3.10.

4.4.1 Results H1: Immatures' tendency to learn socially changes with age and differs by sex

To address our first hypothesis, we tested how (P1a) immatures' social learning changed with age and (P1b) sex (Table 4.2 and Figure 4.2). Our first prediction for H1, P1a, was partially confirmed: scrounging significantly increased up to weaning age and then decreased during juvenescence; the other social learning behaviours (see §4.3), instead, had a significant linear decrease with age, but the quadratic age effect was not significant. Between 1–4 years old, the odds of scrounging decreased by 41.83% and 35.63% in females and males, respectively; the odds of performing other learning behaviours decreased by 41.56% and 58.61% in females and males, respectively (see Appendix 3, §3.9). Our second prediction, P1b, was not confirmed: the interactions between age (linear and quadratic) and sex were not significant in either model, although the linear age-sex interaction was marginally significant for the other learning

behaviours model (p -value = 0.052, but odd's confidence intervals crossing one). Finally, higher-ranking immatures were relatively more likely to learn from others, but the effect of relative rank was significant only for the scrounging model. At the increase of one rank position, the odds of scrounging increased by 114.85%.

4.4.2 Results H2: Immatures' learning from different demonstrators depends on their own age and on the demonstrators' characteristics

To address our second hypothesis, we tested whether immatures preferred to learn from (P2a) individuals in proximity at different ages, (P2b) older and philopatric (female) individuals, (P2c) grooming affiliates and lower- or similarly ranked individuals. The best models comprised all the predictors (those not constrained to appear in all candidate models; see §4.3) except the relative rank difference between the immature and the demonstrator, which was included only in the other social learning behaviours (but not scrounging) best models. Among the unconstrained variables, the interaction between immatures' age and a (immature-demonstrator) dyad's proximity during foraging, and a dyad's grooming allocation were present in all best models ($RVI = 1$), both for scrounging and the other learning behaviours, while the immatures' relative rank was present in all the scrounging (but not the other learning behaviours) best models (Table 4.3). Because scrounging is defined as foraging within 1 m of another individual and our scrounging model included a dyad's foraging proximity among the predictors (see §4.3.5), we checked whether our results were affected by circularity. We run another model substituting foraging proximity with proximity outside of a foraging context (i.e., during grooming, travelling, resting). The results of this alternative model and of the main scrounging model were

qualitatively similar, indicating that circularity was not a concern (see Appendix 3, §3.9).

In the (final) averaged scrounging and other learning behaviours models, immatures' and demonstrators' characteristics had different effects on the odds of learning socially from a particular demonstrator (Table 4.2 and Figure 4.3; see also Appendix 3, §3.9). First (ordered based on significant effect size), immatures' age had the strongest significant effect on the odds of learning from a particular demonstrator in both models. For one standard deviation (SD) increase in age (approx. 16 months), there was an 81.75% and 111.45% increase in the odds of scrounging from and performing other learning behaviours towards a certain demonstrator, respectively. Second, the significant effect of a dyad's grooming allocation confirmed the first part of our P2c prediction: the odds of scrounging and performing other learning behaviours increased by 65.68% and 92.64%, respectively, with a one SD increase (approx. 0.11) in grooming allocation. Third, the effect of a dyad's proximity during foraging partially confirmed our P2a prediction since the predicted proximity effect was significant only for the scrounging model. For one SD increase in the proximity index (approx. 0.07), the odds of scrounging increased by 61.22%. As predicted, the odds of scrounging from and performing other learning behaviours towards individuals in proximity significantly decreased by 42.55% and 41.31%, respectively, with each increase in one SD in immatures' age. Fourth, higher-ranking immatures were relatively less likely to learn from a specific demonstrator, but relative rank had a significant effect only for the scrounging model. The odds of scrounging from a certain demonstrator decreased of 24.06% at the increase in one SD (approx. 0.23) in immature's relative rank. Fifth, demonstrators' age and sex had non-significant effects in either model, thus not supporting our P2b prediction. However,

demonstrators' age, included in most scrounging best models (RVI = 0.89), was marginally significant in the scrounging model (p -value = 0.054 and odd's confidence intervals not crossing one), with an opposite trend to what we predicted: the odds of scrounging from a certain demonstrator decreased by 11.65% at the increase in one SD (approx. 50 months) in demonstrators' age. Lastly, the predicted effect of a dyad's relative rank difference on the odds of performing the other learning behaviours (not present in the scrounging model) was not significant, thus not confirming the second part of our P2c prediction.

Table 4.2: Models' results for hypotheses **H1** (full models) and **H2** (averaged models). Variables of interest (depending on the model) include immatures' linear (H1 and H2) and quadratic (H1) age; immatures' sex and age-sex interactions (':') (H1); immatures' (relative) rank (H1 and H2); demonstrators' age and sex (H2); a (immature-demonstrator) dyad's grooming (Groom.) allocation, proximity (Prox.) in the foraging network, and (relative) rank difference (H2). The values reported for Sex refer to males. For each variable/ model are shown the estimate, the standard (Std.) error, the z value, the p -value ('NS' = not significant), the odds ratio (OR), the lower (LCI) and upper (UCI) 97.5% confidence intervals, and the percentage change in the odds of scrounging (Models 1 and 3) and performing other social learning behaviours (Models 2 and 4) at the increase of one unit (Models 1 and 2) or standard deviation (Models 3 and 4) in the independent variable. Significant (p -value ≤ 0.05) variables are highlighted (grey).

Model	Variable	Estimate	Std. Error	z value	p -value	OR	LCI	UCI	Percentage change
1	Age immature	-11.3419	4.7092	-2.4085	< 0.05	0.00	0.00	0.46	-100.00
	Age:Sex	1.1684	7.4901	0.1560	NS	3.22	0.00	6.29E+07	221.69
	Age ² immature	-18.6803	3.9576	-4.7201	< 0.001	0.00	0.00	0.00	-100.00
	Age ² :Sex	6.3010	6.2056	1.0154	NS	545.09	0.00	5.99E+08	5.44E+04
	Rank immature	0.7648	0.2262	3.3805	< 0.001	2.15	1.29	3.57	114.85
	Sex immature	0.0116	0.1176	0.0987	NS	1.01	0.78	1.32	1.17
2	Age immature	-16.1940	3.7098	-4.3652	< 0.001	0.00	0.00	0.00	-100.00
	Age:Sex	-11.8188	6.0851	-1.9422	NS	0.00	0.00	6.17	-100.00
	Age ² immature	-3.9443	3.4911	-1.1298	NS	0.02	0.00	48.46	-98.06
	Age ² :Sex	1.6544	5.7195	0.2893	NS	5.23	0.00	1.93E+06	423.00
	Rank immature	0.1907	0.1877	1.0159	NS	1.21	0.79	1.84	21.01
	Sex immature	-0.0601	0.0932	-0.6456	NS	0.94	0.76	1.16	-5.84
3	Age demonstrator	-0.1238	0.0642	1.9275	NS	0.88	0.79	0.96	-11.65
	Age immature	0.5975	0.0652	9.1520	< 0.001	1.82	1.60	2.07	81.75
	Age:Proximity	-0.5542	0.1050	5.2755	< 0.001	0.57	0.47	0.71	-42.55
	Groom. allocation	0.5049	0.0417	12.1068	< 0.001	1.66	1.53	1.80	65.68
	Prox. foraging	0.4776	0.0634	7.5235	< 0.001	1.61	1.42	1.83	61.22
	Rank immature	-0.2752	0.0661	4.1609	< 0.001	0.76	0.67	0.86	-24.06

Model	Variable	Estimate	Std. Error	z value	p-value	OR	LCI	UCI	Percentage change
	Sex demonstrator	0.0191	0.0400	0.4759	NS	1.02	0.95	1.16	1.92
4	Age demonstrator	-0.0059	0.0294	0.1992	NS	0.99	0.84	1.10	-0.58
	Age immature	0.7488	0.0852	8.7773	< 0.001	2.11	1.79	2.50	111.45
	Age:Proximity	-0.5329	0.1539	3.4580	< 0.001	0.59	0.43	0.79	-41.31
	Groom. allocation	0.6557	0.0519	12.6292	< 0.001	1.93	1.74	2.13	92.64
	Prox. foraging	0.1608	0.1067	1.5049	NS	1.17	0.95	1.45	17.44
	Rank difference	-0.0329	0.0580	0.5669	NS	0.97	0.82	1.07	-3.24
	Rank immature	-0.0220	0.0527	0.4171	NS	0.98	0.83	1.09	-2.18
	Sex demonstrator	0.0145	0.0489	0.2962	NS	1.01	0.90	1.23	1.46

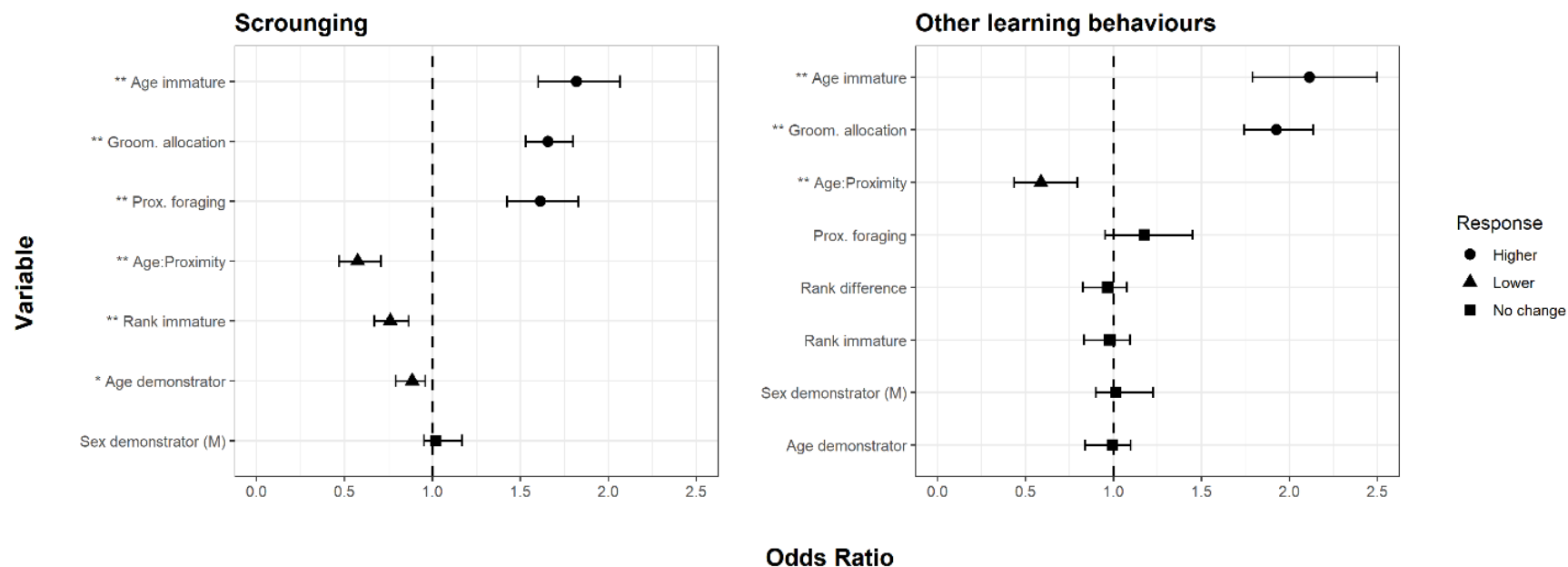
Table 4.3: Relative importance of hypothesis **H2** averaged models' (scrounging: 3; other social learning behaviours: 4) variables of interest, including immatures' age and (relative) rank; demonstrators' age and sex (male); a (immature-demonstrator) dyad's grooming (Groom.) allocation, proximity (Prox.) in the foraging network, and (relative) rank difference. Variables present in all best models (RVI = 1) are highlighted (grey).

Model	Variable	RVI
3	Age demonstrator	0.89
	Age immature	1.00
	Age:Proximity	1.00
	Groom. allocation	1.00
	Prox. foraging	1.00
	Rank immature	1.00
	Sex demonstrator	0.37
4	Age demonstrator	0.13
	Age immature	1.00
	Age:Proximity	1.00
	Groom. allocation	1.00
	Prox. foraging	1.00
	Rank difference	0.54
	Rank immature	0.46
	Sex demonstrator	0.30

Figure 4.2: Hypothesis **H1** models' **significant results** for scrounging (left) and the other social learning behaviours (right, top): (top) immatures' age changes in the odds of learning socially for females (F, red smooth line) and males (M, blue dotted line); (bottom, left) changes in the odds of scrounging with immatures' (relative) rank. Higher odds ratios mean a relatively higher likelihood of an event (*y*-axis variable) to occur. Ribbons represent 97.5% confidence intervals. The last section (bottom, right) shows the age changes in social learning behaviours (ordered in Legend based on their appearance on the *y*-axis) from raw data (behaviours summed across focal individuals in each time period).



Figure 4.3: Hypothesis H2 averaged models' results for scrounging (left) and the other social learning behaviours (right). Variables of interest include immatures' age and (relative) rank; demonstrators' age and sex (male); a (immature-demonstrator) dyad's grooming (Groom.) allocation, proximity (Prox.) in the foraging network, and (relative) rank difference. Independent variables' points represent odds ratios and whiskers are 97.5% confidence intervals (CIs). Points have different shapes depending on whether their CIs overlap with 1 (the odds of learning from a certain demonstrator – response – do not change at the increase in the independent variable), they are < 1 (the response decreases at the increase in the independent variable), or they are > 1 (the response increases at the increase in the independent variable). Variables are ordered based on effect size and significance ('**' = significant; '*' = marginally significant).



4.5 DISCUSSION

In this study, we explored when and to whom wild immature chacma baboons direct social learning behaviours. We first analysed (hypothesis H1) how social learning changes throughout development and differs by sex and then (hypothesis H2) the characteristics of the individuals to whom immatures pay attention (demonstrators). Here, we discuss our results and comment on the potential implications of the observed patterns on social information transmission at the group level.

4.5.1 Age changes in immatures' social learning occurrence

We first found that immature baboons' learning from others is heightened around the weaning period, while it is lower during juvenile years. Our results broadly align with the current literature describing social learning changes during infancy and juvenescence, supporting our hypothesis that young immatures learn from others more than older ones in order to reach foraging independence when they cease to be nursed (Bray *et al.* 2018, Carvajal and Schuppli 2022). Infant baboons start to feed on solid food when they are around four months old (Altmann 1980) and are weaned between 12–18 months at Tsaobis (Huchard *et al.* 2013, Carboni *et al.* 2022). Accordingly, the odds of scrounging, which involved the ingestion of solid food, were relatively low for young infants and increased throughout infancy until weaning age before declining. Instead, the odds of performing other social learning behaviours, which mainly involved the collection of foraging-related information, were relatively high from a young age and decreased steadily throughout the immature period. Social learning for infants and young juveniles could be facilitated by conspecifics' tolerance towards

young age classes and by young immatures' high centrality in the group's social network, offering them a wider choice of demonstrators compared to older immatures (Rapaport and Brown 2008, Whiten and van de Waal 2018). Despite the potential roles of tolerance and social connectedness, the weaning-centred timing of baboons' learning behaviours may point towards the greater importance of immatures' need to learn from others in explaining the observed patterns (Carvajal and Schuppli 2022). Indeed, these behaviours were linked to social learning in other studies (Whiten and van de Waal 2018, Schuppli and van Schaik 2019), explored below.

Our data showed that chacma baboons' observation of others during foraging was higher than scrounging until approx. three months of age (here and below: see Figure 4.2 for raw data patterns). The observation of others is related to how much immatures need to learn and can stimulate their independent learning (Whiten and van de Waal 2018). Young orangutans' observation increases with food processing complexity, while it decreases with an item's frequency in the diet and their increasing foraging competence (Schuppli, Meulman, *et al.* 2016). In addition, in both immature orangutans (Schuppli, Meulman, *et al.* 2016) and Japanese macaques (Tarnaud and Yamagiwa 2008), observation is followed by increasing manipulation of the same kind of items. This exploration behaviour is not a simple by-product of occupying the same environment: immature eastern chimpanzees manipulate the same kind of objects as their mothers more than expected based on their availability (Lamon *et al.* 2018). Observational learning may thus help immatures to acquire fundamental social information, to the point that it can affect their survival (Whiten and van de Waal 2018). For instance, juvenile black-tailed prairie dogs (Shier and Owings 2007) and Siberian jays (Griesser and Suzuki 2017) are more likely to

survive their first year of life if they observed experienced adults interacting with predators.

The inspection of food items accessed by others rapidly decreased in our study when infant baboons started scrounging. Baboons do not use tools for foraging and difficult-to-access foods may be rare in their diet compared to species that regularly process embedded food items (Perry and Manson 2003, Cheney and Seyfarth 2007). Therefore, infant baboons may be more likely to feed on a food item than inspecting it. On the other hand, in species with relatively more complex foraging habits, such as tool use (van Schaik *et al.* 1999) or predation (Thornton and Clutton-Brock 2011), immatures may frequently inspect the materials or the locations used by others, which could aid them in reaching a level of competence sufficient to forage independently (Rapaport and Brown 2008). Immature capuchins (Ottoni and Izar 2008) and western chimpanzees (Biro *et al.* 2003) explore others' tools and artefacts (e.g., broken nutshells), which continues, in parallel with individual practice, until young adults succeed in nut-cracking (de Resende *et al.* 2008, Whiten and van de Waal 2018). Similarly, meerkat pups (Thornton and Hodge 2009) and juvenile tufted capuchins (Gunst, Boinski, *et al.* 2010) inspect the locations where others' have been hunting. This decreases with age as juveniles develop adult-like preferences for foraging microhabitats and dedicate more time hunting on their own (Thornton and Hodge 2009, Gunst, Boinski, *et al.* 2010).

Feeding on food gained by others, in the form of feeding on scraps or tolerated stealing (Brown *et al.* 2004), was relatively uncommon in our study. Because, as mentioned, baboons do not normally process difficult-to-access foods (Cheney and Seyfarth 2007), infants fed on foods already gained by others only for a small variety of food types (see Appendix 3, §3.11), for which their

strength may not have been sufficient to access them. Similarly, immature capuchins, who lack the necessary manual dexterity and strength to crack nuts, feed on the seeds left from adults' nut-cracking activity (Ottoni and Izar 2008). These 'food transfers' are related to immatures' need to learn rather than their nutritional requirements (Jaeggi *et al.* 2008). In eastern chimpanzees, orangutans, and western lowland gorillas (*Gorilla gorilla gorilla*) food solicitations occur mainly when the food is difficult to process or rare (Silk 1978, Jaeggi *et al.* 2008), they are unrelated to food quality (Jaeggi *et al.* 2008), and decrease with increasing foraging competence (Nowell and Fletcher 2006, Jaeggi *et al.* 2008, Mikeliban *et al.* 2021). In addition, food transfers may affect immatures' foraging choices (Thornton and Clutton-Brock 2011). For example, following food provision by conspecific helpers, juvenile golden lion tamarins (*Leontopithecus rosalia*) (Troisi *et al.* 2021) and meerkat pups (Thornton 2008) were more likely to eat the same food item when tested alone compared to those who had no previous provisioning.

Both the acquisition of olfactory information from others' mouths and scrounging increased until weaning and decreased gradually during juvenescence in our sample. First, sniffing others' mouths is common in baboons (Cheney and Seyfarth 2007, Alberts 2019) and may drive immatures' foraging choices. For example, dogs (*Canis familiars*) (Lupfer-Johnson and Ross 2007) and brown rats (Galef and Wigmore 1983) interacting with another individual who had previously been fed preferred to eat the food with the same flavour as the one eaten by the first individual. Second, scrounging may aid the acquisition of a species' typical diet (Hauser 1993, Tarnaud 2004), independently from encountering a similar food availability (Jaeggi *et al.* 2010). In Mayotte brown lemurs (*Eulemur fulvus*) (Tarnaud 2004) and vervet monkeys (Hauser 1993),

infants gradually synchronise their daily feeding rhythms with their mothers' and mother-offspring diets largely overlap by weaning. In addition, the diets of immature Bornean orangutans are similar to their mothers' despite the fact that mothers inhabiting the same territory have different diets (Jaeggi *et al.* 2010). The social information that immatures gain through foraging together with others may also increase their chances of survival (Hauser 1993). In vervet monkeys, there is a positive association between scrounging with the mother and infants' survival (Hauser 1993), and juvenile marsh harriers (*Circus aeruginosus*) are more successful in catching prey when hunting in a group with experienced adults than with peers or alone (Kitowski 2009). In sum, these studies indicate that immatures collect social information when they direct social learning behaviours towards their group mates (Whiten and van de Waal 2018, Schuppli and van Schaik 2019), which may allow them to become foraging independent by weaning (Carvajal and Schuppli 2022). However, because young primates often require a vast dietary knowledge to reach an adult-level foraging competence (Bray *et al.* 2018, Alberts 2019), they may refine their foraging skills beyond weaning age (Bray *et al.* 2018, Carvajal and Schuppli 2022).

The age changes in baboons' social learning behaviours show that immatures keep collecting foraging information from others even after they have been weaned. In particular, the odds of scrounging remained stable until approx. 30 months of age, more than 10 months later than the age at which infants are weaned at Tsaobis (Huchard *et al.* 2013, Carboni *et al.* 2022). Juvenile baboons may learn socially more than adults in order to acquire the species' full dietary repertoire and improve their abilities to find suitable foraging patches (Whiten and van de Waal 2018). First, baboons can feed on up to 250 different types of plants (Alberts 2019), and may encounter rare or seasonal foods for the first time only

during juvenescence (Carvajal and Schuppli 2022). Accordingly, the relatively higher dietary complexity of Sumatran orangutans results in a later acquisition of the adult-level feeding rates compared to the Bornean peers (Schuppli, Forss, *et al.* 2016). Second, juveniles' lower efficiency in locating food compared to adults was reported in another chacma baboon population (Johnson and Bock 2004). Similarly, juvenile marsh harriers select the best habitats to catch prey when hunting in a group with others, while, when alone, they choose habitats based on their availability (Kitowski 2009). Overall, there are numerous examples that may support immature baboons' need to learn socially as an explanation of the observed patterns, although social factors could also have an influence.

An alternative, or complimentary, explanation for the patterns of learning behaviours seen in this population could be that social factors affect younger and older immatures differently. Infants and young juveniles may have enhanced social learning opportunities because they are well tolerated by other group members and, perhaps as a result, because they have numerous proximity associates (Berman 1982b, Silk 1999). Both tolerated proximity (Ottoni and Izar 2008, Rapaport and Brown 2008) and centrality in a group's proximity network (Aplin *et al.* 2012, Carter, Torrents Ticó, *et al.* 2016) may facilitate immatures' access to social information, but they decrease with immatures' age. The social learning opportunities of older juveniles may thus be more limited compared to younger immatures (Pereira 1988a, Mikeliban *et al.* 2021). The vicinity of older juveniles is relatively less tolerated (Pereira 1988a, Tarnaud and Yamagiwa 2008) and they have lower proximity associations compared to younger immatures (Vilette *et al.* 2022, Roatti *et al.* 2023a). In addition, immatures become less bonded to their maternal kin with age (Berman 1982a, Roatti *et al.* 2023a). This may reduce the availability of tolerant demonstrators in proximity because

close kin tend to be more tolerant towards each other than non-kin (Chapais and Belisle 2001, Silk 2009). Proximity tolerance and connectedness may thus contribute to explain why younger immatures learn more from others than older ones. However, immatures' weaning-centred learning suggests that learning from others derives mainly from their need to become competent foragers (Whiten and van de Waal 2018, Carvajal and Schuppli 2022). This is also supported by our results on the effects of immatures' sex and dominance rank on social learning occurrence (see below).

4.5.2 Immatures' choice of demonstrators

We then found that, as predicted, immature baboons preferred to learn from individuals closer in their proximity and grooming networks. However, contrary to our prediction, they tended to choose younger over older demonstrators. Learning from individuals in proximity decreased with age independently from the number of partners with whom immatures associated. In addition, the odds of learning from a certain demonstrator increased with age, which was the factor affecting immatures' learning allocations the most. Taken together, these findings indicate that, as they aged, immatures shifted their learning from a wide range of individuals to specific demonstrators. Infants and young juveniles are constrained by the proximity of caring figures for nurture (Altmann 1980) and agonistic support when their dominance rank is not yet established (Holekamp and Smale 1991). Therefore, infants and young juveniles may learn from anyone in proximity, including mainly individuals from their mother's network (vervet monkeys (Grampp *et al.* 2019), long-tailed macaques (Tan *et al.* 2018)), such as maternal kin (Holekamp *et al.* 1997, Silk *et al.* 2010a). The tolerance of close kin may allow youngsters to exploit foraging resources that they could not access on their own

(Chapais and Belisle 2001, Silk 2009). For instance, juvenile chacma and olive (*P. anubis*) baboons associating with their mother and father feed in/on relatively higher quality patches/ foods (Huchard *et al.* 2013, Lynch *et al.* 2020). On the other hand, older juveniles may actively look for specific demonstrators beyond their regular foraging associates (vervet monkeys (Grampp *et al.* 2019), tufted capuchins (de Resende *et al.* 2004)). Because older immatures are less bonded to maternal kin (Berman 1982a, Roatti *et al.* 2023a) and their proximity may be less tolerated by others (Pereira 1988b, 1988a) compared to younger immatures, they may concentrate their learning efforts towards fewer tolerant demonstrators, such as grooming partners (Lonsdorf and Bonnie 2010).

Grooming affiliation was more important than spatial proximity in determining immatures' choice of demonstrators. Immature baboons, independently from how much grooming they gave and received, preferred to learn from their grooming partners. Grooming is a form of social affiliation that can be traded for tolerance by primates living in despotic societies (Sick *et al.* 2014, Borgeaud and Bshary 2015). Sharing strong social bonds may enable immatures to access better learning and foraging opportunities independently from their kinship and dominance relationships (King, Clark, *et al.* 2011). For example, adult chacma baboons tend to scrounge with close grooming partners, while kinship does not affect their scrounging patterns (King *et al.* 2009, King, Clark, *et al.* 2011). Social affiliation also reduces the agonism received by low ranking baboons during foraging (Marshall *et al.* 2015). Although immatures still need to integrate themselves into the adults' grooming network (Vilette *et al.* 2022, Roatti *et al.* 2023a), unrelated conspecifics' tolerance during foraging may explain the importance of grooming interactions in choosing from whom to learn (long-tailed macaques (Tan *et al.* 2018), tufted capuchins (Coelho *et al.* 2015)). Grooming

bonds may also allow immatures to access better foraging patches by scrounging from unrelated dominant individuals (tufted capuchins (Coelho *et al.* 2015)). Concurrently, grooming tolerance may derive from nepotism (Chapais and Belisle 2001, Silk 2009) because, in matrilineal societies, close maternal relatives preferentially groom together (Charpentier *et al.* 2012, Kulik *et al.* 2015, Lange *et al.* 2023). Indeed, immatures' grooming allocations were positively correlated with maternal relatedness (Spearman's rank correlation: 0.30, p -value < 0.001). Overall, our results are consistent with the hypothesis that social tolerance enhances social information transmission (Bonnie and de Waal 2006, Pasquaretta *et al.* 2014), which was also supported by our findings on demonstrators' age.

Immature baboons tended to learn from other immatures and young sub/adults, independently from their shared proximity and grooming associations. The odds of scrounging decreased with demonstrators' age, although the effect was only marginally significant. Because the distribution of the immature-demonstrator age differences peaked around zero, with most values within a 60-month age difference (see Appendix 3, §3.9), the preferred demonstrators included the younger age classes independently from their availability in the troop. We expected that immatures would learn from older individuals, who are knowledgeable on the local food resources (Lonsdorf and Bonnie 2010). However, because baboons do not need extensive experience in food processing skills (Cheney and Seyfarth 2007), immatures may not target older demonstrators as in species that regularly extract embedded foods (long-tailed macaques (Tan *et al.* 2018), tufted capuchins (Coelho *et al.* 2015)). Instead, immatures may choose younger demonstrators because they are among their play partners and are thus more tolerant towards them (Shimada and Sueur 2017). Social play,

which decreases with age as grooming increases, may have a similar social bonding function as grooming for juvenile primates (Shimada and Sueur 2014, 2017), especially for males (Lonsdorf 2017, Amici, Kulik, *et al.* 2019) (see below).

4.5.3 The effects of immatures' sex and dominance rank

We then found that immature baboons' sex and dominance rank affected their social learning occurrence and their choice of demonstrators. While all similarly aged immatures may have an equal *need* to learn, sex and rank differences may translate into higher or lower social learning opportunities. However, our results suggest that lower-opportunity immatures at least partially overcome their phenotypical constraints by being relatively more active in looking for suitable demonstrators. Immature males may have less social learning opportunities than females but learn from others as much as them. Because baboon females and males are weaned at similar ages at Tsaobis (Carboni *et al.* 2022), both sexes may need to collect foraging information at the same pace in order to reach independence (Carvajal and Schuppli 2022). While infants of both sexes have a similar social centrality, in female-philopatric species, juvenile males become relatively less integrated in the grooming network (Vilette *et al.* 2022, Roatti *et al.* 2023a) and less bonded to their matriline (Kulik *et al.* 2015, Roatti *et al.* 2023a) with age. This could limit males' choice of tolerant demonstrators from grooming affiliates (Coelho *et al.* 2015, Tan *et al.* 2018) and maternal kin in proximity (Chapais and Belisle 2001, Silk 2009), and reduce their overall learning from others (Hollén and Manser 2006). Indeed, for males, the amount of grooming shared with an individual was relatively less important in determining their learning allocations, and the decrease in learning from individuals in proximity with age was more prominent compared to female peers.

Nevertheless, the absence of significant sex differences in social learning occurrence in both of our models suggests that immature males compensate by looking for different kinds of tolerant demonstrators. In particular, because juvenile males engage in more social play than female peers (Lonsdorf 2017, Amici, Kulik, *et al.* 2019), they may learn relatively more from play partners, who could constitute a source of affiliates comparable to grooming partners (Shimada and Sueur 2014, 2017).

Higher-ranking immatures may have more social learning opportunities than lower-ranking peers, but this translated into greater learning from others only for scrounging. In addition, the odds of scrounging from a certain demonstrator decreased with an increase in immatures' dominance rank. Independently from their age and their number of proximity associates, higher-ranking immatures had relatively more scrounging partners. Dominant immatures may access social information relatively more easily due to their better competitive abilities (Pereira 1989, Holekamp and Smale 1991) and/or their higher social connectedness (Wooddell *et al.* 2020, Liu *et al.* 2022). First, dominance rank had a stronger effect than age on scrounging occurrence (see Appendix 3, §3.10), in accordance with chacma baboons' strictly hierarchical society (King *et al.* 2008, Silk *et al.* 2017). Indeed, scrounging involves the depletion of another individual's patch and may lead to agonistic competition (King *et al.* 2009, Marshall *et al.* 2012). Higher-ranking immatures can be supported by a greater number of individuals (i.e., close kin and individuals ranking in-between the two opponents) in case of an agonistic interaction (Pereira 1989, Holekamp *et al.* 1997), and this can work as a deterrent against them being attacked (Horrocks and Hunte 1983, Prud'Homme and Chapais 1993). Therefore, compared to lower-ranking peers, dominant immatures may be: (1) more willing to scrounge from a demonstrator (2), more

likely to win a between-immatures competition for the same demonstrator; (3) and able to scrounge more opportunistically from any available demonstrator (Chapais 1988, Markham *et al.* 2015). Because dominant matriline units are not larger than subordinate ones (Cheney *et al.* 2004) (see also Appendix 2, §2.3), having more scrounging partners may mean learning from individuals outside the matriline unit (see below). On the other hand, low ranking peers could benefit more from selecting tolerant demonstrators (Sick *et al.* 2014, Borgeaud and Bshary 2015). For example, low ranking chacma baboons who groom relatively more their dominant group mates receive less agonism during foraging, which translates into a better foraging performance (Marshall *et al.* 2015).

Second, dominant immatures may be more likely to acquire information from others because of their relatively higher centrality in the group's network (Carter, Torrents Ticó, *et al.* 2016, Kulahci *et al.* 2016). Because dominant matriline units are more cohesive (Holekamp *et al.* 1997, Koyama 2003), higher-ranking immatures may also have a relatively wider choice of tolerant demonstrators in proximity (Chapais and Belisle 2001, Silk 2009). For instance, dominant adult chacma baboons are more central in the co-feeding network, sharing food patches with multiple individuals (King, Clark, *et al.* 2011). Nevertheless, the fact that age had the strongest effect on the occurrence of the other learning behaviours (see Appendix 3, §3.10), while dominance rank had no significant effect, could mean that social connectedness had a relatively small role in the observed scrounging patterns. Because the other learning behaviours involve mainly the collection of foraging-related information without reducing a demonstrator's foraging efficiency, immatures' competitive abilities may affect their social learning opportunities less than for scrounging. This suggests that, in general, lower-ranking immatures could buffer their lower social connectedness, perhaps by

actively searching for more tolerant demonstrators. However, this was not enough to offset for their lower competitive abilities in scrounging. Similarly, low ranking chacma baboons could maintain stable foraging levels in low- but not in high-competition artificial foraging patches, despite their tendency to scrounge with grooming affiliates in both cases (Marshall *et al.* 2015).

4.5.4 Implications for social information transmission

Our study confirmed that immatures acquire social information more than adults. Because information acquisition is the first step of social information transmission in a group (Carter, Torrents Ticó, *et al.* 2016), immatures could play a fundamental role in information transmission at the group level (Whiten and van de Waal 2018, Schuppli and van Schaik 2019). When maintained through time, a socially-learned behaviour can form a local culture (Laland and Janik 2006, Allen 2019). Determining what constrains or enhances immatures' social learning could thus help to understand why culture develops in some social groups and not others.

In this baboon population, information transmission may be constrained in some instances, and enhanced in others. First, immatures' age changes in social learning patterns and the need to learn from tolerant demonstrators could constrain social information transmission. Because matriline members tend to associate in proximity and groom together (Holekamp *et al.* 1997, Silk *et al.* 2010a), the demonstrator preferences of both younger and older immature baboons (see above) may indicate that matriline units are important centres of information acquisition. The presence of these matrilineal social clusters could limit the spread of social information across different matriline, potentially leading to the formation of 'matrilineal cultures' as opposed to group cultures (van

de Waal *et al.* 2012). For example, vervet monkeys' techniques to clean sand-covered grapes were more similar within than across matriline. Individuals maintained their cleaning preferences through time and in the absence of matriline members nearby. A genetic explanation is unlikely because the mother-offspring similarity in cleaning techniques was higher than that between full sisters (van de Waal *et al.* 2012).

Second, immatures' sex and dominance rank differences in learning from others may enhance social information transmission. Because juvenile males and higher-ranking immatures may learn relatively more from individuals outside their matriline (see above), they could facilitate social information flow across matriline. However, the effects of sex and dominance rank were relatively limited. Immature males' learning allocations did not differ greatly from those of females (see Appendix 3, §3.6) and immatures' dominance rank affected only the scrounging patterns. In addition, although social rank had a strong influence on the occurrence of scrounging, its effect on demonstrator choice was weaker than those of proximity and grooming associations. We conclude that chacma baboons' high nepotistic biases (Silk *et al.* 2010a) may limit group-level social information transmission and potentially the formation of culture (van de Waal *et al.* 2012, Pasquaretta *et al.* 2014). This may contribute to explain why cultural behaviours were not reported in chacma baboons, while olive baboons, a species with a lower degree of nepotism (Silk *et al.* 2017, Fischer *et al.* 2019), show evidence of culture (Strum 1975, Sapolsky and Share 2004).

5 CHAPTER 5: THE ROLE OF MATERNAL WARMTH ON SOCIAL INFORMATION ACQUISITION IN WILD BABOONS

5.1 ABSTRACT

Maternal warmth, a poorly studied dimension of maternal style, may enhance immatures' learning from others. This is important because immature age classes could have a fundamental role in social information transmission, and ultimately the rise of culture in wild social groups. Our aim was to determine whether grooming received from the mother – a behaviour associated with warmth – during infancy and juvenescence affected juveniles' tendency to learn socially. We had two alternative mutually exclusive predictions: (1) based on the results of previous studies of secure attachment and exploration, we predicted that maternal grooming would increase learning from others; (2) because three features potentially associated with lower maternal grooming (i.e., the number of maternal siblings, dominance rank, and social integration), could increase social learning, we predicted that maternal grooming would be associated with lower learning from others. While we confirmed that juveniles' number of siblings, dominance rank, and grooming network centrality increased social learning, we did not find any support for our predictions on maternal grooming. We discuss the possible reasons behind the absence of a role of maternal warmth on juvenile baboons' learning propensities.

5.2 INTRODUCTION

Mothers are the primary caring figure in most species of mammals (Broad *et al.* 2006, Okabe *et al.* 2012). The bond formed between mothers and their infants accompanies the offspring throughout the dependency period, when mothers provide nutrition and protection (Altmann 1980, Maestripieri 2018). Mothers may, however, differ in their maternal style, defined as consistent between-individual variation in infant care behaviours (Berman 1990, Fairbanks 1996). Maternal style may cause a non-genetic imprint on the offspring's phenotype, for example affecting their neuroendocrine system and behaviour (Wolf and Wade 2009, Von Borell *et al.* 2019). Despite genetics contributing to individual differences (Von Borell *et al.* 2019), the non-genetic influence of maternal style on her offspring's physiology and behaviour has been confirmed by cross-fostering studies (Liu *et al.* 2000, Maestripieri 2005, Maestripieri *et al.* 2006).

Mother-infant bonding and maternal style have been studied mainly in non-human primates (hereafter primates), particularly Cercopithecine monkeys (e.g., macaques *Macaca* spp. and baboons *Papio* spp.), and in humans (Maestripieri 1999, Maestripieri and Roney 2006, Gholampour *et al.* 2020). In primates, maternal style has been described as varying along two main independent dimensions: protectiveness and rejection. Protectiveness describes the frequency with which a mother maintains contact and/or proximity with her infant, and prevents the infant from leaving her contact and/or proximity (Maestripieri 1994, 2001, Sekizawa and Kutsukake 2019). Rejection describes the frequency with which a mother breaks contact and/or proximity with her infant, and prevents the infant from making contact with her (Fairbanks and McGuire 1985, Schino *et al.* 1995, Liu *et al.* 2018). A relatively less studied third dimension is warmth,

which correlates with being in ventral-ventral contact with the infant (Hinde and Simpson 1975), cradling and grooming the infant (Hinde and Simpson 1975, Maestriperi 1998, Bardi *et al.* 2001, Maestriperi *et al.* 2009), and allowing nursing (Maestriperi *et al.* 2009). Warmth may also be present in brown rats (*Rattus norvegicus*) in the form of licking-grooming (hereafter grooming) (Champagne *et al.* 2003), and common bottlenose dolphins (*Tursiops truncatus*) as pectoral fin contacts (Dudzinski *et al.* 2021).

Similar to Cercopithecines, human parental style is formed by two main dimensions. These are responsiveness (i.e., recognising the child's individuality and needs) and demandingness (i.e., setting and enforcing limits on the child's behaviour) (Maestriperi 1999). Responsiveness, often described as being affectionate and responding to signs of distress in the child (Tamis-LeMonda *et al.* 2001, McFadden and Tamis-Lemonda 2013), may be the human equivalent of warmth in other primates (Mason and Mendoza 1998, Maestriperi and Roney 2006). The degree to which caregivers express responsive behaviours may determine the infant's attachment security, i.e., a measure of how much a caregiver represents a secure base to explore the surrounding environment, both in humans (Susman-Stillman *et al.* 1996, Waters *et al.* 2000) and other primates (Kondo-Ikemura and Waters 1995, McCormack *et al.* 2015). Securely attached individuals, who have warm mothers, may be more willing to explore the social and physical environment surrounding their caregivers compared to insecurely attached ones (Spencer-Booth and Hinde 1971, Kondo-Ikemura and Waters 1995, Waters and Cummings 2000).

Maternal style (or parental style in humans) may influence individuals' development (Maestriperi 2018) by having both short- and long-term effects on the offspring's behaviour and/or physiology (Mogi *et al.* 2011, Parker and

Maestriperi 2011). However, little is known about how maternal style could affect social learning (i.e., learning from others (Laland 2004)) (Lindeyer *et al.* 2012). This is important because behaviours transmitted socially in a group and maintained through time can form a local culture (Laland and Janik 2006, Allen 2019) and contribute to between-population variation in fitness (McComb *et al.* 2001, Marcoux *et al.* 2007). Immature age classes may have a fundamental role in group-level social information transmission because they learn socially more than adults due to their inexperience with the environment (Laland 2004, Whiten and van de Waal 2018). Maternal style could thus add to the social and behavioural factors underlying the social information transmission process (Mesoudi *et al.* 2016) (see also Chapter 4). Because social learning is widespread in the animal kingdom (Whiten 2017, Allen 2019) and it assumes a special importance in humans through cumulative culture (Tennie *et al.* 2009, Dean *et al.* 2012), increasing our knowledge on the link between maternal style and social learning may help understanding the evolutionary bases of maternal behaviour in primates and potentially other mammals (Mason and Mendoza 1998, Maestriperi and Roney 2006).

Maternal warmth has been shown to increase the offspring's tendency to learn from others (Lindeyer *et al.* 2012), which could constitute a form of non-genetic inheritance (English *et al.* 2015, Sproul Bassett *et al.* 2020). For example, adult brown rats who received more maternal grooming as pups learn conspecifics' food preferences more than those who were maternally deprived (Lévy *et al.* 2003, Melo *et al.* 2006) or who received less maternal grooming (Lindeyer *et al.* 2012). Variation in maternal warmth may provide information on the current value of social *versus* personal information (Lindeyer *et al.* 2012). Although maternal style consists of relatively stable individual traits, there may be

within-individual changes due to environmental and/or social factors (Fairbanks 1996, Maestripieri 2018). For instance, mothers tend to show greater warmth when the environment poses risks to their offspring (Maestripieri 1998), who could, as a result, be securely attached and potentially relatively more willing to initiate learning interactions with other group mates (Kondo-Ikemura and Waters 1995). This may be advantageous because relying on social learning allows for greater vigilance for threat compared to individual exploration (Mathot and Giraldeau 2007). On the other hand, mothers tend to be less warm when having high stress levels due to, e.g., food scarcity (Bardi *et al.* 2004, Champagne and Meaney 2006), thus predisposing the offspring to be insecurely attached and, potentially, relatively less inclined to learn from others (Kondo-Ikemura and Waters 1995). In this case, collecting personal rather than social information may benefit the offspring to avoid intra-group competition (Chapman *et al.* 2008) and because social information on food availability may be unreliable (Boogert *et al.* 2013). The effects of receiving more or less maternal warmth could be, at least partially, reversed by later life events, which may ‘update’ the offspring’s learning strategies based on what is most advantageous in that moment (Melo *et al.* 2006).

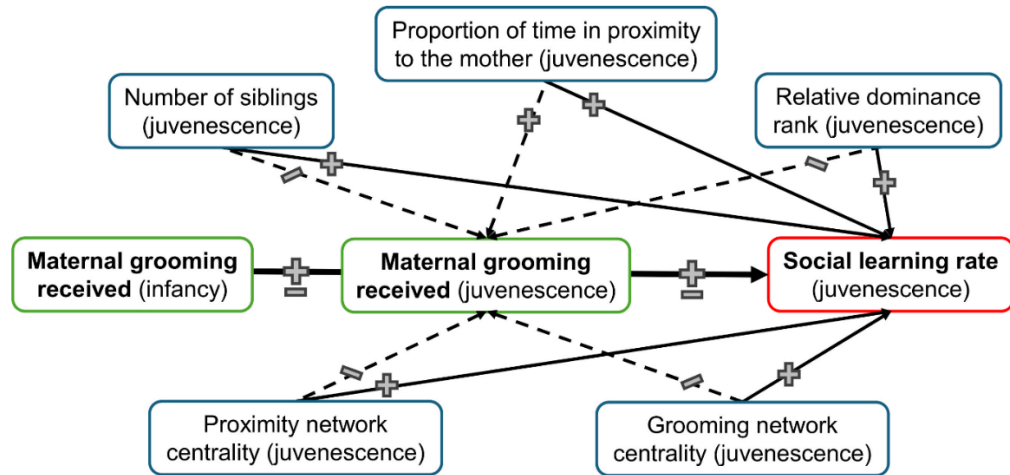
In this study, we investigated the effects of the grooming received from the mother, a behaviour associated with maternal warmth (Maestripieri *et al.* 2009), on the offspring’s tendency to acquire social information (hereafter learn socially) in a wild primate, the chacma baboon (*P. ursinus*). We focused on grooming because it has an important social bonding function in primates (Dunbar 1991, 2010) and because, unlike other warmth-related behaviours (i.e., ventral-ventral contact, cradling, and nursing) that are limited to infancy (Altmann 1980), maternal grooming occurs throughout development (Delaunay *et al.* 2023) (see

also Chapter 3). This characteristic allowed us to assess the influence of both a mother's earlier grooming investment towards her offspring and of her current investment on the immatures' tendency to learn socially around weaning, a period critical for the acquisition of feeding independence (Bray *et al.* 2018, Carvajal and Schuppli 2022) (see also Chapter 4). Baboons are an ideal taxon for this study because they live in large multi-male-multi-female social groups (Cheney and Seyfarth 2007), offering numerous opportunities to learn socially (van Boekholt *et al.* 2021). In addition, baboons' social learning abilities have been confirmed by information transmission experiments (Carter *et al.* 2014, Carter, Torrents Ticó, *et al.* 2016). Because baboons' societies are considered similar to those of early hominins, this study could provide insights on the evolution of human parental behaviour (Swedell and Plummer 2012, King 2022).

We tested the hypothesis that maternal warmth affects the offspring's tendency to acquire social information as young juveniles. Because other factors may have contrasting effects on social learning both directly and/or indirectly through maternal grooming (Figure 5.1), we proposed two alternative predictions for this hypothesis. First, we predicted that (P1) individuals who receive *more* maternal grooming during infancy and juvenescence would learn more from others. This prediction stems from (i) previous studies finding a positive influence of brown rats' maternal grooming on social learning in the offspring (Lindeyer *et al.* 2012), and (ii) from the fact that securely attached individuals (having warm mothers) may be more likely to initiate learning interactions (Kondo-Ikemura and Waters 1995). In addition, maternal grooming may increase with the time spent in proximity to the mother, which may also heighten social learning because the mother could be an important source of information for young juveniles (Whiten and van de Waal 2018) (see Chapter 4, §4.5). Alternatively, we predicted that

(P2) individuals who receive less maternal grooming during infancy and juvenescence would learn more from others. This is because three characteristics that may result in lower grooming received from the mother could be associated with higher learning from others. First, the more (maternal) siblings an immature has, the less grooming s/he may receive from the mother because offspring compete for maternal care (Lee 1987a, Delaunay *et al.* 2023). The number of siblings may, however, increase immatures' integration in the group's social network (Brent 2015), and thus their opportunities to collect social information (van Boekholt *et al.* 2021) (see Chapter 3, §3.4 and §3.5). Second, dominance rank may affect both maternal grooming and immatures' learning from others in despotic societies such as chacma baboons' (King *et al.* 2008). While dominant mothers may groom their offspring less than subordinate ones (Maestriperi 1998), higher-ranking immatures were found to acquire social information more frequently and from a wider variety of individuals than lower-ranking ones (see Chapter 4, §4.4 and §4.5). Third, social integration may drive down the relative time dedicated to grooming with the mother: highly socially central immatures may already groom with numerous individuals other than the mother (Wooddell *et al.* 2020, Liu *et al.* 2022). Nevertheless, social centrality predicted social information transmission in foraging patch discovering experiments (Carter, Torrents Ticó, *et al.* 2016).

Figure 5.1: Schematic representation of the considered direct (solid arrows) and/or indirect (dotted arrows) effects on immatures' social learning rate during juvenescence (response – red). The predictors (green) are the proportion of grooming received from the mother (duration over the total focal observation time) during infancy (6–11 months of age) and juvenescence (15–21 months of age). These predictors may be affected by other variables (controls; blue), which may also influence immatures' learning from others directly. The plus (increase) and minus (decrease) signs indicate the predicted directions of the variables' effects.



5.3 METHODS

5.3.1 Study site and species

This research was carried out at the Tsaobis Baboon Project, a long-term, individual-based study of a wild chacma baboon population (TBP 2019). Tsaobis, located on the edge of the Namib desert in central Namibia (22°22'S, 15°44'E), is a semi-desertic area, divided from east to west by the ephemeral Swakop River. The river hosts dense patches of woodland, while the surrounding hills have scarce vegetation (see Cowlshaw and Davies 1997 for a full description of the area). The study involves two troops (J and L) that range across Tsaobis Nature Park and the surrounding farmland. The troops are habituated to the presence of observers on foot and the majority of the individuals are recognisable through a unique combination of ear marks (proportion recognisable: 1 in 2021

and 0.98 in 2022) (see Chapter 4, §4.3, and Appendix 3, §3.1, for more details on the troops' composition).

Baboons' society is organised into matrilineal groups where females are philopatric (Silk *et al.* 1999, Cheney and Seyfarth 2007), while males disperse at maturity (around eight years old) (Alberts and Altmann 1995a, 1995b). Females' dominance hierarchy is linear and stable, with offspring inheriting their mothers' ranks (Cheney 1977, Pereira 1989). Adult females give birth to an infant approx. every two years (Dezeure, Baniel, *et al.* 2021) and infants of both sexes are weaned around 12–18 months of age at Tsaobis (Huchard *et al.* 2013, Carboni *et al.* 2022). For the purposes of this study, individuals ≤ 5 years old are considered immatures, among whom individuals ≤ 12 months of age are infants and those > 12 months of age are juveniles (Altmann 1980, Cheney *et al.* 2004). Females typically start menstruating around five years old and males enter sub-adulthood (before reaching full adult size) around six years old (Altmann *et al.* 1981, Alberts and Altmann 1995a, Altmann and Alberts 2003).

5.3.2 Data collection

Observations were conducted on the two study troops during two field seasons in 2021 (approx. six months) and 2022 (approx. three months), totalling nine months of data collection over the two years. Baboons were followed daily from dawn to dusk while collecting observational data with the application CyberTracker, which records time-stamped behaviours, allowing the calculation of both their frequency and duration (Liebenberg 2022).

We collected data on 13 immatures (J: 5; L: 8), including nine females and four males, born from different mothers. Infants' sex and the mother's identity

were determined through direct observation (nursing). The study subjects were followed both as infants in 2021 and as juveniles in 2022, allowing us to test our hypothesis on the effects of maternal grooming early in life and of current maternal grooming on social learning. The study subjects were observed as infants when they were six to 11 months old (mean age: 7.62 months) (see Chapter 4, §4.3, for details on date of birth estimates and age calculations). This first age period served to determine whether maternal care, in the form of grooming during infancy, affects the offspring's tendency to learn from others later in life (Lindeyer *et al.* 2012). Then, the same individuals were observed again as juveniles when they were 15 to 21 months old (mean age: 18.46 months). This second age period is characterised by an intense social learning activity (see Chapter 4, §4.4 and §4.5) and served to assess whether current maternal grooming affects immatures' social learning tendency during juvenescence.

To test our hypothesis, we collected data on both our variables of interest (i.e., immatures' learning from others and maternal grooming) and on other factors that may affect social learning directly and/or indirectly through maternal grooming (see Figure 5.1 and §5.3.2). We first obtained measures of immatures' social learning, the amount of grooming received by the mother, and their tendency to be in proximity to the mother, by collecting 20-min focal observations. Observations per individual were distributed evenly in four daily periods and each individual was observed as a focal only up to twice per day in two different and non-consecutive time periods. Focal observations per individual were also spread evenly throughout the field season (see Chapter 4, §4.3, for more details).

The frequency of immatures' social learning was derived from behaviours that may be indicative of social information acquisition during foraging. While we cannot know whether immatures are learning when performing these behaviours,

based on the previous literature (Brown *et al.* 2004, Rapaport and Brown 2008) and for simplicity, we refer to them as ‘social learning’ (see also Chapter 4). The six behaviours considered, previously used to assess immatures’ age changes in learning from others and demonstrator (i.e., the individual to whom they pay attention) preferences (see Chapter 4), included: ‘observe feed,’ defined as peering for ≥ 3 s at another individual while the latter is foraging (Biro *et al.* 2003, Schuppli, Meulman, *et al.* 2016); ‘inspect food,’ defined as manipulating the food accessed by another individual without eating it (Schiel and Huber 2006, Rapaport and Brown 2008); ‘feed scraps,’ defined as feeding on the scraps dropped by another individual (Ottoni *et al.* 2005, Tan *et al.* 2018); ‘sniff mouth,’ defined as smelling the mouth of another individual (Gunst, Leca, *et al.* 2010, Alberts 2019); ‘steal food,’ defined as grabbing a food item in possession of another individual (Brown *et al.* 2004, Mikeliban *et al.* 2021); ‘scrounging,’ defined as foraging on the same food as another individual within 1 m of the latter (in the same patch) (Ueno 2005, O’Mara and Hickey 2012) (see Chapter 4, §4.3, for more details). In all cases, we noted the identity of the individual to whom a learning behaviour was directed. To increase data independence, we did not record observations of the same dyad within the same 30 s.

During focal observations, we also recorded the amount of grooming that each immature received from the mother and their tendency to be in proximity to the mother. First, we collected the duration (in seconds) of a mother-to-offspring grooming bout. If grooming was interrupted for < 3 s, it was considered as an uninterrupted grooming bout. Second, immatures’ proximity within 5 m of the mother was assessed through scan samples performed every 5 min (five in a 20-min observation).

We then collected data on immatures' proximity and grooming associations to determine their social integration in the troop's network (see below). First, we performed troop-level proximity scans on all the recognisable individuals, recording the neighbours within 10 m of 'focal' individuals. To increase data independence, focal individuals were chosen from a randomised list of all troop members, and both focal individuals and their neighbours were not re-sampled within an hour (as focal individuals) if appearing again in a list (Carter, Torrents Ticó, *et al.* 2016) (see Chapter 4, §4.3, for more details). Second, we recorded *ad libitum* grooming interactions while moving through the troops to avoid a bias towards the individuals easier to find. A grooming dyad was not recorded more than once within the same half an hour (Carter, Torrents Ticó, *et al.* 2016).

Finally, we recorded data on dominance interactions to control for immatures' rank (see below) and used long-term demographic data. Dominance interactions were collected on all the recognisable troop members, both *ad libitum* and during focal observations. Dominance behaviours comprised displacements, supplants, threats, chases, and attacks (Huchard and Cowlshaw 2011). When these behaviours happened in combination, they were recorded as a single dominance interaction (Huchard and Cowlshaw 2011). Demographic data included each immature's number of maternal siblings in the troop, derived from troop composition data.

5.3.3 Data analysis

Data analyses were performed with R 4.3.0 (R Core Team 2022) using a longitudinal approach. We divided the data into three time periods of approx. three months each: two in 2021 (first and second half of the six-month field season) and one in 2022. We chose these time windows because they fit our

data resolution and could capture developmental changes (see Chapter 4, §4.3, for more details). Overall, we recorded 163.13 h of focal observation during infancy and 121.42 h during juvenescence, approx. evenly spread among the focal individuals (Table 5.1).

The measures (see below) used in our analyses were calculated for each immature individual in each 3-month time period in which s/he was observed. The immature study subjects were then divided into two groups corresponding to the previously-mentioned two age periods: (1) late infancy (6–11 months of age) and (2) early juvenescence (15–21 months of age). We thus had one set of behavioural measures per each immature individual, computed on 3-month time period data for each age period (13 rows). Because of the relatively narrow age range considered (five months during infancy and six months during juvenescence), we assumed that the amount of maternal grooming received by immatures within the same age period was not affected by their age. Because individuals entered our study at different ages, they may have been observed in different 3-month time periods while belonging to the same age period. We believe that the time period in which immatures were followed did not affect the amount of grooming received from the mother in the two age periods: during infancy, eight individuals were sampled in winter 2021 and five in summer 2021, but the mean grooming received during the first and the second 2021 time periods did not differ significantly (see Appendix 4, §4.1); during juvenescence, all individuals were sampled in winter 2022 but one immature followed in summer 2021 (Table 5.1). In addition, baboons do not have distinct mating and breeding seasons (Cheney *et al.* 2004, Dezeure, Baniel, *et al.* 2021) that could affect the troops' social structure (Brent, MacLarnon, *et al.* 2013).

Table 5.1: Summary of each immature study subject's (named by individual code) characteristics during infancy (first age period: 6–11 months of age) and juvenescence (second age period: 15–21 months of age). These include troop, sex ('F' = female; 'M' = male), age (in months), maternal identity, number (Nb.) of *maternal* siblings in the troop, the 3-month time period in which s/he was observed ('1' = winter 2021; '2' = summer 2021; '3' = winter 2022), and the focal observation hours (Obs. h) collected (per individual and in total per age period).

Troop	Sex	Immature	Mother	First age period (infancy)				Second age period (juvenescence)			
				Age (months)	Nb. siblings	Time period	Obs. h	Age (months)	Nb. siblings	Time period	Obs. h
J	F	JF58	JF39	8	1	1	12.84	21	2	3	9.63
		JF60	JF02	6	3	1	14.08	19	3	3	8.85
		JF61	JF30	8	4	2	11.77	17	5	3	8.79
	M	JM78	JF27	8	4	1	13.28	21	5	3	9.07
		JM85	JF36	8	3	2	11.47	18	4	3	8.72
L	F	LF58	LF17	6	5	2	11.84	15	5	3	9.65
		LF59	LF29	9	2	1	12.76	21	3	3	9.44
		LF56	LF33	11	1	1	13.00	15	1	2	11.38
		LF60	LF39	8	1	1	12.16	21	2	3	9.22
		LF61	LF38	8	1	1	12.52	21	2	3	9.80
		LF1212	LF23	6	3	2	11.91	15	3	3	8.60
	M	LM67	LF14	6	4	1	13.11	19	5	3	8.90
		LM68	LF13	7	5	2	12.39	17	5	3	9.37
J-L Troop				Total obs. h in first age period			163.13	Total obs. h in second age period			121.42

We first computed immatures' social learning, grooming received from the mother, and proximity to the mother in each 3-month time period. First, we derived the total number of times that each immature directed social learning behaviours to other group members. Second, we obtained the proportion of the total focal observation time that each immature received grooming from the mother. Third, we subset a random proximity scan from each focal observation (to increase data independence) and calculated the proportion of scans in which each immature was within 5 m of the mother.

We then built proximity and grooming networks in each 3-month time period. Both networks were weighted (i.e., values indicate both the presence and strength of a social connection) (Croft *et al.* 2011), and the grooming network was also directed. Associations were not filtered based on edge weight because this may eliminate important ties (Brent, MacLarnon, *et al.* 2013, Sosa 2016) and generate errors in the network structure (Farine and Whitehead 2015). Network graphs were created using the package *igraph* (Csardi and Nepusz 2006) and the function *graph_adjacency*. For the proximity data, we used a simple ratio index (SRI; i.e., the proportion of time two individuals associated) (Hoppitt and Farine 2018) (see Chapter 4, §4.3, for more details). For the grooming data, we used count matrices (i.e., the number of interactions per dyad). From network graphs, we calculated each immature's proximity and grooming (total) eigenvector centrality (hereafter centrality), i.e., the sum of the centralities of an individual's social partners, with *igraph*'s *eigen_centrality* function (Sosa *et al.* 2021). To make metrics comparable across networks of different sizes, we standardised them within each time period by mean-centring them around zero with a standard deviation of one through the function *scale* (Wey *et al.* 2008).

Finally, dominance ranks were determined for each troop member in each time period through the 'I & SI' method (de Vries 1998, Schmid and de Vries 2013). The method is appropriate for linear dominance hierarchies (de Vries 1995, Sánchez-Tójar *et al.* 2018) and has been applied in other studies on this population (Huchard and Cowlshaw 2011) (see Chapter 4, §4.3, for more details). Ordinal ranks were computed through the package *compete* and the function *isi13* (500 iterations) (Sánchez-Tójar *et al.* 2018, Vilette *et al.* 2020). Because infants were involved in very few or no dominance interactions, they were excluded from the rank calculation and assigned one ordinal rank below their mothers'. Absolute ranks were standardised by controlling for group size using the formula $1 - [(1 - r) / (1 - n)]$, where r is an individual's absolute rank and n is the group size. We thus obtained relative ranks ranging from '0' (lowest) to '1' (highest) (Baniel *et al.* 2018a).

To test our hypothesis, we used negative binomial models with the package *MASS* (Venables and Ripley 2002) and the function *glm.nb* (*link* = 'log'). We chose negative binomial models because the residuals' distribution of models run with a Poisson family was over-dispersed (> 2 (Thomas *et al.* 2015)). The base logarithm of each immature's focal observation time was added as an offset. Significance was accepted at $p\text{-value} \leq 0.05$ (Chowdhury and Turin 2020, Tredennick *et al.* 2021). We obtained R^2 values (coefficient of determination) from the package *MuMIn* (Bartoń 2022) and the function *r.squaredGLMM*. Before running the models, we checked for independent variables' linear correlations by computing their Pearson's correlation coefficients (r) (Thomas *et al.* 2015). We did not include in the same model variables with $r \geq 0.5$ (Suzuki *et al.* 2008, Dormann *et al.* 2013) (see below and Appendix 4, §4.2). In addition, we assessed multi-collinearity after running the models using variance inflation factors (VIFs)

with the package *car* (Fox *et al.* 2023) and the function *vif*. In all cases, VIFs were < 2 , indicating low collinearity (Dormann *et al.* 2013). We verified under/overdispersion with the package *DHARMA* (Hartig 2022) and the function *testDispersion*. In all cases, significant dispersion values were within the distribution's normal range of variation (0.7–2) (Thomas *et al.* 2015). We also checked the overall model fit plotting *DHARMA*'s simulated residuals through the function *simulateResiduals*. For each model variable, we obtained both the risk ratios (RR) by exponentiating the estimates and the 97.5% confidence intervals (CIs; function *confint*). RR represent an individual's relative risk (dependent variable) based on an exposure (independent variable). When $RR = 1$ and/or CIs cross one, there is no change in relative risk; when RR are < 1 or > 1 (and CIs do not cross one), the relative risk decreases or increases, respectively (George *et al.* 2020). The percentage change in RR per each unit variation in an independent variable was expressed as $(RR - 1) \times 100$.

The models tested featured immatures' social learning rates as the dependent variable. The independent variables of interest (predictors) were the proportion of total focal observation time in which immatures received grooming from the mother (hereafter maternal grooming) during infancy and during juvenescence. We then considered other independent variables that may affect learning from others during juvenescence directly and/or indirectly through maternal grooming: juveniles' number of maternal siblings in the troop, relative dominance rank, proportion of time spent in proximity to the mother, and centrality in the proximity and grooming social networks. These variables, inserted as fixed factors, served as controls in order to detect the independent effects of maternal grooming (see Figure 5.1 and §5.2). To control for the effect of troop, which was sometimes significant in previous analyses on social learning behaviours (see

Appendix 3, §3.9), we added it as a fixed variable (< 5 levels (Harrison *et al.* 2018)). We did not control for immatures' age because of the relatively small age range (see above) and because the occurrence of social learning behaviours during early juvenescence is relatively stable (see the results for scrounging – the most common social learning behaviour – in Chapter 4, §4.4 and §4.5). We also did not consider sex because the occurrence of social learning behaviours was not significantly predicted by sex and immatures' demonstrator preferences were similar in the two sexes (see Chapter 4, §4.4 and §4.5; and Appendix 3, §3.6). Finally, we did not include the time period in which each immature was observed during juvenescence because, as mentioned, they were mostly sampled in the same year and season (Table 5.1).

To test the effect of different variables while having a small sample size, we compared different models using an information theoretic approach (Chowdhury and Turin 2020, Tredennick *et al.* 2021) based on Akaike's Information Criterion (AIC) (Anderson *et al.* 2000). We used *MuMIn*'s *dredge* to calculate AICc values (corrected for small sample size) and weights (i.e., models' relative likelihood) for a set of candidate models (Symonds and Moussalli 2011, Thomas *et al.* 2015) (see Appendix 4, §4.3). We constrained the model set to insert 1–2 independent variable(s) per model to avoid over-parametrization (Thomas *et al.* 2015), and to include only variables not highly correlated with each other in the same model (see above and Appendix 4, §4.2). We then selected the best models as those with a sum of AICc weights < 0.95 using *MuMIn*'s *get.models* (Thomas *et al.* 2015), which included the models with $\Delta AICc < 7$ (Burnham *et al.* 2011) (see Appendix 4, §4.3). Because of the small sample size, the best models could not be averaged, and were thus assessed separately. We determined the relative importance of each independent variable (RVI) by summing its best models'

Akaike weights. When $RVI = 1$, it means that the variable is present in all the best models and thus explains a large part of the variance in the dependent variable (Grampp *et al.* 2019). Comparisons among the best models' variables through standardized (i.e., all variables on the same scale) estimates are shown in Appendix 4, §4.4.

5.4 RESULTS

To address our hypothesis, we tested whether juvenile baboons' social learning rate was positively (P1) or negatively (P2) affected by the grooming received from the mother during infancy and juvenescence. The best models selected were six out of 31 possible combinations (see Appendix 4, §4.3). Our predictions were not supported: among our predictors, only maternal grooming during juvenescence was included in one of the best models with a non-significant effect. However, other variables that we inserted as controls because of their potential effects on social learning and/or maternal grooming significantly affected juveniles' relative risk of learning from others (Table 5.2). We describe the variables included in the best models in order of standardised effect size (see Appendix 4, §4.4). Variables' relative importance is shown in Table 5.3.

The best models comprised the following variables with a significant positive effect: juveniles' number of maternal siblings in the troop, relative dominance rank, and grooming network centrality (see Figure 5.2 for predicted social learning rates from unstandardised variables and Figure 5.3 for best models' standardised predicted risk ratios). The non-significant proximity network centrality and maternal grooming during juvenescence were each included in one of the two best models with highest AICc (Models 5 and 6, respectively). Maternal grooming

had the weakest overall standardised effect. Among the significant variables, juveniles' number of siblings was present in five (out of six) best models (Models 1–3, 5, 6), including the top model. The number of siblings had the highest RVI (0.96) and, in general, the strongest (standardised) effect on the response variable. With the addition of one sibling, juveniles' relative risk of learning from others increased between (range of values) 20.21–27.11% (Models 6 and 2, respectively; unstandardised effects). Juveniles' relative rank was present in two best models (Models 1 and 4), including the top model. Relative rank had the second highest RVI (0.64) and second strongest (standardised) effect on the response variable. With an increase in one position in relative rank, juveniles' relative risk of learning from others increased by 189.88% and 244.02% (Models 1 and 4, respectively; unstandardised effects). Finally, juveniles' grooming network centrality was included in one best model (Model 2) with the lowest RVI (0.29) among the significant variables, but a similar (standardised) effect size as relative rank. At the increase in one unit of grooming centrality, juveniles' relative risk of learning from others increased by 23.87% (unstandardised effect).

Table 5.2: Best models' results including the following variables: juveniles' (15–21 months of age) grooming (Groom.) and proximity (Prox.) centrality, proportion of grooming received from the mother (#2; duration over total focal observation time), number (Nb.) of siblings, (relative) rank. For each variable/ model are shown the (unstandardised) estimate, the standard (Std.) error, the z value, the *p*-value ('NS' = not significant), the risk ratio (RR), the lower (LCI) and upper (UCI) 97.5% confidence intervals, and the percentage change in the relative risk of performing social learning behaviours at the increase of one unit in the independent variable. Significant (*p*-value ≤ 0.05) model variables are highlighted (grey).

Model	Variable	Estimate	Std. Error	z value	<i>p</i> -value	R ²	RR	LCI	UCI	Percentage change
1	Nb. siblings	0.1871	0.0475	3.9400	< 0.001	0.74	1.21	1.10	1.33	20.57
	Rank immature	1.0643	0.2897	3.6739	< 0.001	0.74	2.90	1.66	5.11	189.88
2	Groom. centrality	0.2140	0.0656	3.2612	< 0.05	0.71	1.24	1.09	1.41	23.87
	Nb. siblings	0.2399	0.0504	4.7609	< 0.001	0.71	1.27	1.15	1.41	27.11
3	Nb. siblings	0.2155	0.0684	3.1526	< 0.05	0.46	1.24	1.08	1.42	24.05
4	Rank immature	1.2355	0.4263	2.8986	< 0.05	0.41	3.44	1.52	8.04	244.02
5	Nb. siblings	0.2113	0.0652	3.2426	< 0.05	0.52	1.24	1.08	1.41	23.53
	Prox. centrality	0.1442	0.1140	1.2654	NS	0.52	1.16	0.92	1.46	15.52
6	Groom. received #2	-5.4828	6.6281	-0.8272	NS	0.48	0.00	0.00	1406.78	-99.58
	Nb. siblings	0.1841	0.0732	2.5141	< 0.05	0.48	1.20	1.04	1.40	20.21

Table 5.3: Best models' variables' relative importance (RVI; 1 = highest), including juveniles' (15–21 months of age) grooming (Groom.) and proximity (Prox.) centrality, proportion of grooming received from the mother (#2; duration over total observation time), number (Nb.) of siblings, and (relative) rank. The two variables with the highest RVIs are highlighted (grey).

Variable	RVI
Groom. centrality	0.29
Groom. received #2	0.01
Nb. siblings	0.96
Prox. centrality	0.01
Rank immature	0.64

Figure 5.2: Predicted juveniles' (15–21 months of age) **social learning behaviours** in function of their number (Nb.) of siblings, (relative) rank, and grooming (Groom.) centrality (in descending order of standardised effect size). The relationship is shown for different best models in ascending AICc order (1 to 6) from the top model (1 = lowest AICc). Ribbons represent 97.5% confidence intervals. Each variable's unstandardised effect is plotted only once even when appearing in more than one best model (same trend and similar effect sizes across models), choosing the model with lowest AICc.

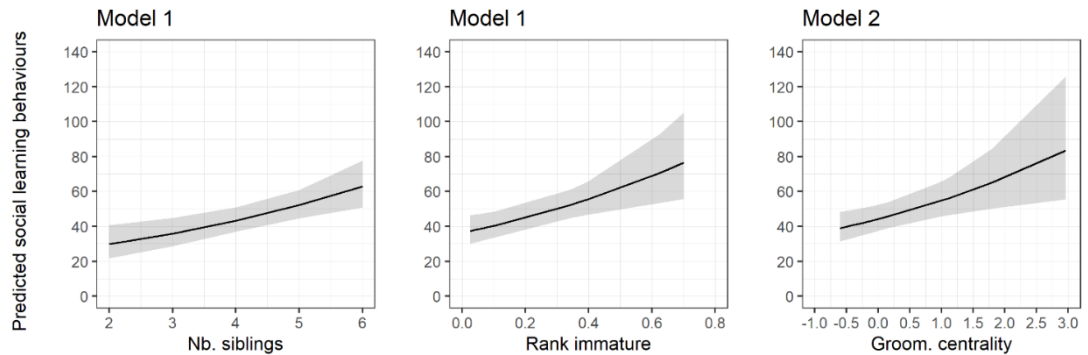
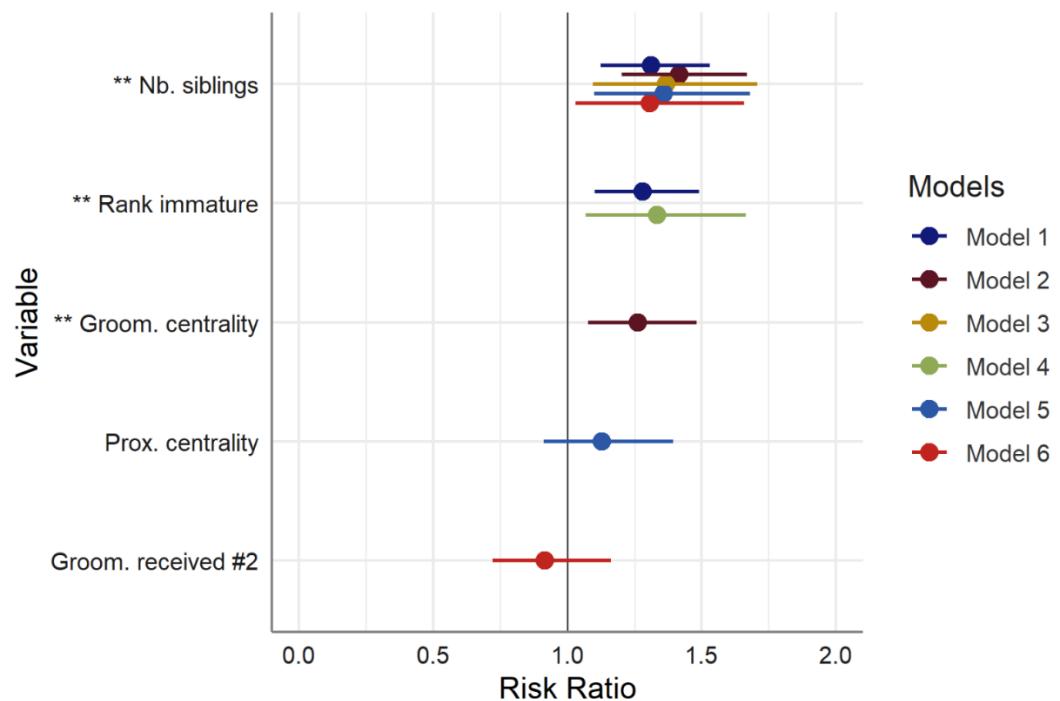


Figure 5.3: Overall **best models' standardised results**. Models are numbered in ascending AICc order (1 to 6) from the top model (1 = lowest AICc). Variables include juveniles' grooming (Groom.) and proximity (Prox.) centrality, proportion of grooming received from the mother (#2; duration over total focal observation time), number (Nb.) of siblings, and (relative) rank. Independent variables' points represent risk ratios and whiskers are 97.5% confidence intervals (CIs). When CIs overlap with 1, the relative risk of performing social learning behaviours does not change at the increase in the independent variable; when CIs are < 1, the relative risk decreases at the increase in the independent variable; when CIs are > 1, the relative risk increases at the increase in the independent variable. Significant variables are indicated with '**'.



5.5 DISCUSSION

In this chapter, we investigated whether maternal warmth, in the form of maternal grooming received during infancy and juvenescence, affected juveniles' tendency to learn socially in wild chacma baboons. We did not find any significant effect of maternal grooming, but other factors influenced juveniles' learning from others. Here, we first briefly interpret our results on the significant effects of juveniles' number of maternal siblings in the troop, dominance rank, and grooming network centrality. Subsequently, we discuss the possible reasons behind the lack of support to our hypothesis.

5.5.1 Predictors of juveniles' social learning rate

Juveniles' number of siblings, dominance rank, and grooming network centrality all enhanced learning from others, which agrees with our previous findings in this population (see previous Chapters). First, siblings may increase immature baboons' social learning opportunities by providing indirect social connections (Brent 2015) and thus heightening their social integration (Carter, Torrents Ticó, *et al.* 2016) (see Chapter 3, §3.4 and §3.5). In addition, close maternal relatives may be preferred as demonstrators because of their relatively greater tolerance (Chapais and Belisle 2001), which could be an important driver of demonstrator choice in despotic societies, such as chacma baboons' (King *et al.* 2008) (see Chapter 4, §4.5). Second, higher-ranking juveniles may have greater competitive abilities because they can receive support from relatively more individuals (i.e., their maternal kin and matriline ranking in-between the two opponents) (Pereira 1989). Therefore, dominant juveniles may be relatively more willing to initiate a learning interaction because they are unlikely to be

aggressed (Pereira 1988b), and they may win a between-peer competition for the same demonstrator (Markham *et al.* 2015). Indeed, higher-ranking immature baboons are more likely to learn from others and they acquire information from more diverse individuals than lower-ranking ones (see Chapter 4, §4.4 and §4.5). Third, juveniles' centrality in the group's network may increase their opportunities to acquire foraging information from others: centrality in the grooming network predicted social information transmission in this population (Carter, Torrents Ticó, *et al.* 2016). Immature baboons become more integrated in the grooming network as they age (Lange *et al.* 2023, Roatti *et al.* 2023a). Nevertheless, grooming affiliates, who may be relatively more tolerant of each other's proximity (Marshall *et al.* 2015), are the preferred demonstrators of immature baboons independently from the immatures' age (see Chapter 4, §4.4 and §4.5).

5.5.2 The absent role of maternal warmth?

Maternal warmth is the only maternal style dimension that has been reported to have a direct (positive) effect on the offspring's social learning in captive brown rats (Lévy *et al.* 2003, Melo *et al.* 2006, Lindeyer *et al.* 2012). In these studies, learning from others was measured as adopting or not the food preference of a conspecific whose mouth they could sniff, a behaviour also measured in our study (see §5.3). There are two possible mutually exclusive explanations for why our results contrasted with those of these previous studies: (1) maternal warmth has no role (at least *per se*) in shaping wild baboons' propensity to learn from others, or (2) we did not detect a significant effect of maternal warmth although such effect is present (Visentin *et al.* 2020).

The discrepancy between the results of our study and those of the previous ones on rats may derive from differences between species and/or between study

environments (experimental captive *versus* wild). First, immature primates may receive more diverse and extended maternal care compared to rats (Altmann 1980, Maestripieri 2018). While between-individual differences in rats' maternal care have been described in terms of frequency of grooming the pups and nursing positions (Champagne *et al.* 2003), primates' maternal style comprises a wider variety of behaviours (Fairbanks 1996). Some of these maternal behaviours could have an indirect influence on learning from others in the offspring. For example, in Japanese macaques (*M. fuscata*), juveniles who experienced higher maternal protectiveness as infants spend relatively less time away from the mother and initiate fewer social interactions (Bardi and Huffman 2002), which could limit their social learning (van Boekholt *et al.* 2021); maternal rejection, instead, promotes infants' independence (Bardi and Huffman 2002), and potentially learning from others. Therefore, it is possible that no primate maternal style dimension has an effect alone, but it is their combination that influences immatures' social learning. In addition, primates have a longer immature period compared to similarly-sized mammals (Jones 2011) and mothers maintain a strong bond with their offspring beyond weaning (Maestripieri 2018). Immature primates' early experiences with the mother could thus be modulated by changes in the mother-offspring relationship later in life (e.g., the birth of a younger sibling (Lee 1987a, Delaunay *et al.* 2023)).

Second, our results may be different from those obtained from experiments in captivity because, in natural conditions, an individual's opportunity to learn from others may be more important than their tendency, and/or social experiences outside the family group may affect individuals' learning propensity. The experiments on rats involved each test rat encountering a single conspecific from whom they could acquire information. Individuals thus all had equal opportunities

to acquire social information, but different propensities, explained by the level of maternal care received (Lévy *et al.* 2003, Melo *et al.* 2006, Lindeyer *et al.* 2012). In our wild settings, individuals may not have equal opportunities to learn socially, e.g., due to differences in social connectedness and dominance rank (see above). In addition, in the previous experiments, post-weaning rats were housed with one or more littermate(s), while immature baboons in our study grew up in larger social groups formed by both kin and non-kin individuals (Cheney and Seyfarth 2007). Immature baboons' relatively more diverse sociality may have affected their learning propensity more than what previous studies' captive rats experienced. Social stimulation can promote social learning (Melo *et al.* 2006) and, in general, a species' typical behavioural development (Rommeck *et al.* 2011, Wooddell *et al.* 2020). Overall, these additional factors may reduce the importance of maternal warmth, compared to a captive setting, to the point that it has no effect in a wild or naturalistic social context.

Alternatively, the reason behind not finding any significant effect of maternal warmth may lie in our study design. In particular, our results could have been affected by the small sample size and/or by how we characterised maternal warmth. First, our sample size (13 mother-offspring pairs) may have been too small to detect a significant effect of maternal warmth if the effect size was relatively small with a relatively large between-individual variation (Visentin *et al.* 2020). Because individual mothers change their level of care based on their offspring's age, maternal style may need to be determined within a relatively narrow age range (Dura *et al.* 2018, Arlet *et al.* 2019). This approach generally constrains the sample size of studies investigating the long-term effects of maternal style on the offspring's behaviour because: (i) few individuals of similar age can be observed in species with low fecundity, such as primates (Jones

2011); and (ii) the same individuals need to survive for observation later in life (Fairbanks and McGuire 1993, Bardi and Huffman 2006, Sekizawa and Kutsukake 2019). This small-sample-size problem could be solved by implementing a different analytical approach (Houslay and Wilson 2017). Multivariate modelling (involving multiple response variables) could control for the offspring's characteristics (such as age) that affect maternal behaviour when testing for the effects of maternal style on the offspring's behaviour (Houslay and Wilson 2017). The multivariate solution may also solve multicollinearity issues. For instance, we could not insert maternal grooming during juvenescence and juveniles' rank in the same model (see §5.3 and Appendix 4, §4.2), which were significantly negatively correlated (Spearman's rank correlation: -0.58, p -value = 0.04). Because juveniles' rank had a relatively strong (see §5.4 and Appendix 4, §4.4) positive effect on social learning rate, it is possible that it cancelled out the effect of maternal grooming, which had a relatively weak negative effect on the response variable.

Second, our lack of maternal warmth's significance could derive from the fact that grooming received from the mother is not a good measure of warmth in baboons. In addition to grooming the offspring, warmth was previously associated with other behaviours in captive macaques, i.e., ventral-ventral contact, cradling, and nursing (Hinde and Simpson 1975, Maestripieri *et al.* 2009). Because we wanted to assess the effects of the degree of maternal warmth experienced by the offspring during both infancy and juvenescence, we opted for a behaviour – grooming – that mothers can direct towards their offspring at any age (Delaunay *et al.* 2023). While we did not find any significant effect of maternal grooming, other aspects of maternal warmth could have an influence on the offspring's social learning. However, it may be necessary to first understand more precisely

what constitutes maternal warmth in primates because: (i) it is a poorly studied maternal style dimension, addressed only in a few species of macaques in captivity (Maestriperi *et al.* 2009); and (ii) the behaviours associated with warmth are not always consistent across studies (Hinde and Simpson 1975, Bardi *et al.* 2001, Maestriperi *et al.* 2009).

5.5.3 Conclusions

In conclusion, further studies will be necessary to determine whether maternal warmth has truly no influence on the offspring's tendency to learn socially or if we were not able to detect it. However, it may be necessary to first increase our knowledge of how maternal warmth affects the offspring's behaviour in general and, in turn, how these behavioural aspects may influence social learning. For example, warmth is known to enhance the offspring's cognitive abilities (Liu *et al.* 2000, Deneault *et al.* 2023), but it is not clear whether higher cognition would promote more social (van de Waal and Bshary 2011) or individual (Bandini and Tennie 2020) learning, or both (van Schaik and Pradhan 2003). A consistent higher propensity to engage in social interactions could improve individuals' social integration (Kulahci *et al.* 2018b) and thus their opportunities to acquire information from others (van Boekholt *et al.* 2021). Yet, studies do not agree on whether maternal warmth enhances (Hane *et al.* 2010, Starr-Phillips and Beery 2013) or constrains (Parent and Meaney 2008, Franks *et al.* 2015) the offspring's sociability. Finally, higher warmth has been generally associated with better stress-coping abilities (Liu *et al.* 1997, Parker and Maestriperi 2011), but these could either increase (Carter *et al.* 2014) or decrease (Bangasser and Shors 2010) learning from others. It is thus fundamental to consider multiple aspects of maternal style and the offspring's behaviour to understand their roles

on social information acquisition and potentially the formation of culture in wild social groups.

6 CHAPTER 6: GENERAL DISCUSSION

6.1 IMPORTANCE OF THE STUDY

Social learning and culture are a fundamental part of human lives and have long been considered a unique human feature (Sommer and Parish 2010, Dean *et al.* 2012). However, given that a large amount of evidence accumulated on taxa ranging from invertebrates to mammals, it is now clear that social learning and culture are rooted in animals' evolutionary history (Whiten 2017, Allen 2019). Despite this common evolutionary background, there are quantitative differences in the cultural capacity of different taxa, with non-human primates (hereafter primates) being the most similar to humans from a cultural perspective (Whiten and van de Waal 2017, 2018). Despite primate taxa sharing characteristics linked to the emergence of culture (e.g., large relative brain size (van Schaik and Burkart 2011, Street *et al.* 2017)), great apes show far more evidence of culture than most monkeys (Perry and Manson 2003, Whiten and van de Waal 2017). On the one hand, this may derive from methodological issues, such as how culture is defined and how much a taxon has been studied from a cultural perspective (Perry and Manson 2003, Schuppli and van Schaik 2019). On the other hand, some taxa may experience stronger constraints on the formation of culture than others (Koops *et al.* 2014, Carter, Torrents Ticó, *et al.* 2016) (see also Chapter 1, §1.1 and §1.2).

Culture arises through three main steps: first, novel information needs to be discovered (innovation), then, it needs to spread in a social group (transmission) and, eventually, it has to be passed to the next generation (maintenance) in order

to be considered a cultural variant (McGrew 1998, Perry and Manson 2003). Because some species show little evidence of culture despite the occurrence of innovations (e.g., baboons (Beck 1974); see below), investigating the constraints on horizontal (between peers) and vertical (from older to younger individuals) information transmission may help to elucidate the reasons behind species' abilities to sustain culture (van Schaik 2010, Whiten and van de Waal 2018). Importantly, individuals may have different roles in the cultural process: adults may lead the innovation phase because their greater experience facilitates the discovery of novel information (Reader and Laland 2001, Amici, Widdig, *et al.* 2019); immatures may promote the social transmission of such information because, due to their inexperience with the environment, they learn from others more than adults (Laland 2004, Rapaport and Brown 2008) (see also Chapter 1, §1.3 and §1.4).

To understand why some primate species are less 'cultural' than others, I addressed the possible constraints on social learning in wild immature chacma baboons (*Papio ursinus*), female-philopatric (i.e., females remain in their natal group for life while males disperse at maturity), stable group living primates. In baboons, only two cases of culture have been reported (Strum 1975, Sapolsky and Share 2004). This is paradoxical because baboons possess several characteristics that may favour the emergence of culture (Cheney and Seyfarth 2007, Fischer *et al.* 2019). Baboons can, at least occasionally, innovate behaviours (Beck 1974) and they readily learn from others (Carter *et al.* 2014, Carter, Torrents Ticó, *et al.* 2016). In addition, baboons live in large and cohesive social groups, which may facilitate information acquisition and diffusion (Pasquaretta *et al.* 2014, van Boekholt *et al.* 2021); they are terrestrial omnivorous foragers, which has been linked to material culture in primates (van

Schaik *et al.* 1999, Falótico and Ottoni 2023); and they are aware of the relationships between their group mates, indicating that they can memorise a large amount of information (Crockford *et al.* 2007b, Seyfarth and Cheney 2013). Because baboons are considered model species to understand the evolution of early hominins (Codron *et al.* 2008, King 2022), identifying the constraints on the formation of culture in baboons may increase our understanding of how humans developed cumulative culture (Tennie *et al.* 2009, Dean *et al.* 2012) (see also Chapter 1, §1.5 and §1.6).

In the next sections, I summarise the main findings of this thesis (§6.2) and highlight their implications for the formation of culture in baboons (§6.3). Finally, I address some aspects that emerged from this research that need further investigation (§6.4).

6.2 SUMMARY OF FINDINGS

To understand why baboons show little evidence of culture, I explored different aspects of immatures' behavioural development linked to social information acquisition. First, I investigated how proximity and grooming social networks change with age and differ by sex during the immature period (Roatti *et al.* 2023a) (Chapter 2). The results showed that immature baboons inherited their mothers' networks and differentiated from them as they aged, although maternal social connections continued to affect their offspring's connections throughout development. As they aged, juveniles increased their association with partners of similar age and the same sex. In general, immatures grew more socially selective in their proximity associations, while they integrated themselves more into the grooming network. However, immature males became relatively more socially

peripheral with age: compared to female peers, males were less bonded to their matriline, they were less integrated into the grooming network, and they had a stronger preference for same-sex peer partners. These results largely confirm previous studies' findings on immature primates' network inheritance and differentiation, and sex differences in sociality in female-philopatric societies (Amici, Kulik, *et al.* 2019, Vilette *et al.* 2022).

Second, I analysed how maternal social features affect their offspring's social connections. I focused on three maternal features: a mother's number of offspring in the group (matriline size), her dominance rank, and her social network integration (Chapter 3). The results showed that, independently from age and sex, immatures from larger and higher-ranking matriline inherited relatively more their mothers' proximity and grooming networks, and they kept bonding with maternal grooming partners throughout development more than peers from smaller and lower-ranking matriline. Immatures' social integration increased with both matriline size and a mother's own network integration, while dominance rank negatively affected immatures' ability to connect different social clusters. Finally, both matriline size and dominance rank increased immatures' association with partners of similar age and the same sex. These results generally support previous studies on the roles of matriline bonds and dominance rank, and of maternal social integration (Silk 2009, Brent 2015). The negative effect of dominance rank on immatures' ability to connect social clusters was unexpected but it may reflect dominant mothers' stronger role in bridging across different subgroups compared to her offspring (Silk *et al.* 2010a, Brent 2015).

Third, I examined how behaviours associated with social learning change with age and sex during the immature period and to whom immatures direct these learning behaviours (hereafter learn socially) (Chapter 4). The results showed

that both immature females and males concentrated their social learning during infancy and around the weaning period and decreased social learning during juvenescence. Immatures tended to learn from demonstrators (i.e., the individuals to whom they pay attention) closer to them in their proximity network when they are young, while they actively looked for specific demonstrators when older. In general, they preferred to learn from grooming affiliates and individuals of similar age. Grooming affiliates largely included close maternal kin (the mother and maternal siblings; the two variables were strongly positively correlated). However, compared to females, males learnt less from grooming partners and more from peers, with whom they could be affiliated through the play network. Finally, higher-ranking immatures were more likely to learn from others than lower-ranking peers and they also learnt from a relatively wider variety of demonstrators. These results broadly confirm other studies' findings on the importance of learning from others to become competent foragers by weaning, the positive effect of tolerance on social learning, and the tendency of dominant individuals to monopolise resources (King *et al.* 2008, Carvajal and Schuppli 2022).

Fourth, I tested whether maternal warmth, in the form of grooming received by the offspring during infancy and juvenescence, affected immatures' tendency to learn from others around weaning. At the same time, I controlled for other factors that were linked to social learning in previous Chapters and that may affect maternal grooming (Chapter 5). The results did not find any support for the role of maternal warmth but confirmed that juveniles' number of maternal siblings in the group, dominance rank, and centrality in the grooming network enhance social learning. Dominance rank and network centrality were linked to social information use in this population (Carter, Torrents Ticó, *et al.* 2016) and, in

Chapter 3, larger matriline size was found to increase social integration, and thus social learning opportunities. The lack of support of an effect of maternal warmth was unexpected based on previous studies' results (Kondo-Ikemura and Waters 1995, Lindeyer *et al.* 2012) and may derive either from maternal grooming not having an effect on immature baboons' social learning in the wild or from methodological issues (e.g., small sample size).

6.3 WHAT MAY CONSTRAIN CULTURE IN BABOONS?

The results obtained on immature baboons' social development may have important implications for social information transmission at the group level. In particular, social clustering around matriline and within immature same-sex subgroups may constrain the formation of culture in baboons because information remains confined within social clusters instead of reaching the whole group (van de Waal *et al.* 2012, Pasquaretta *et al.* 2014). Because social clustering may be present relatively more in female-philopatric societies, culture could be constrained in primate species with female philopatry compared to those where males are philopatric (van de Waal and Whiten 2012). I found that social clustering regards both immature baboons' patterns of association (social partners in the proximity and grooming networks) and learning interactions (to whom they pay attention) and is linked to behavioural sex differences. Finally, dominance asymmetry may further constrain social information spread in baboon groups.

6.3.1 Matrilineal clustering

Matrilines may be repositories of social knowledge more in female-philopatric societies compared to male-philopatric ones because, in the former, matriline are relatively more cohesive, and females have a relatively deeper local knowledge. First, matriline, defined as units formed by a mother and her offspring, are present in most primate societies because mothers are the primary caretakers in most species (Maestripieri 2018). However, because, in general, daughters have stronger bonds with their mothers than sons (Lonsdorf 2017), when females are philopatric, they maintain strong relationships with close maternal kin for life (Silk, Altmann, *et al.* 2006, Silk *et al.* 2010a), while, when females disperse at maturity, they break bonds with maternal kin (e.g., in chimpanzees (Langergraber *et al.* 2009)). In female-philopatric species, matriline thus form cohesive units through generations, where not only mothers and their offspring, but also adult sisters, share stronger bonds between each other than with more distantly related individuals (Chapais *et al.* 1997, Chapais 2001).

Second, matriline are pivotal centres of information acquisition for young immatures. Indeed, in all primate societies, young immatures first learn from their close maternal kin (Whiten and van de Waal 2018) (see above). However, matriline may represent repositories of social knowledge relatively more in female-philopatric primates, where mothers have been in their natal group for their whole life, having both a deep personal (from repeated experience with the same environment) and social (accumulated within their matriline through generations) knowledge of the local environment (van de Waal *et al.* 2010). This is exacerbated by females' tendency to learn socially more than males (Watson *et al.* 2018, Canteloup, Cera, *et al.* 2021): philopatric females have a relatively

greater access to social information by being both more socially central and more connected to their matriline (Lehmann and Ross 2011, Sosa 2016). Because dispersing males are less socially central, they may both have a greater tendency to produce information (Reader and Laland 2001, Amici, Widdig, *et al.* 2019) and be facilitated in doing so by being at the edges of the group (King *et al.* 2009, Carter, Torrents Ticó, *et al.* 2016). Importantly, because males are less bonded to their matriline, they could act as ‘information bridges’ across matriline. However, since individuals may prefer to learn from the philopatric sex (Bono *et al.* 2018, Grampp *et al.* 2019) and because socially central individuals are more likely to be observed as demonstrators (Kulahci *et al.* 2018a, Kulahci and Quinn 2019), philopatric, and more socially central, females may be more likely to serve as demonstrators rather than dispersing, and more peripheral, males.

My results largely corroborate this framework. Immature baboons tend to associate with their close maternal kin and learn from their matriline, and both these tendencies are stronger in immature females than in male peers. As mentioned, this could concentrate the local knowledge within the philopatric sex and thus favour information spread within rather than across matriline (van de Waal *et al.* 2012, 2014). In addition, immature males’ spatial and learning patterns may maintain social information within matriline. Contrary to what reported in other species (e.g., vervet monkeys *Chlorocebus pygerythrus* (Bono *et al.* 2018, Canteloup, Cera, *et al.* 2021)), I did not find sex differences in the likelihood to learn from others or a bias towards observing female demonstrators. This could mean that males, who are relatively less bonded to their matriline and learn less from maternal kin than females, could spread social information across different matriline. However, this potential may be hindered by the fact that they are socially separated from the group members who produce most information, that

is adults (Carter *et al.* 2015, Amici, Widdig, *et al.* 2019). Indeed, males have a greater tendency to associate with same-sex peers and to learn from peers than females (see also §6.3.2).

6.3.2 Age- and sex-driven clustering

In primates in general, immatures tend to associate with same-sex peers as they age, and this occurs more in males than in females (Lonsdorf 2017). Age and sex-driven social clustering may hinder social information transmission because the individuals who tend to produce information (i.e., adults and males (Reader and Laland 2001, Amici, Widdig, *et al.* 2019)) are socially separated from those who tend to acquire it (i.e., immatures and females (Carter *et al.* 2014, Canteloup, Cera, *et al.* 2021)) (Carter *et al.* 2015). As mentioned, in female-philopatric societies, the fact that juvenile males have a stronger preference for same-sex peer partners could maintain social information within matriline. Indeed, juvenile males have more opportunities to acquire information from peers rather than from adults, who may provide different kinds of social information. Although immatures acquire the basic skills necessary for survival during infancy, they may not learn about the edibility and processing of rare or seasonal food items until juvenescence (Bray *et al.* 2018, Carvajal and Schuppli 2022). Adult demonstrators, who are more experienced (Schuppli, Meulman, *et al.* 2016, Barrett *et al.* 2017), may be more likely to provide information on such long-lasting skills (that could give rise to culture) compared to peers, who may instead supply, e.g., information on food location or patch quality (that rapidly becomes outdated). The fact that fine dietary information may be less available for immature males compared to female peers could produce, e.g., within-matriline dietary

differences that do not converge at the group level (van de Waal *et al.* 2012, 2014).

My results generally confirm this framework. Immature baboons increase their association with same-sex peers while they age, and this tendency is relatively greater in juvenile males. While, as mentioned, males do not learn socially less than females, the likelihood to learn from others for immatures of both sexes decreases as they approach sexual maturity. This indicates that immature baboons learn socially more than adults, thus supporting the view that age-driven clustering constrains information spread. In addition, because immature males learn both less from their matriline and more from peers compared to females, this may preserve information clustering within matriline (see above). As mentioned, juvenile males could be constrained in learning certain skills from adults, which limits their potential in disseminating information across matriline.

6.3.3 Dominance asymmetry

The presence of a steep dominance gradient may increase matrilineal clustering because individuals tend to learn from social affiliates, who are tolerant of their proximity (King, Clark, *et al.* 2011, Coelho *et al.* 2015). Because of the strong nepotism that characterises despotic societies (Silk 2009, Thierry 2013), social affiliates may largely include close maternal kin (Chapais and Belisle 2001, Tan *et al.* 2018). Again, this pattern may be predominant in female-philopatric societies, where females maintain their mother's dominance rank through the agonistic support of maternal kin (Silk *et al.* 1999, 2004). Indeed, dominant matriline are relatively more cohesive because, as mentioned, their members support each other, while subordinate matriline bond with unrelated higher-

ranking individuals to gain social tolerance (Sick *et al.* 2014, Marshall *et al.* 2015). In addition, because of their ability to acquire resources from subordinates, higher-ranking individuals tend to learn from others more than lower-ranking ones (King *et al.* 2009, Carter, Marshall, *et al.* 2013). While this may favour across-matriline information transmission, dominant individuals could be more likely to acquire ephemeral information (e.g., about food location) than potentially long-lasting skills related to, e.g., the processing of a rare high-quality food item. This is because subordinates may refrain from applying their knowledge in the presence of dominant individuals who could steal their resources (Drea and Wallen 1999, Lonsdorf *et al.* 2016).

Baboons are a despotic taxon and dominance asymmetry is highest in groups of the chacma species (Fischer *et al.* 2019). This may contribute to explain why the only two cases of culture in baboons have been reported in olive baboons (*P. anubis*) (Strum 1975, Sapolsky and Share 2004) despite the fact that, e.g., chacma baboons (Cheney and Seyfarth 2007) and yellow baboons (*P. cynocephalus*) (Alberts 2019) have been equally well studied. Compared to chacma and yellow baboons, olive baboons have a more relaxed dominance hierarchy and a lower degree of nepotism (Silk *et al.* 2017, Fischer *et al.* 2019), which may facilitate information spread across their social groups (Pasquaretta *et al.* 2014, van Boekholt *et al.* 2021).

My results support this framework in chacma baboons. Higher-ranking immatures' association and learning patterns could intensify matrilineal clustering. Dominant immatures associate relatively more with their matriline and with same-sex peers, which may both increase within-matriline information transmission (see above). In addition, higher-ranking immatures learn from others more than lower-ranking ones. Although dominant immatures learn from

a wider variety of individuals compared to subordinate ones, the effect of grooming affiliation in determining demonstrator choice was more than two times stronger. Because, as mentioned, grooming affiliation was positively correlated with matrilineal kinship, dominance ultimately increases information acquisition from matriline members.

6.3.4 Matrilineal cultures?

Overall, my results support the hypothesis that, in female-philopatric societies, social information tends to remain ‘stuck’ within matrilineal clusters. As reported in vervet monkeys, this may lead to the formation of ‘matrilineal cultures’ as opposed to group cultures (van de Waal *et al.* 2012). Instead, in male-philopatric species, the lack of matrilineal clustering could allow social information to travel relatively more easily across the whole group. For example, in male-philopatric chimpanzees (*Pan troglodytes*), the primate species that shows the most evidence of culture after humans (Whiten and van de Waal 2017, Whiten *et al.* 2021), females may share strong bonds with the same sex, but, unlike in female-philopatric societies, they form few bonds with close kin (Lehmann and Boesch 2008, Langergraber *et al.* 2009). Perhaps as a result, social information spreads across matrilineal lines and causes most behavioural variants to converge at the group level (Whiten *et al.* 1999). This qualifies many chimpanzee behaviours as culture according to its traditional definition (McGrew 1998, Perry and Manson 2003).

The question remains about whether behaviours that are socially transmitted and maintained across generations within matrilineal lines should be considered cultural (e.g., matriline-specific preferences in the food cleaning techniques of wild vervet monkeys (van de Waal *et al.* 2012)), ultimately challenging the view

of culture as a group-level phenomenon. Indeed, a recent study proposed that any naturally-occurring behaviour that is acquired socially should be part of a species' cultural repertoire (Schuppli and van Schaik 2019). This includes basic subsistence behaviours, reaching beyond the historical focus on material culture that excludes most monkey species from cultural studies (Perry and Manson 2003, Schuppli and van Schaik 2019).

Recognising social transmission biases in the information that spreads in species with different social organisation (i.e., within or beyond matriline) may improve our understanding of the roles played by matrilineal clustering and group conformity and, ultimately, of primates' cultural evolution. For example, conformity to a group's norm, which may maintain, e.g., chimpanzee between-group cultural diversity (Luncz and Boesch 2014), was also reported in vervet monkeys (van de Waal *et al.* 2013), suggesting that matrilineal clustering does not always prevent the emergence of group-level behaviours (van de Waal *et al.* 2017). Because culture may affect groups' fitness and potentially their evolution, determining the fitness consequences of differential social information transmission patterns may inform how primate cultures are linked to their taxonomic diversity (Whiten 2017, Brakes *et al.* 2019, 2021).

6.4 FUTURE DIRECTIONS

This thesis highlighted various aspects of immatures' behavioural development that may favour the formation of matrilineal cultures in baboons and other female-philopatric primates. In addition to the factors addressed here, other behavioural aspects may need to be investigated to confirm the existence of matrilineal cultures and further clarify the reasons behind their emergence. First,

although the social learning behaviours analysed have been linked to social information acquisition in other species (Rapaport and Brown 2008) (see also Chapter 4), it may be important to understand to which extent they predict the acquisition of foraging competence in immature baboons and how much they, instead, reflect social affiliation (e.g., for foraging in close proximity of another individual) (Huchard *et al.* 2013). In addition, performing a fine-grained analysis of between-matriline differences in diet and/or food processing techniques could determine the presence of matrilineal cultures in baboons (van de Waal *et al.* 2012). Second, while I found that immatures prefer to learn from grooming affiliates, who largely belong to close maternal kin, the roles of close compared to more distant maternal kin and of paternal kin need further study. In particular, because paternal relatives tend to be of similar age (Altmann 1979), they may be important learning partners for juvenile males, who learn relatively more from peers. The affiliated adult male (often the biological father (Huchard *et al.* 2010)) could also be a source of information for juvenile males, who associate with the same sex more than females.

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AUTHOR CONTRIBUTION STATEMENT

The research chapters (2–5) of this thesis are a series of papers that are either published or intended for publication. Although I performed the majority of the work that forms this thesis, a number of colleagues, who are included as co-authors (in order of appearance below) in the related publications, contributed to this research (see specific contributions below). Data collection was funded by different grants (indicated below for each co-author). Finally, this work was possible thanks to many people who worked at/ supported the Tsaobis Baboon Project (see Acknowledgments).

Chapters 2 and 3:

- Vittoria Roatti: conceptualisation, formal analysis, data curation, writing – original draft, visualisation.
- Guy Cowlshaw: writing – review and editing, project administration, project funding (Research England).
- Elise Huchard: writing – review and editing, project administration, project funding (Agence Nationale de la Recherche 616 – ANR ERS-17-CE02-0008, 2018–2021).
- Alecia Carter: conceptualisation, formal analysis, writing – review and editing, supervision, project administration, project funding (Leakey Foundation Research Grant and Templeton World Charity Foundation Grant – TWCF0509).

Chapters 4 and 5:

- Vittoria Roatti: conceptualisation, data collection, formal analysis, data curation, writing – original draft, visualisation.
- Axelle Delaunay: data collection, data curation, writing – review and editing.
- Guy Cowlshaw: writing – review and editing, project administration, project funding (Research England).
- Elise Huchard: writing – review and editing, project administration, project funding (Agence Nationale de la Recherche 616 – ANR ERS-17-CE02-0008, 2018–2021).
- Alecia Carter: conceptualisation, formal analysis, writing – review and editing, supervision, project administration, project funding (Templeton World Charity Foundation Grant – TWCF0509).

APPENDICES

1 APPENDIX 1: SOCIAL NETWORK INHERITANCE AND DIFFERENTIATION IN WILD BABOONS

1.1 MOTHER-OFFSPRING COSINE SIMILARITY

In order to test whether there was a positive correlation between mothers' and offspring's social networks and how this changed through time, we used the Pearson's correlation (MP1b; see Chapter 2, §2.3) and the cosine similarity. Cosine models' structure (LMM) and dependent variables were the same as MP1b. Cosine (calculated through the package *lsa* (Wild 2022) and the function *cosine*) is nearly identical to a correlation except for a coefficient (*cosine = correlation x coefficient*). Cosine similarity is the cosine of the angle between two vectors and represents how similar two sets of values are. Cosine's values are bounded between '0' (no similarity) and '1' (identical vectors) (Jarrett *et al.* 2018).

Our correlation and cosine values were correlated between each other (Figure A1.1). The cosine similarity values were comparable to those found for juvenile female vervet monkeys (Jarrett *et al.* 2018) (Table A1.1, Figure A1.2; see Chapter 2, §2.5). The number of observations and sample size for the cosine models were the same as for the correlation ones (MP1b; see Appendix 1, §1.3). The results of the models in which either the Pearson's correlation (see Appendix 1, §1.5.1) or the cosine similarity were used as dependent variables were qualitatively similar (Table A1.2, Figure A1.3).

Table A1.1: Mean and standard deviation (SD) values (divided per sex and overall) of the mother-offspring social network cosine similarity for the proximity and grooming (Groom.) networks.

Network	Sex	Mean	SD	Mean Total	SD Total
Proximity	Male	0.69	0.19	0.71	0.18
	Female	0.73	0.17		
Groom. Given	Male	0.16	0.22	0.22	0.24
	Female	0.29	0.23		
Groom. Received	Male	0.26	0.26	0.29	0.27
	Female	0.32	0.27		
Groom. Total	Male	0.27	0.26	0.3	0.25
	Female	0.35	0.24		

Figure A1.1: Relationship between the mother-offspring social network correlation and cosine similarity for the proximity and grooming (Groom.) networks.

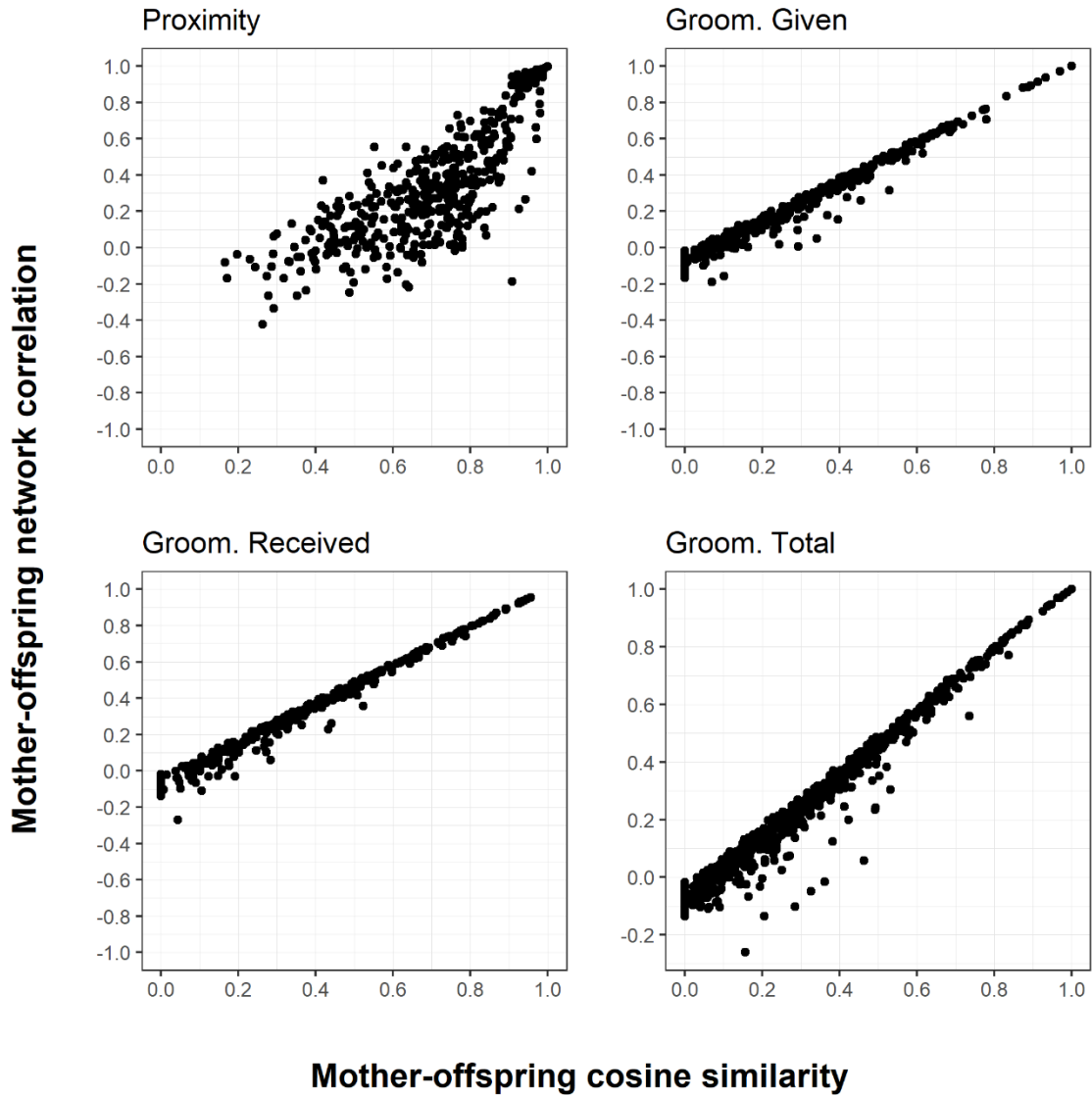


Table A1.2: Results of the models using the mother-offspring cosine similarity for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, degrees of freedom (df), test statistic (t value), *p*-value ('NS' = not significant), and conditional R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	df	t value	<i>p</i> -value	R ²
Cosine Proximity	(Intercept)	0.7184	0.0432	41.2886	16.6293	-	0.21
	Age immature	-0.0016	0.0007	490.8138	-2.2524	0.05	
	Age:Sex	-0.0004	0.0009	487.5010	-0.3843	NS	
	Nb. offspring	0.0030	0.0063	490.6398	0.4837	0.05	
	Relative rank	0.1171	0.0243	488.6101	4.8214	0.05	
	Sex immature	-0.0276	0.0356	487.7934	-0.7758	NS	
	TroopL	0.0018	0.0153	489.4841	0.1180	0.05	
	TroopM	0.1286	0.0390	490.2589	3.2946	0.05	
Cosine Groom. Given	(Intercept)	0.2301	0.0562	127.1824	4.0934	-	0.26
	Age immature	0.0027	0.0010	321.7047	2.7200	0.05	
	Age:Sex	-0.0027	0.0014	466.3230	-1.8845	0.05	
	Nb. offspring	-0.0009	0.0106	102.2239	-0.0825	NS	
	Relative rank	-0.0298	0.0437	41.2530	-0.6818	NS	
	Sex immature	-0.0300	0.0573	356.8361	-0.5235	NS	
	TroopL	-0.0497	0.0285	24.4016	-1.7445	0.05	
	TroopM	0.0344	0.0604	133.7057	0.5706	NS	
Cosine Groom. Received	(Intercept)	0.2458	0.0902	54.9564	2.7264	-	0.43
	Age immature	-0.0038	0.0012	166.9317	-3.1052	0.05	
	Age:Sex	0.0004	0.0015	233.1550	0.2397	NS	
	Nb. offspring	0.0519	0.0158	104.6907	3.2755	0.05	
	Relative rank	0.1127	0.0712	44.7523	1.5825	0.05	
	Sex immature	-0.0280	0.0533	157.1257	-0.5258	NS	
	TroopL	-0.0977	0.0724	31.2981	-1.3496	0.05	
	TroopM	0.0240	0.0877	49.9544	0.2741	0.05	
Cosine Groom. Total	(Intercept)	0.3010	0.0597	81.8294	5.0405	-	0.28
	Age immature	0.0000	0.0009	381.8015	0.0197	NS	
	Age:Sex	-0.0016	0.0011	481.4835	-1.4114	0.05	
	Nb. offspring	0.0133	0.0110	134.0009	1.2068	0.05	
	Relative rank	0.0305	0.0496	63.3822	0.6151	NS	
	Sex immature	-0.0231	0.0411	318.3726	-0.5632	NS	
	TroopL	-0.0559	0.0346	34.7602	-1.6147	0.05	
	TroopM	0.1561	0.0847	411.6301	1.8420	NS	

Figure A1.2: Mother-offspring social network cosine similarity for the proximity and grooming (Groom.) networks. Frequencies are presented by sex ('F' = female, 'M' = male). Dotted lines represent mean values.

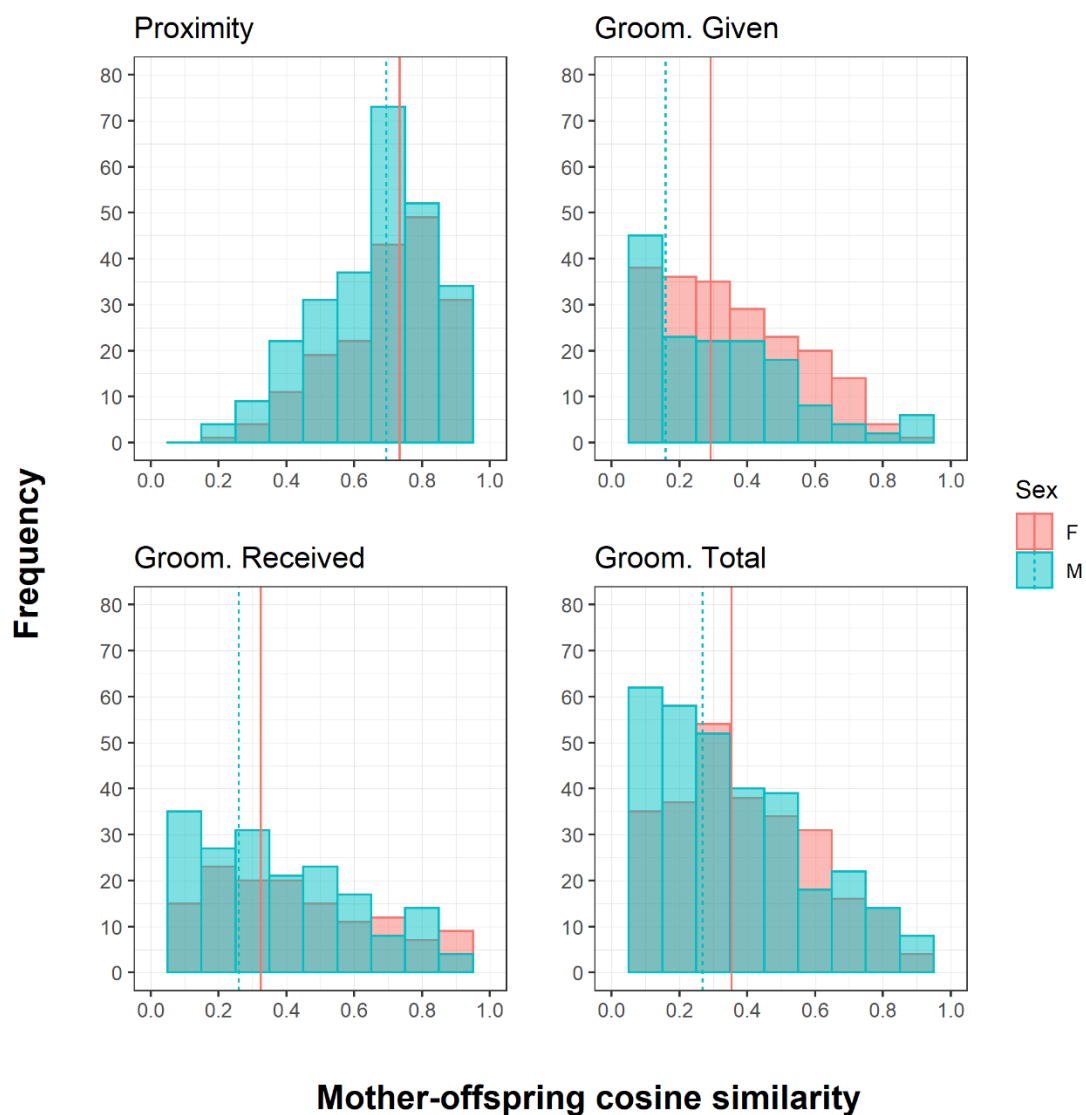
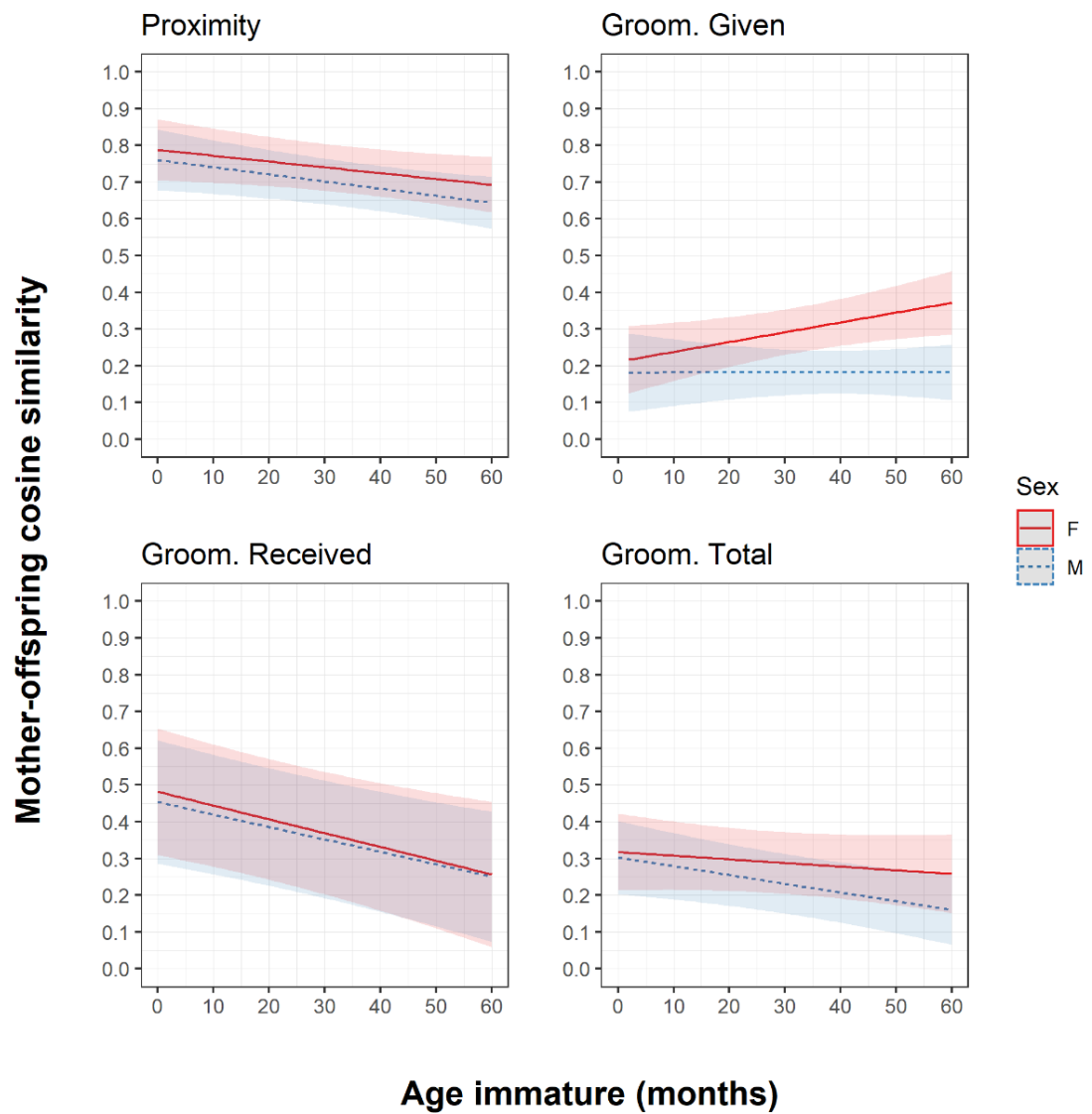


Figure A1.3: Changes in the mother-offspring social network cosine similarity with immatures' age, divided by sex ('F' = female, 'M' = male), for the proximity and grooming (Groom.) networks. Ribbons represent 97.5% confidence intervals.



1.2 CONTROLLING FOR THE MOTHER'S PROXIMITY

The grooming networks of immatures may be constrained by their mothers' presence: if immature baboons tend to be in proximity to their mothers (Berman 1982a), they have a limited choice of partners with whom they can share grooming. Controlling for the mother's proximity would potentially solve this issue (Albery *et al.* 2021). To control for the mother's proximity, we calculated the proportion of time spent with the mother from the proximity network (as for MP1a; see Chapter 2, §2.3) and inserted this variable in models testing changes in mother-offspring social network correlations (MP1b). These models were structured as MP1b. Datastream permutations were performed to obtain *p*-values (see Chapter 2, §2.3).

The mother's presence had no effect on the grooming partner choices of her offspring: the proportion of time with the mother was never significant (Table A1.3). The models' results were sometimes different from the ones presented for MP1b (see Appendix 1, §1.5.1) because we used a reduced dataset to control for the mother's proximity. Because our grooming networks had a higher resolution than the proximity networks, controlling for the mother's proximity reduced the number of overall data available to build the grooming networks (full dataset): for some of the 30-day grooming periods no proximity records were collected (in the same month and year), and the correspondent grooming data were excluded (reduced dataset). The number of observations in the full and reduced datasets, respectively, were: 554 versus 375 for grooming given, 441 versus 246 for grooming received, and 741 versus 430 for grooming total.

Table A1.3: Results of the mother-offspring grooming (Groom.) correlation models (MP1b) when controlling or not for the mother's proximity (Prop. time with mother). Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, degrees of freedom (df), test statistic (t value), *p*-value ('NS' = not significant), and conditional R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	df	t value	<i>p</i> -value	R ²
P1b Groom. Given No prop. time with mother	(Intercept)	0.2312	0.0774	133.6825	2.9865	-	0.31
	Age immature	0.0012	0.0014	244.3996	0.9087	NS	
	Age:Sex	-0.0027	0.0019	319.0646	-1.4400	0.05	
	Nb. offspring	0.0013	0.0133	101.0555	0.0989	NS	
	Relative rank	-0.0262	0.0555	41.6211	-0.4716	NS	
	Sex immature	-0.0126	0.0756	276.3233	-0.1671	NS	
	TroopL	-0.0822	0.0365	26.6804	-2.2495	0.05	
	TroopM	-0.1497	0.0908	190.4379	-1.6481	0.05	
P1b Groom. Given Prop. time with mother	(Intercept)	0.2340	0.0776	134.5674	3.0141	-	0.31
	Age immature	0.0012	0.0014	242.8170	0.8894	NS	
	Age:Sex	-0.0027	0.0019	319.7221	-1.4653	0.05	
	Nb. offspring	0.0018	0.0133	100.5986	0.1352	NS	
	Prop. time with mother	-0.0271	0.0561	357.9001	-0.4831	NS	
	Relative rank	-0.0232	0.0558	42.8407	-0.4148	NS	
	Sex immature	-0.0121	0.0757	276.1822	-0.1596	NS	
	TroopL	-0.0818	0.0365	26.7179	-2.2409	0.05	
	TroopM	-0.1433	0.0918	193.9437	-1.5612	NS	
P1b Groom. Received No prop. time with mother	(Intercept)	0.2195	0.1161	48.5789	1.8912	-	0.37
	Age immature	-0.0049	0.0017	97.9853	-2.8406	0.05	
	Age:Sex	0.0023	0.0023	134.2315	1.0247	0.05	
	Nb. offspring	0.0508	0.0204	73.8033	2.4868	0.05	
	Relative rank	0.0391	0.0902	29.6949	0.4337	NS	
	Sex immature	-0.1096	0.0878	119.6928	-1.2481	0.05	
	TroopL	-0.0413	0.0869	23.0152	-0.4755	0.05	
	TroopM	0.1596	0.1269	44.3265	1.2584	NS	
P1b Groom. Received Prop. time with mother	(Intercept)	0.2124	0.1153	48.6858	1.8425	-	0.37
	Age immature	-0.0047	0.0018	100.1589	-2.6620	0.05	
	Age:Sex	0.0026	0.0023	136.7604	1.1223	NS	
	Nb. offspring	0.0496	0.0203	72.3145	2.4402	0.05	
	Prop. time with mother	0.0211	0.0192	221.5423	1.0999	NS	
	Relative rank	0.0394	0.0893	29.0018	0.4407	NS	
	Sex immature	-0.1221	0.0887	123.3428	-1.3758	0.05	
	TroopL	-0.0437	0.0859	22.7982	-0.5090	0.05	
	TroopM	0.1436	0.1266	45.4278	1.1342	NS	
P1b Groom. Total No prop. time with mother	(Intercept)	0.2690	0.0876	118.4649	3.0703	-	0.39
	Age immature	-0.0015	0.0015	287.0269	-1.0092	0.05	
	Age:Sex	-0.0002	0.0018	361.4817	-0.1359	NS	
	Nb. offspring	0.0251	0.0149	124.9503	1.6885	0.05	
	Relative rank	0.0052	0.0664	53.7168	0.0775	NS	

Model	Variable	Estimate	Std. Error	df	t value	p-value	R ²
	Sex immature	-0.0530	0.0742	276.5909	-0.7148	0.05	
	TroopL	-0.0823	0.0450	30.0337	-1.8293	0.05	
	TroopM	-0.0564	0.1872	294.8999	-0.3014	0.05	
P1b Groom. Total Prop. time with mother	(Intercept)	0.2676	0.0878	119.7075	3.0463	-	0.39
	Age immature	-0.0014	0.0015	287.3789	-0.9873	NS	
	Age:Sex	-0.0002	0.0018	361.4181	-0.1179	NS	
	Nb. offspring	0.0250	0.0149	124.4154	1.6795	0.05	
	Prop. time with mother	0.0045	0.0173	371.7432	0.2584	NS	
	Relative rank	0.0046	0.0665	53.5912	0.0693	NS	
	Sex immature	-0.0540	0.0743	276.9816	-0.7267	NS	
	TroopL	-0.0826	0.0450	30.0573	-1.8344	0.05	
	TroopM	-0.0670	0.1918	308.3337	-0.3491	NS	

1.3 NUMBER OF OBSERVATIONS AND SAMPLE SIZE

Here we show the number of observations and sample size (immature individuals and their mothers) for each model (see Chapter 2, Table 2.1 for the models' summary) for the proximity (Table A1.4) and grooming (Table A1.5) networks. In models where the networks of mothers and offspring were compared (MP1b and MP1c), the number of observations was different for the various grooming components. This is because, for each individual and 30-day period, both a mother's and her offspring's records needed to be present to be included in the model, thus producing different numbers if a mother or her offspring were never observed giving and/or receiving grooming.

Table A1.4: Number of observations (Nb. Obs.) and sample size (Individuals, divided by sex, and Mothers) of each analysis on the proximity network.

Model	Nb. Obs.	Individuals (Male, Female)	Mothers
P1a	467	109 (64, 45)	40
P1b	499	115 (66, 49)	40
P1c.1	499	115 (66, 49)	40
P1c.2			
P1c.3			
P1c.4			
P2a	489	111 (64, 47)	39
P2b.1	489	111 (64, 47)	39
P2b.2			
P2c.1	503	116 (66, 50)	40
P2c.2			
P2c.3			

Table A1.5: Number of observations (Nb. Obs.) and sample size (Individuals, divided by sex, and Mothers) of each analysis on the grooming network.

Model	Grooming	Nb. Obs.	Individuals (Male, Female)	Mothers
P1a	Total	837	142 (80, 62)	43
P1b	Given	554	108 (59, 49)	40
	Received	441	93 (52, 41)	32
	Total	741	135 (77, 58)	42
P1c.1	Given	587	111 (62, 49)	41
	Received	536	97 (54, 43)	32
	Total	837	142 (79, 63)	43
P1c.2	Given	587	111 (62, 49)	41
	Received	536	97 (54, 43)	32
	Total	837	142 (79, 63)	43
P1c.3	Given	587	111 (62, 49)	41
	Received	536	97 (54, 43)	32
	Total	837	142 (79, 63)	43
P1c.4	Given	587	111 (62, 49)	41
	Received	536	97 (54, 43)	32
	Total	837	142 (79, 63)	43
P2a	Given	837	142 (79, 63)	43
	Received			
	Total			
P2b.1	Total	837	142 (79, 63)	43
P2b.2				
P2c.1	Given	851	142 (79, 63)	43
	Received			
	Total			
P2c.2	Given			
	Received			
	Total			
P2c.3	Given			
	Received			
	Total			

1.4 SUPPLEMENTARY MATERIAL FOR NETWORK CORRELATION AND BINOMIAL MODELS

Here we present the supplementary tables and figure for network correlation models (MP1b and MP1c) and binomial models (MP1a, MP1c, and MP2c). The values of the mother-offspring social network correlation (MP1b) are shown in Table A1.6 and Figure A1.4. The number of observations in which the mother-offspring social network correlation was higher or lower compared to the correlation with other individuals' networks are listed in Table A1.7 for each MP1c model (see Appendix 1, §1.4). Finally, changes in the odds ratios (binomial models) at different age stages (1 and 4 years old; see Appendix 1, §1.3) and in the two sexes are summarized in Table A1.8.

Table A1.6: Mean and standard deviation (SD) values (divided per sex and overall) for the mother-offspring social network correlation for the proximity and grooming (Groom.) networks.

Network	Sex	Mean	SD	Mean Total	SD Total
Proximity	Male	0.33	0.32	0.36	0.33
	Female	0.41	0.33		
Groom. Given	Male	0.11	0.23	0.16	0.25
	Female	0.23	0.25		
Groom. Received	Male	0.21	0.28	0.24	0.29
	Female	0.28	0.28		
Groom. Total	Male	0.21	0.28	0.24	0.27
	Female	0.29	0.28		

Figure A1.4: Mother-offspring social network correlation for the proximity and grooming (Groom.) networks. Frequencies are presented by sex ('F' = female, 'M' = male). Dotted lines represent mean values.

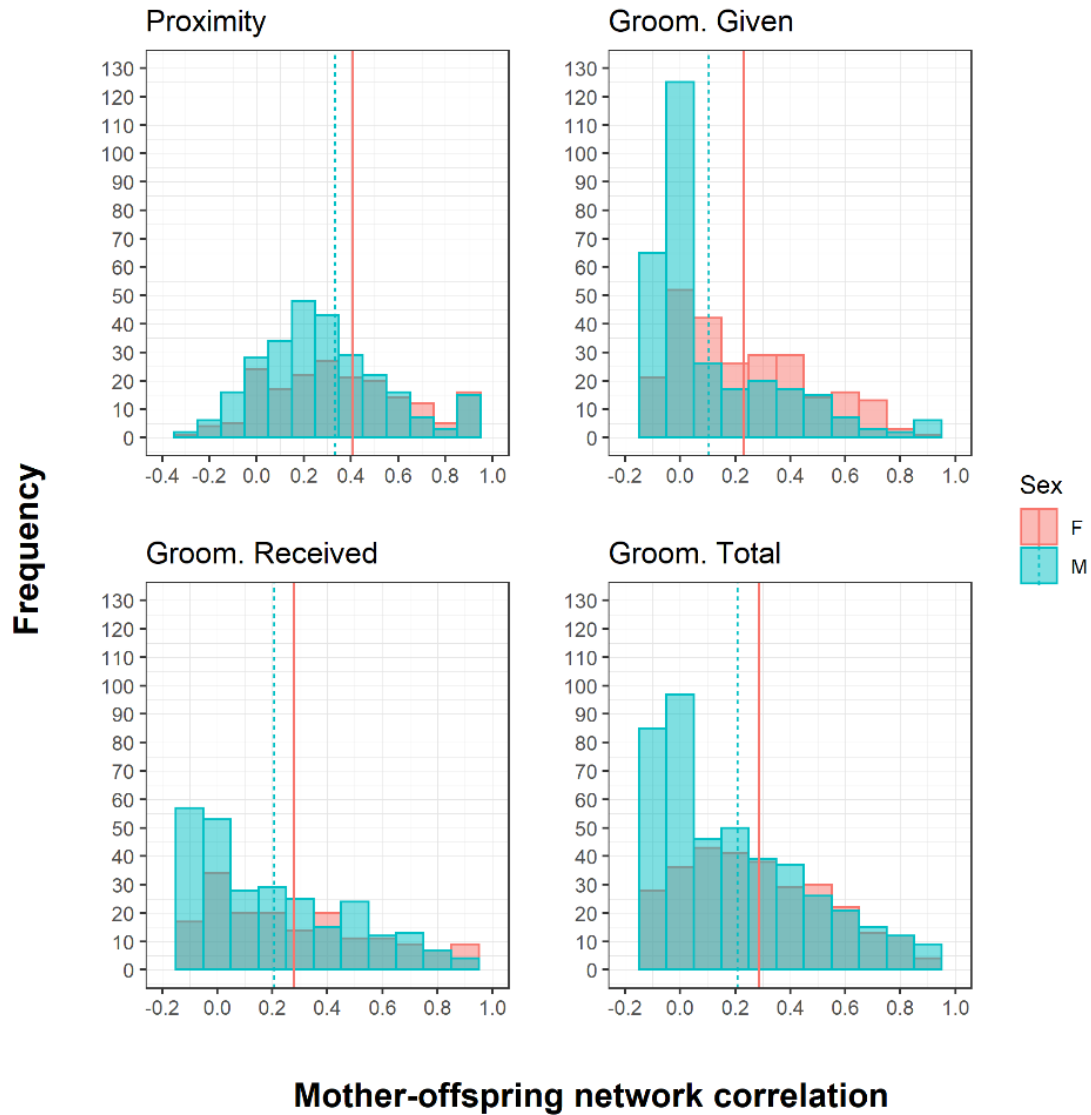


Table A1.7: Number of cases, for the proximity and grooming (Groom.) networks, in which (1) the correlation with the mother's network was higher or lower than the correlation with a random individual's network (MP1c.1) and the mean correlation with other individuals' networks (MP1c.2); (2) the rank of the mother-offspring social network correlation was ≥ 0.9 (MP1c.3) or > 0.5 (MP1c.4), or not; and (3) total number of observations.

Model	Higher	Lower	Total
P1c.1 Proximity	304	195	499
P1c.1 Groom. Given	345	234	579
P1c.1 Groom. Received	273	262	535
P1c.1 Groom. Total	467	367	834
P1c.2 Proximity	330	169	499
P1c.2 Groom. Given	275	312	587
P1c.2 Groom. Received	204	332	536
P1c.2 Groom. Total	396	441	837
P1c.3 Proximity	77	422	499
P1c.3 Groom. Given	143	444	587
P1c.3 Groom. Received	102	434	536
P1c.3 Groom. Total	191	646	837
P1c.4 Proximity	307	191	498
P1c.4 Groom. Given	370	212	582
P1c.4 Groom. Received	283	253	536
P1c.4 Groom. Total	532	304	836

Table A1.8: Odds ratios (OR) for each significant GLMM binomial model for the proximity and grooming (Groom.) networks, divided by immatures' age (year) and sex, and the percentage increase or decrease between 1–4 years old in the two sexes.

Model	Age	Sex	OR	Percentage change
P1a Proximity	1	Female	0.13	-33.27
	4		0.09	
	1	Male	0.15	-58.89
	4		0.06	
P1a Groom. Total	1	Female	1.25	-56.63
	4		0.54	
	1	Male	2.77	-76.74
	4		0.64	
P1c.1 Groom. Given	1	Female	1.08	104.29
	4		2.21	
	1	Male	0.77	9.89
	4		0.84	
P1c.2 Proximity	1	Female	0.41	119.79
	4		0.90	
	1	Male	0.47	20.07

Model	Age	Sex	OR	Percentage change
	4		0.56	
P1c.2 Groom. Given	1	Female	0.50	78.44
	4		0.90	
	1	Male	0.18	63.67
	4		0.30	
P1c.2 Groom. Total	1	Female	0.34	104.32
	4		0.69	
	1	Male	0.28	26.25
	4		0.35	
P1c.3 Groom. Received	1	Female	0.03	-67.17
	4		0.01	
	1	Male	0.04	-51.89
	4		0.02	
P1c.4 Proximity	1	Female	0.54	88.68
	4		1.02	
	1	Male	0.61	2.01
	4		0.62	
P1c.4 Groom. Given	1	Female	0.59	287.23
	4		2.28	
	1	Male	0.61	-29.35
	4		0.43	
P1c.4 Groom. Total	1	Female	0.56	166.10
	4		1.49	
	1	Male	0.41	24.59
	4		0.51	
P2c.1 Proximity	1	Female	0.86	2.43
	4		0.88	
	1	Male	0.81	10.57
	4		0.89	
P2c.1 Groom. Given	1	Female	0.04	247.30
	4		0.13	
	1	Male	0.01	330.47
	4		0.05	
P2c.1 Groom. Received	1	Female	0.04	53.57
	4		0.06	
	1	Male	0.04	66.93
	4		0.06	
P2c.1 Groom. Total	1	Female	0.08	126.01
	4		0.18	
	1	Male	0.05	118.38
	4		0.11	
P2c.2 Groom. Given	1	Female	0.06	197.47
	4		0.19	
	1	Male	0.03	387.93
	4		0.12	
P2c.2 Groom. Received	1	Female	0.04	156.45
	4		0.10	

Model	Age	Sex	OR	Percentage change
	1	Male	0.04	226.80
	4		0.13	
P2c.2 Groom. Total	1	Female	0.09	169.57
	4		0.25	
	1	Male	0.06	272.73
	4		0.22	
P2c.3 Proximity	1	Female	0.82	3.51
	4		0.85	
	1	Male	0.74	16.28
	4		0.86	
P2c.3 Groom. Given	1	Female	0.04	270.69
	4		0.14	
	1	Male	0.01	391.22
	4		0.04	
P2c.3 Groom. Received	1	Female	0.07	33.52
	4		0.10	
	1	Male	0.01	184.75
	4		0.04	
P2c.3 Groom. Total	1	Female	0.10	103.26
	4		0.21	
	1	Male	0.02	258.60
	4		0.07	

1.5 SUPPLEMENTARY MATERIAL FOR MODEL RESULTS

In this section, we show the descriptive tables for each model (see Chapter 2, Table 2.1 for the models' summary) for hypothesis H1 (Appendix 1, §1.5.1) and hypothesis H2 (Appendix 1, §1.5.2). Compared to the tables presented in the Chapter 2, which focus on age and sex variables, these tables also include the control variables (maternal features and troop; see Chapter 2, §2.3). In addition, we present here the significant ($p\text{-value} \leq 0.05$; see Chapter 2, §2.3) results of part of the models used to test P1c (Appendix 1, §1.5.1).

1.5.1 Results H1: Inheritance of maternal social networks

This section shows the full tables for each model used to test the predictions of hypothesis H1: P1a, P1b, and P1c (Tables A1.9–A1.13). We also report a third approach (Tables A1.12 and A1.13; Figure A1.5) to test P1c (i.e., whether immatures' ego-networks were more similar to their mothers' ego-networks than to those of other group mates and how this changed with age), involving two different sets of models (see Chapter 2, §2.3 and §2.4 for the first two approaches: MP1c.1 and MP1c.2).

In the third approach to test P1c, we used the Pearson's correlation coefficient (r) of the mother-immature dyad with combinations of other dyads from the proximity networks or grooming proportions networks (as for the first two approaches). We ranked the r values of the immature-others' ego-networks, which were then standardised with the same function used for dominance ranks (see Chapter 2, §2.3), thus obtaining relative correlation ranks. We ran two binomial GLMM with a 1/0 score as the dependent variable (as for the first two approaches), scoring a '1' when the rank position of the mother-immature r was:

(1) ≥ 0.9 , i.e., the mother-immature's r was in the top 10% of the immatures' r (MP1c.3), and (2) > 0.5 , i.e., the mother-immature's r was above chance (MP1c.4).

For the proximity network, MP1c.4 had the same qualitative results as MP1c.2: between 1–4 years old, the odds of having a proximity network relatively more similar to the mother's one increased by 88.68% and 2.01% in females and males, respectively. Age and the age-sex interaction were not significant in MP1c.3. For the grooming network, MP1c.4 total had qualitatively similar results as MP1c.1 given and MP1c.2 given and total: between 1–4 years old, the odds of having a network relatively more similar to the mother's one increased by 166.10% and 24.59% in females and males, respectively. The pattern was significantly less marked in males (while the age-sex interaction was not significant in MP1c.1 and MP1c.2). In addition, according to our prediction and contrary to the results of the other four models (MP1c.1 and MP1c.2 given, and MP1c.4 total), in MP1c.3, immatures' grooming received networks became significantly less similar to their mothers' networks than to those of other individuals with age. This pattern was less marked in males (contrary to our prediction), but the age-sex interaction was not significant. Between 1–4 years old, the odds of having a grooming received network relatively more similar to the mother's one decreased by 67.17% and 51.89% in females and males, respectively. Finally, in MP1c.4 for grooming given, there was an opposite pattern for females and males, which was significantly less marked in males than in females: females' networks became significantly more similar to their mothers' ones than to those of other individuals with age, while males' networks became significantly less similar. Between 1–4 years old, the odds of having a grooming given network relatively more similar to the mother's one increased by 287.23%

in females and decreased by 29.35% in males. Instead, age and the age-sex interaction were not significant in MP1c.3 given and total, and in MP1c.4 received. Overall, there was stronger support against our P1c prediction than in favour of it (see Chapter 2, §2.5).

Figure A1.5: Changes in the odds that the rank of the mother-offspring social network correlation was ≥ 0.9 (MP1c.3) or > 0.5 (MP1c.4). These changes are related to immatures' age and divided between the two sexes ('F' = female, 'M' = male) for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y -axis variable) to occur. Ribbons represent 97.5% confidence intervals.

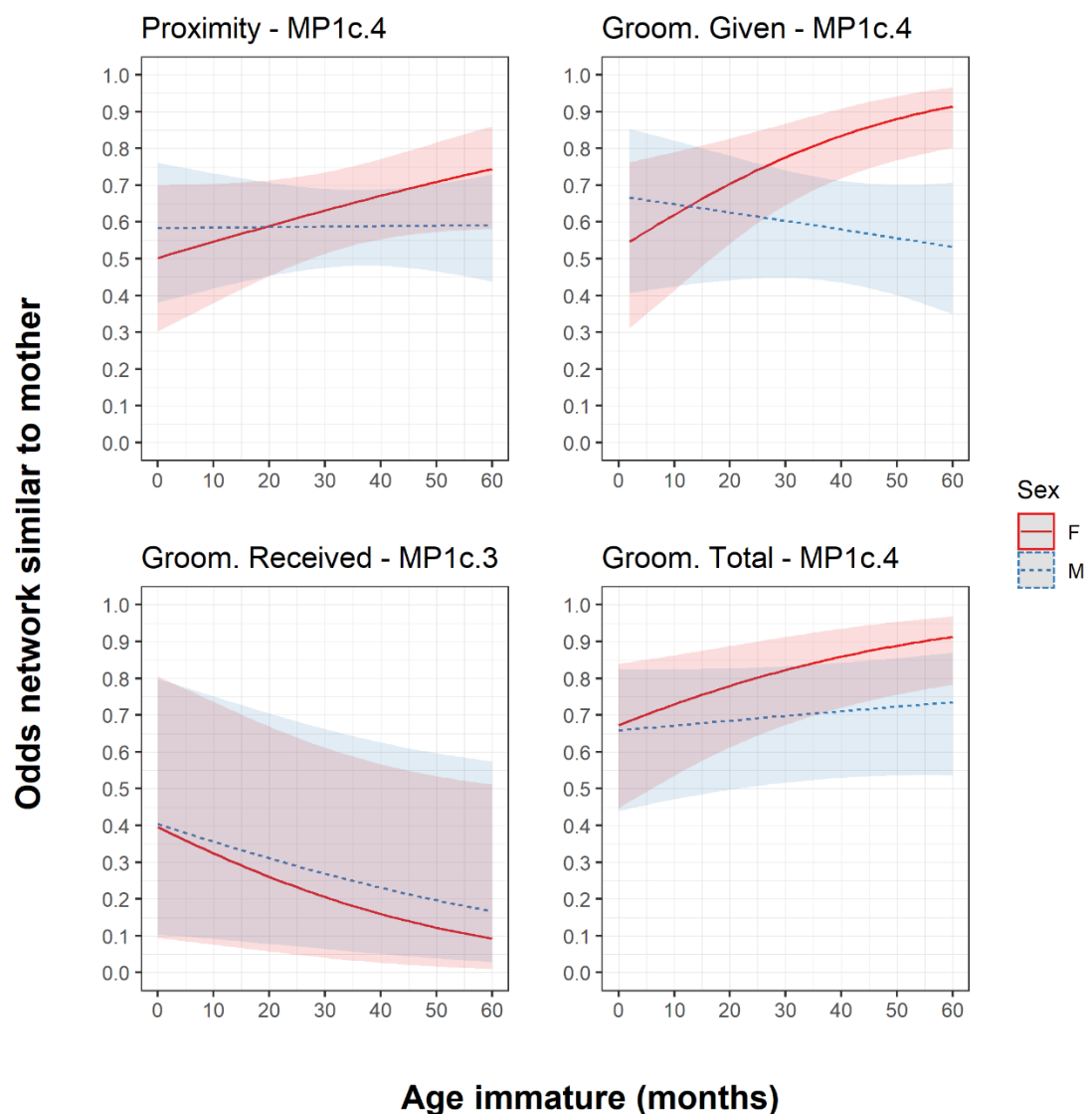


Table A1.9: Results of MP1a for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, test statistic (z value), *p*-value ('NS' = not significant), and conditional delta R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	z value	<i>p</i> -value	R ²
P1a Proximity	(Intercept)	-1.8889	0.2895	-6.5246	0.0000	0.27
	Age immature	-0.0112	0.0051	-2.1943	0.0282	
	Age:Sex	-0.0135	0.0067	-2.0162	0.0438	
	Nb. offspring	0.0300	0.0498	0.6017	0.5474	
	Relative rank	0.4667	0.2129	2.1920	0.0284	
	Sex immature	0.2702	0.2529	1.0687	0.2852	
	TroopL	0.1144	0.1428	0.8013	0.4230	
	TroopM	1.0131	0.2075	4.8816	0.0000	
P1a Groom. Total	(Intercept)	0.5005	0.2603	1.9228	0.0545	0.84
	Age immature	-0.0232	0.0035	-6.6501	0.0000	
	Age:Sex	-0.0173	0.0038	-4.5779	0.0000	
	Nb. offspring	-0.2177	0.0452	-4.8168	0.0000	
	Relative rank	-0.0057	0.2284	-0.0247	0.9803	
	Sex immature	1.0043	0.2027	4.9534	0.0000	
	TroopL	0.3741	0.2012	1.8595	0.0630	
	TroopM	0.1094	0.4163	0.2628	0.7927	

Table A1.10: Odds ratio (OR), lower and upper 97.5% confidence intervals (LCI and UCI, respectively), and percentage increase or decrease in odds for each variable of MP1a, for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males.

Model	Variable	OR	LCI	UCI	Percentage change
P1a Proximity	Age immature	0.99	0.98	1.00	-1.12
	Age:Sex	0.99	0.97	1.00	-1.34
	Nb. offspring	1.03	0.93	1.14	3.04
	Relative rank	1.59	1.05	2.42	59.48
	Sex immature	1.31	0.80	2.15	31.03
	TroopL	1.12	0.85	1.48	12.12
	TroopM	2.75	1.83	4.14	175.42
P1a Groom. Total	Age immature	0.98	0.97	0.98	-2.29
	Age:Sex	0.98	0.98	0.99	-1.72
	Nb. offspring	0.80	0.74	0.88	-19.56
	Relative rank	0.99	0.64	1.56	-0.56
	Sex immature	2.73	1.83	4.06	172.99
	TroopL	1.45	0.98	2.16	45.36
	TroopM	1.12	0.49	2.52	11.56

Table A1.11: Results of MP1b for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, degrees of freedom (df), test statistic (t value), *p*-value ('NS' = not significant), and conditional R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	df	t value	<i>p</i> -value	R ²
P1b Proximity	(Intercept)	0.2978	0.0786	46.8025	3.7887	-	0.20
	Age immature	-0.0029	0.0013	438.1043	-2.1852	0.05	
	Age:Sex	-0.0021	0.0018	431.8567	-1.1637	0.05	
	Nb. offspring	0.0179	0.0121	68.0345	1.4797	0.05	
	Relative rank	0.1911	0.0476	33.5945	4.0125	0.05	
	Sex immature	-0.0007	0.0670	433.0557	-0.0097	NS	
	TroopL	0.0977	0.0301	24.9783	3.2434	NS	
	TroopM	0.0988	0.0741	201.7839	1.3325	NS	
P1b Groom. Given	(Intercept)	0.1834	0.0597	130.1407	3.0742	-	0.25
	Age immature	0.0022	0.0010	322.6699	2.1597	0.05	
	Age:Sex	-0.0027	0.0015	464.5972	-1.7789	0.05	
	Nb. offspring	0.0025	0.0112	103.7697	0.2211	NS	
	Relative rank	-0.0337	0.0466	41.2485	-0.7224	NS	
	Sex immature	-0.0227	0.0607	355.6844	-0.3735	NS	
	TroopL	-0.0586	0.0304	24.3322	-1.9271	0.05	
	TroopM	-0.0848	0.0641	133.8744	-1.3228	NS	
P1b Groom. Received	(Intercept)	0.2006	0.0992	54.6323	2.0218	-	0.44
	Age immature	-0.0042	0.0013	166.9474	-3.2314	0.05	
	Age:Sex	0.0003	0.0016	236.2819	0.1745	NS	
	Nb. offspring	0.0557	0.0172	107.2775	3.2343	0.05	
	Relative rank	0.1151	0.0786	46.2955	1.4637	0.05	
	Sex immature	-0.0222	0.0575	154.4023	-0.3853	NS	
	TroopL	-0.1036	0.0806	31.1944	-1.2860	0.05	
	TroopM	-0.0413	0.0967	49.1936	-0.4272	0.05	
P1b Groom. Total	(Intercept)	0.2337	0.0644	100.5932	3.6276	-	0.28
	Age immature	-0.0010	0.0010	385.5281	-1.0401	0.05	
	Age:Sex	-0.0014	0.0012	487.6465	-1.1416	0.05	
	Nb. offspring	0.0207	0.0121	140.3337	1.7086	0.05	
	Relative rank	0.0225	0.0554	64.4210	0.4068	NS	
	Sex immature	-0.0147	0.0449	317.6541	-0.3284	NS	
	TroopL	-0.0540	0.0391	34.0437	-1.3788	0.05	
	TroopM	0.1457	0.0927	406.0224	1.5727	0.05	

Table A1.12: Results of MP1c.1–4 for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, test statistic (z value), *p*-value ('NS' = not significant), and conditional delta R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	z value	<i>p</i> -value	R ²
P1c.1 Proximity	(Intercept)	0.0547	0.4678	0.1170	-	0.03
	Age immature	0.0053	0.0090	0.5841	NS	
	Age:Sex	0.0017	0.0120	0.1412	NS	
	Nb. offspring	-0.0427	0.0791	-0.5396	NS	
	Relative rank	0.7873	0.3135	2.5111	NS	
	Sex immature	-0.3070	0.4550	-0.6748	NS	
	TroopL	0.3212	0.1946	1.6500	NS	
	TroopM	-0.6895	0.4964	-1.3889	NS	
P1c.1 Groom. Given	(Intercept)	-0.1617	0.4566	-0.3542	-	0.08
	Age immature	0.0198	0.0091	2.1908	0.05	
	Age:Sex	-0.0172	0.0126	-1.3698	NS	
	Nb. offspring	0.0664	0.0781	0.8505	NS	
	Relative rank	0.2714	0.2952	0.9192	NS	
	Sex immature	-0.1326	0.4849	-0.2735	NS	
	TroopL	-0.1472	0.1835	-0.8021	NS	
	TroopM	-1.4341	0.4874	-2.9421	0.05	
P1c.1 Groom. Received	(Intercept)	-0.8808	0.5331	-1.6520	-	0.13
	Age immature	-0.0088	0.0092	-0.9570	NS	
	Age:Sex	0.0108	0.0115	0.9376	NS	
	Nb. offspring	0.3278	0.1035	3.1680	0.05	
	Relative rank	0.8691	0.4383	1.9830	0.05	
	Sex immature	-0.4860	0.3657	-1.3287	NS	
	TroopL	-0.2242	0.4062	-0.5519	NS	
	TroopM	-0.6664	0.5665	-1.1763	NS	
P1c.1 Groom. Total	(Intercept)	-0.7639	0.4600	-1.6609	-	0.17
	Age immature	0.0096	0.0072	1.3354	NS	
	Age:Sex	-0.0022	0.0092	-0.2346	NS	
	Nb. offspring	0.3399	0.0842	4.0354	0.05	
	Relative rank	0.0217	0.3497	0.0620	NS	
	Sex immature	-0.3061	0.3116	-0.9823	NS	
	TroopL	-0.4084	0.2308	-1.7690	0.05	
	TroopM	-1.1853	0.4596	-2.5790	0.05	
P1c.2 Proximity	(Intercept)	-1.1590	0.4949	-2.3417	-	0.08
	Age immature	0.0219	0.0097	2.2548	0.05	
	Age:Sex	-0.0168	0.0128	-1.3111	NS	
	Nb. offspring	0.1617	0.0850	1.9029	NS	
	Relative rank	1.1377	0.3410	3.3367	NS	
	Sex immature	0.3355	0.4720	0.7109	NS	
	TroopL	0.3926	0.2078	1.8896	NS	
	TroopM	-1.1366	0.5210	-2.1817	NS	
P1c.2 Groom. Given	(Intercept)	-0.8772	0.5492	-1.5974	-	0.19
	Age immature	0.0161	0.0100	1.6035	0.05	
	Age:Sex	-0.0024	0.0143	-0.1681	NS	

Model	Variable	Estimate	Std. Error	z value	p-value	R ²
	Nb. offspring	0.1519	0.1016	1.4946	NS	
	Relative rank	0.5948	0.4090	1.4542	NS	
	Sex immature	-0.9799	0.5681	-1.7248	0.05	
	TroopL	-0.3134	0.2531	-1.2380	NS	
	TroopM	-0.4935	0.5658	-0.8723	NS	
P1c.2 Groom. Received	(Intercept)	-1.3871	0.6682	-2.0759	-	0.25
	Age immature	-0.0112	0.0114	-0.9879	NS	
	Age:Sex	0.0021	0.0141	0.1508	NS	
	Nb. offspring	0.4990	0.1434	3.4803	0.05	
	Relative rank	0.6419	0.5136	1.2499	0.05	
	Sex immature	-0.1466	0.4497	-0.3259	NS	
	TroopL	-0.9844	0.5090	-1.9338	0.05	
	TroopM	-1.3873	0.6753	-2.0544	0.05	
P1c.2 Groom. Total	(Intercept)	-1.3208	0.5172	-2.5540	-	0.24
	Age immature	0.0198	0.0079	2.5243	0.05	
	Age:Sex	-0.0134	0.0101	-1.3239	NS	
	Nb. offspring	0.2737	0.0901	3.0396	0.05	
	Relative rank	0.3147	0.3604	0.8730	NS	
	Sex immature	-0.0312	0.3522	-0.0885	NS	
	TroopL	-0.5200	0.2356	-2.2072	0.05	
	TroopM	-1.4387	0.4972	-2.8934	0.05	
P1c.3 Proximity	(Intercept)	-4.0354	0.7492	-5.3862	-	0.05
	Age immature	0.0218	0.0125	1.7441	NS	
	Age:Sex	-0.0060	0.0173	-0.3461	NS	
	Nb. offspring	0.2426	0.1135	2.1384	0.05	
	Relative rank	1.3955	0.4538	3.0751	0.05	
	Sex immature	-0.1009	0.7009	-0.1439	NS	
	TroopL	0.1362	0.2768	0.4920	NS	
	TroopM	-0.4824	0.8076	-0.5974	NS	
P1c.3 Groom. Given	(Intercept)	-1.5094	0.6919	-2.1815	-	0.19
	Age immature	0.0072	0.0119	0.6090	NS	
	Age:Sex	-0.0115	0.0172	-0.6700	NS	
	Nb. offspring	-0.0315	0.1352	-0.2331	NS	
	Relative rank	0.0220	0.5454	0.0404	NS	
	Sex immature	0.3187	0.6876	0.4635	NS	
	TroopL	-0.0911	0.3551	-0.2567	NS	
	TroopM	-2.2174	1.1383	-1.9480	NS	
P1c.3 Groom. Received	(Intercept)	-2.9905	1.0553	-2.8338	-	0.31
	Age immature	-0.0309	0.0159	-1.9440	0.05	
	Age:Sex	0.0106	0.0193	0.5497	NS	
	Nb. offspring	0.6603	0.2155	3.0638	0.05	
	Relative rank	0.7888	0.8169	0.9655	0.05	
	Sex immature	0.0339	0.5762	0.0588	NS	
	TroopL	-1.2460	0.8049	-1.5480	0.05	
	TroopM	-2.1100	1.0431	-2.0228	0.05	
P1c.3 Groom. Total	(Intercept)	-1.8260	0.6128	-2.9796	-	0.20
	Age immature	-0.0068	0.0099	-0.6851	NS	

Model	Variable	Estimate	Std. Error	z value	p-value	R ²
	Age:Sex	0.0082	0.0124	0.6627	NS	
	Nb. offspring	0.1743	0.1167	1.4934	NS	
	Relative rank	0.0538	0.4700	0.1145	NS	
	Sex immature	0.0039	0.4446	0.0089	NS	
	TroopL	-0.5550	0.3176	-1.7478	0.05	
	TroopM	-1.8340	0.7602	-2.4125	0.05	
P1c.4 Proximity	(Intercept)	-0.8236	0.4804	-1.7145	-	0.06
	Age immature	0.0176	0.0093	1.8872	0.05	
	Age:Sex	-0.0171	0.0123	-1.3881	NS	
	Nb. offspring	0.1288	0.0808	1.5942	0.05	
	Relative rank	0.7484	0.3187	2.3487	NS	
	Sex immature	0.3261	0.4614	0.7067	NS	
	TroopL	0.1941	0.1976	0.9822	NS	
	TroopM	-1.2261	0.5284	-2.3204	NS	
P1c.4 Groom. Given	(Intercept)	-0.9815	0.5736	-1.7110	-	0.21
	Age immature	0.0376	0.0113	3.3146	0.05	
	Age:Sex	-0.0473	0.0152	-3.1133	0.05	
	Nb. offspring	0.1684	0.1070	1.5739	0.05	
	Relative rank	0.9692	0.4502	2.1526	0.05	
	Sex immature	0.5954	0.5876	1.0134	NS	
	TroopL	-0.2785	0.3016	-0.9233	NS	
	TroopM	-1.2734	0.5981	-2.1289	0.05	
P1c.4 Groom. Received	(Intercept)	-0.9456	0.5832	-1.6215	-	0.20
	Age immature	0.0002	0.0105	0.0164	NS	
	Age:Sex	-0.0050	0.0130	-0.3864	NS	
	Nb. offspring	0.3939	0.1231	3.2007	0.05	
	Relative rank	0.8970	0.4408	2.0348	0.05	
	Sex immature	-0.2735	0.4218	-0.6484	NS	
	TroopL	-0.4817	0.4295	-1.1216	0.05	
	TroopM	-0.8646	0.5959	-1.4509	0.05	
P1c.4 Groom. Total	(Intercept)	-0.9080	0.5432	-1.6717	-	0.29
	Age immature	0.0272	0.0088	3.0948	0.05	
	Age:Sex	-0.0211	0.0110	-1.9170	0.05	
	Nb. offspring	0.4471	0.0992	4.5074	0.05	
	Relative rank	0.1846	0.4013	0.4599	NS	
	Sex immature	-0.0653	0.3631	-0.1798	NS	
	TroopL	-0.6702	0.2644	-2.5351	0.05	
	TroopM	-1.7777	0.5069	-3.5068	0.05	

Table A1.13: Odds ratio (OR), lower and upper 97.5% confidence intervals (LCI and UCI, respectively), and percentage increase or decrease in odds for each variable of MP1c.1–4, for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males.

Model	Variable	OR	LCI	UCI	Percentage change
P1c.1 Proximity	Age immature	1.01	0.99	1.02	0.53
	Age:Sex	1.00	0.98	1.03	0.17
	Nb. offspring	0.96	0.82	1.12	-4.18
	Relative rank	2.20	1.19	4.06	119.75
	Sex immature	0.74	0.30	1.79	-26.44
	TroopL	1.38	0.94	2.02	37.87
	TroopM	0.50	0.19	1.33	-49.82
P1c.1 Groom. Given	Age immature	1.02	1.00	1.04	2.00
	Age:Sex	0.98	0.96	1.01	-1.71
	Nb. offspring	1.07	0.92	1.25	6.87
	Relative rank	1.31	0.74	2.34	31.18
	Sex immature	0.88	0.34	2.27	-12.42
	TroopL	0.86	0.60	1.24	-13.69
	TroopM	0.24	0.09	0.62	-76.17
P1c.1 Groom. Received	Age immature	0.99	0.97	1.01	-0.88
	Age:Sex	1.01	0.99	1.03	1.08
	Nb. offspring	1.39	1.13	1.70	38.79
	Relative rank	2.38	1.01	5.63	138.48
	Sex immature	0.62	0.30	1.26	-38.49
	TroopL	0.80	0.36	1.77	-20.08
	TroopM	0.51	0.17	1.56	-48.64
P1c.1 Groom. Total	Age immature	1.01	1.00	1.02	0.97
	Age:Sex	1.00	0.98	1.02	-0.22
	Nb. offspring	1.40	1.19	1.66	40.48
	Relative rank	1.02	0.51	2.03	2.19
	Sex immature	0.74	0.40	1.36	-26.37
	TroopL	0.66	0.42	1.05	-33.53
	TroopM	0.31	0.12	0.75	-69.44
P1c.2 Proximity	Age immature	1.02	1.00	1.04	2.21
	Age:Sex	0.98	0.96	1.01	-1.67
	Nb. offspring	1.18	1.00	1.39	17.55
	Relative rank	3.12	1.60	6.09	211.97
	Sex immature	1.40	0.55	3.53	39.87
	TroopL	1.48	0.99	2.23	48.09
	TroopM	0.32	0.12	0.89	-67.91
P1c.2 Groom. Given	Age immature	1.02	1.00	1.04	1.62
	Age:Sex	1.00	0.97	1.03	-0.24
	Nb. offspring	1.16	0.95	1.42	16.40
	Relative rank	1.81	0.81	4.04	81.27
	Sex immature	0.38	0.12	1.14	-62.47
	TroopL	0.73	0.45	1.20	-26.90
	TroopM	0.61	0.20	1.85	-38.95
P1c.2	Age immature	0.99	0.97	1.01	-1.11

Model	Variable	OR	LCI	UCI	Percentage change
Groom. Received	Age:Sex	1.00	0.97	1.03	0.21
	Nb. offspring	1.65	1.24	2.18	64.71
	Relative rank	1.90	0.69	5.20	90.01
	Sex immature	0.86	0.36	2.09	-13.63
	TroopL	0.37	0.14	1.01	-62.63
	TroopM	0.25	0.07	0.94	-75.03
P1c.2 Groom. Total	Age immature	1.02	1.00	1.04	2.00
	Age:Sex	0.99	0.97	1.01	-1.33
	Nb. offspring	1.31	1.10	1.57	31.49
	Relative rank	1.37	0.68	2.78	36.98
	Sex immature	0.97	0.49	1.93	-3.07
	TroopL	0.59	0.37	0.94	-40.55
	TroopM	0.24	0.09	0.63	-76.28
P1c.3 Proximity	Age immature	1.02	1.00	1.05	2.20
	Age:Sex	0.99	0.96	1.03	-0.60
	Nb. offspring	1.27	1.02	1.59	27.46
	Relative rank	4.04	1.66	9.82	303.68
	Sex immature	0.90	0.23	3.57	-9.59
	TroopL	1.15	0.67	1.97	14.59
	TroopM	0.62	0.13	3.01	-38.27
P1c.3 Groom. Given	Age immature	1.01	0.98	1.03	0.73
	Age:Sex	0.99	0.96	1.02	-1.14
	Nb. offspring	0.97	0.74	1.26	-3.10
	Relative rank	1.02	0.35	2.98	2.23
	Sex immature	1.38	0.36	5.29	37.54
	TroopL	0.91	0.46	1.83	-8.71
	TroopM	0.11	0.01	1.01	-89.11
P1c.3 Groom. Received	Age immature	0.97	0.94	1.00	-3.05
	Age:Sex	1.01	0.97	1.05	1.07
	Nb. offspring	1.94	1.27	2.95	93.53
	Relative rank	2.20	0.44	10.91	120.07
	Sex immature	1.03	0.33	3.20	3.45
	TroopL	0.29	0.06	1.39	-71.23
	TroopM	0.12	0.02	0.94	-87.88
P1c.3 Groom. Total	Age immature	0.99	0.97	1.01	-0.68
	Age:Sex	1.01	0.98	1.03	0.83
	Nb. offspring	1.19	0.95	1.50	19.05
	Relative rank	1.06	0.42	2.65	5.53
	Sex immature	1.00	0.42	2.40	0.40
	TroopL	0.57	0.31	1.07	-42.59
	TroopM	0.16	0.04	0.71	-84.02
P1c.4 Proximity	Age immature	1.02	1.00	1.04	1.78
	Age:Sex	0.98	0.96	1.01	-1.69
	Nb. offspring	1.14	0.97	1.33	13.74
	Relative rank	2.11	1.13	3.95	111.37
	Sex immature	1.39	0.56	3.42	38.55
	TroopL	1.21	0.82	1.79	21.42

Model	Variable	OR	LCI	UCI	Percentage change
	TroopM	0.29	0.10	0.83	-70.66
P1c.4 Groom. Given	Age immature	1.04	1.02	1.06	3.83
	Age:Sex	0.95	0.93	0.98	-4.62
	Nb. offspring	1.18	0.96	1.46	18.34
	Relative rank	2.64	1.09	6.37	163.58
	Sex immature	1.81	0.57	5.74	81.38
	TroopL	0.76	0.42	1.37	-24.31
	TroopM	0.28	0.09	0.90	-72.01
P1c.4 Groom. Received	Age immature	1.00	0.98	1.02	0.02
	Age:Sex	1.00	0.97	1.02	-0.50
	Nb. offspring	1.48	1.16	1.89	48.28
	Relative rank	2.45	1.03	5.82	145.23
	Sex immature	0.76	0.33	1.74	-23.93
	TroopL	0.62	0.27	1.43	-38.23
	TroopM	0.42	0.13	1.35	-57.88
P1c.4 Groom. Total	Age immature	1.03	1.01	1.05	2.76
	Age:Sex	0.98	0.96	1.00	-2.09
	Nb. offspring	1.56	1.29	1.90	56.38
	Relative rank	1.20	0.55	2.64	20.27
	Sex immature	0.94	0.46	1.91	-6.32
	TroopL	0.51	0.30	0.86	-48.84
	TroopM	0.17	0.06	0.46	-83.10

1.5.2 Results H2: Changes in social network characteristics throughout development

This section shows the full tables for each model used to test the predictions of hypothesis H2: P2a, P2b, and P2c (Tables A1.14–A1.17).

Table A1.14: Results of MP2a for the proximity and grooming (Groom.) networks Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring, relative rank, and social network strength; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, degrees of freedom (df), test statistic (t value), *p*-value ('NS' = not significant), and conditional R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	df	t value	<i>p</i> -value	R ²
P2a Proximity	(Intercept)	0.7731	0.2344	63.8348	3.2982	-	0.41
	Age immature	-0.0211	0.0039	208.4171	-5.4838	0.05	
	Age:Sex	0.0069	0.0050	291.7706	1.3872	NS	
	Nb. offspring	0.0627	0.0385	76.8341	1.6298	0.05	
	Relative rank	0.3433	0.1610	46.4043	2.1326	NS	
	Sex immature	-0.3603	0.1936	224.6261	-1.8610	NS	
	Strength mother	0.1890	0.0387	451.6261	4.8793	0.05	

Model	Variable	Estimate	Std. Error	df	t value	p-value	R ²
	TroopL	-0.1839	0.1008	25.6461	-1.8248	NS	
	TroopM	-0.2242	0.2702	242.6280	-0.8296	0.05	
P2a Groom. Given	(Intercept)	-1.4408	0.1547	25.8753	-9.3147	-	0.72
	Age immature	0.0455	0.0019	476.7874	23.3558	0.05	
	Age:Sex	-0.0199	0.0025	623.1896	-8.0460	0.05	
	Nb. offspring	0.0464	0.0224	114.2184	2.0684	NS	
	Relative rank	0.0634	0.0909	46.8687	0.6982	NS	
	Sex immature	-0.2985	0.0893	349.8585	-3.3429	0.05	
	Strength mother	0.0494	0.0472	454.8695	1.0463	0.05	
	TroopL	-0.0379	0.0609	31.0244	-0.6226	NS	
	TroopM	-0.1682	0.1197	177.9398	-1.4057	NS	
P2a Groom. Received	(Intercept)	-0.1618	0.1298	99.3492	-1.2470	-	0.40
	Age immature	0.0069	0.0020	479.8039	3.4741	0.05	
	Age:Sex	-0.0022	0.0025	659.5725	-0.8993	NS	
	Nb. offspring	0.0136	0.0244	132.7472	0.5572	NS	
	Relative rank	0.0804	0.1060	59.9335	0.7584	NS	
	Sex immature	-0.0613	0.0922	321.7225	-0.6647	NS	
	Strength mother	-0.0369	0.0211	500.9098	-1.7487	NS	
	TroopL	-0.4146	0.0766	40.0373	-5.4137	0.05	
	TroopM	-0.5240	0.1297	194.7066	-4.0394	0.05	
P2a Groom. Total	(Intercept)	-0.9857	0.1272	64.0888	-7.7467	-	0.64
	Age immature	0.0341	0.0019	488.3826	18.2285	0.05	
	Age:Sex	-0.0235	0.0023	669.0969	-10.0356	0.05	
	Nb. offspring	0.0504	0.0228	144.7904	2.2107	NS	
	Relative rank	-0.0383	0.0987	60.7245	-0.3874	NS	
	Sex immature	-0.0125	0.0863	336.6209	-0.1444	NS	
	Strength mother	0.1142	0.0238	425.3126	4.7944	0.05	
	TroopL	-0.3132	0.0691	39.6789	-4.5307	0.05	
	TroopM	-0.5016	0.1199	189.2269	-4.1848	0.05	

Table A1.15: Results of MP2b.1–2 for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring, relative rank, and social network centrality (MP2b.1) and betweenness (MP2b.2); troop. The values reported for sex refer to males. The estimate, standard (Std.) error, degrees of freedom (df), test statistic (t value), *p*-value ('NS' = not significant), and conditional R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	df	t value	p-value	R ²
P2b.1 Proximity	(Intercept)	0.8658	0.2286	50.4055	3.7870	-	0.49
	Age immature	-0.0211	0.0036	203.6444	-5.7929	0.05	
	Age:Sex	0.0047	0.0047	285.4914	1.0004	NS	
	Centrality mother	0.3044	0.0346	447.7050	8.8094	0.05	
	Nb. offspring	0.0481	0.0365	72.8349	1.3186	0.05	
	Relative rank	0.2511	0.1529	43.9671	1.6421	NS	
	Sex immature	-0.2964	0.1831	219.8464	-1.6186	NS	
	TroopL	-0.1701	0.0958	24.3387	-1.7756	NS	

Model	Variable	Estimate	Std. Error	df	t value	p-value	R ²
	TroopM	-0.4302	0.2569	237.1518	-1.6746	0.05	
P2b.1 Groom. Total	(Intercept)	-0.0899	0.1340	97.4781	-0.6710	-	0.49
	Age immature	0.0097	0.0022	451.7644	4.3900	0.05	
	Age:Sex	-0.0068	0.0028	595.7264	-2.4198	NS	
	Centrality mother	0.4283	0.0262	438.8201	16.3550	0.05	
	Nb. offspring	0.0301	0.0250	121.9220	1.2045	NS	
	Relative rank	0.1654	0.1064	51.6199	1.5548	NS	
	Sex immature	-0.0195	0.1005	327.1470	-0.1938	NS	
	TroopL	-0.8069	0.0728	38.2129	-11.0807	0.05	
	TroopM	-0.9460	0.1366	188.9464	-6.9252	0.05	
P2b.2 Proximity	(Intercept)	-0.2590	0.2310	114.3121	-1.1214	-	0.07
	Age immature	0.0054	0.0042	165.0928	1.2980	NS	
	Age:Sex	-0.0055	0.0057	215.9049	-0.9685	NS	
	Betweenness mother	0.1262	0.0468	436.0496	2.6955	NS	
	Nb. offspring	-0.0198	0.0406	86.2569	-0.4881	NS	
	Relative rank	-0.1360	0.1694	45.0581	-0.8033	0.05	
	Sex immature	0.1166	0.2167	192.7433	0.5382	NS	
	TroopL	0.0418	0.1077	31.7890	0.3880	NS	
	TroopM	-0.2419	0.3247	281.1946	-0.7449	NS	
P2b.2 Groom. Total	(Intercept)	-0.9259	0.1440	43.3906	-6.4313	-	0.52
	Age immature	0.0355	0.0023	441.7744	15.5632	0.05	
	Age:Sex	-0.0126	0.0029	515.1513	-4.3043	0.05	
	Betweenness mother	-0.0228	0.0354	439.5192	-0.6442	NS	
	Nb. offspring	0.0656	0.0251	184.4977	2.6165	0.05	
	Relative rank	0.1210	0.0959	151.4199	1.2619	NS	
	Sex immature	-0.2042	0.1020	371.0548	-2.0017	NS	
	TroopL	-0.4345	0.0786	181.2177	-5.5291	0.05	
	TroopM	-0.4651	0.1431	447.2707	-3.2498	0.05	

Table A1.16: Results of MP2c.1–3 for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males. The estimate, standard (Std.) error, test statistic (z value), *p*-value ('NS' = not significant), and conditional delta R² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	z value	p-value	R ²
P2c.1 Proximity	(Intercept)	-0.1545	0.0757	-2.0419	-	0.14
	Age immature	0.0007	0.0013	0.5308	NS	
	Age:Sex	0.0021	0.0017	1.2386	0.05	
	Nb. offspring	0.0025	0.0115	0.2199	NS	
	Relative rank	0.0843	0.0443	1.9018	0.05	
	Sex immature	-0.0922	0.0641	-1.4390	0.05	
	TroopL	-0.1120	0.0280	-4.0034	NS	
	TroopM	0.0442	0.0903	0.4892	NS	
P2c.1 Groom. Given	(Intercept)	-3.6708	0.2736	-13.4147	-	0.64
	Age immature	0.0346	0.0032	10.9346	0.05	
	Age:Sex	0.0060	0.0044	1.3499	NS	

Model	Variable	Estimate	Std. Error	z value	p-value	R ²
	Nb. offspring	0.0080	0.0407	0.1976	NS	
	Relative rank	0.1236	0.1643	0.7521	NS	
	Sex immature	-1.1815	0.1887	-6.2622	0.05	
	TroopL	-0.3559	0.1108	-3.2129	0.05	
	TroopM	0.6507	0.2057	3.1630	NS	
P2c.1 Groom. Received	(Intercept)	-3.3194	0.2277	-14.5789	-	0.36
	Age immature	0.0119	0.0027	4.3346	0.05	
	Age:Sex	0.0023	0.0036	0.6418	NS	
	Nb. offspring	0.0547	0.0339	1.6153	0.05	
	Relative rank	0.0607	0.1410	0.4302	NS	
	Sex immature	-0.1137	0.1339	-0.8486	NS	
	TroopL	-0.4046	0.0948	-4.2689	0.05	
	TroopM	0.7017	0.1734	4.0468	NS	
P2c.1 Groom. Total	(Intercept)	-2.8192	0.2100	-13.4233	-	0.56
	Age immature	0.0227	0.0022	10.1039	0.05	
	Age:Sex	-0.0010	0.0030	-0.3143	NS	
	Nb. offspring	0.0243	0.0287	0.8475	NS	
	Relative rank	0.0726	0.1182	0.6143	NS	
	Sex immature	-0.4327	0.1195	-3.6211	0.05	
	TroopL	-0.3929	0.0798	-4.9257	0.05	
	TroopM	0.6734	0.1490	4.5185	NS	
P2c.2 Proximity	(Intercept)	-0.1206	0.1325	-0.9098	-	0.01
	Age immature	-0.0001	0.0026	-0.0514	NS	
	Age:Sex	0.0018	0.0036	0.5059	NS	
	Nb. offspring	-0.0059	0.0221	-0.2665	NS	
	Relative rank	0.0531	0.0886	0.5994	NS	
	Sex immature	-0.0362	0.1412	-0.2566	NS	
	TroopL	-0.0754	0.0551	-1.3676	NS	
	TroopM	0.0877	0.1914	0.4581	NS	
P2c.2 Groom. Given	(Intercept)	-3.1097	0.3377	-9.2096	-	0.31
	Age immature	0.0303	0.0051	5.9068	0.05	
	Age:Sex	0.0137	0.0073	1.8782	NS	
	Nb. offspring	-0.0315	0.0571	-0.5510	NS	
	Relative rank	0.0897	0.2273	0.3946	NS	
	Sex immature	-1.1021	0.3042	-3.6234	0.05	
	TroopL	-0.2156	0.1466	-1.4714	0.05	
	TroopM	0.3547	0.3304	1.0735	NS	
P2c.2 Groom. Received	(Intercept)	-3.5299	0.3445	-10.2476	-	0.23
	Age immature	0.0261	0.0054	4.8332	0.05	
	Age:Sex	0.0067	0.0070	0.9591	NS	
	Nb. offspring	0.0357	0.0551	0.6485	NS	
	Relative rank	0.0478	0.2121	0.2256	NS	
	Sex immature	-0.0887	0.2828	-0.3136	NS	
	TroopL	-0.2854	0.1363	-2.0941	0.05	
	TroopM	0.5037	0.3137	1.6060	NS	
P2c.2 Groom. Total	(Intercept)	-2.7160	0.2806	-9.6779	-	0.33
	Age immature	0.0275	0.0042	6.5608	0.05	

Model	Variable	Estimate	Std. Error	z value	p-value	R ²
	Age:Sex	0.0090	0.0057	1.5911	NS	
	Nb. offspring	0.0142	0.0447	0.3185	NS	
	Relative rank	0.0507	0.1748	0.2899	NS	
	Sex immature	-0.5450	0.2297	-2.3724	0.05	
	TroopL	-0.3158	0.1123	-2.8130	0.05	
	TroopM	0.2726	0.2700	1.0097	NS	
P2c.3 Proximity	(Intercept)	-0.2048	0.0748	-2.7362	-	0.18
	Age immature	0.0010	0.0012	0.7998	0.05	
	Age:Sex	0.0032	0.0016	1.9666	0.05	
	Nb. offspring	0.0022	0.0109	0.1971	NS	
	Relative rank	0.0872	0.0422	2.0676	0.05	
	Sex immature	-0.1528	0.0627	-2.4379	0.05	
	TroopL	-0.1006	0.0266	-3.7866	0.05	
	TroopM	0.0597	0.0881	0.6780	NS	
P2c.3 Groom. Given	(Intercept)	-3.7472	0.2693	-13.9164	-	0.70
	Age immature	0.0364	0.0029	12.5025	0.05	
	Age:Sex	0.0078	0.0044	1.7784	NS	
	Nb. offspring	0.0291	0.0407	0.7138	NS	
	Relative rank	0.1874	0.1697	1.1038	NS	
	Sex immature	-1.5735	0.1916	-8.2145	0.05	
	TroopL	-0.0907	0.1178	-0.7696	0.05	
	TroopM	0.5454	0.2217	2.4596	0.05	
P2c.3 Groom. Received	(Intercept)	-2.6930	0.1926	-13.9817	-	0.57
	Age immature	0.0080	0.0023	3.5225	0.05	
	Age:Sex	0.0210	0.0038	5.4663	0.05	
	Nb. offspring	0.0649	0.0303	2.1442	0.05	
	Relative rank	0.1066	0.1174	0.9079	NS	
	Sex immature	-1.9513	0.1537	-12.6991	0.05	
	TroopL	-0.2826	0.0754	-3.7485	0.05	
	TroopM	0.4125	0.1634	2.5239	0.05	
P2c.3 Groom. Total	(Intercept)	-2.5047	0.1901	-13.1774	-	0.72
	Age immature	0.0197	0.0020	9.8845	0.05	
	Age:Sex	0.0158	0.0032	4.9161	0.05	
	Nb. offspring	0.0440	0.0271	1.6264	0.05	
	Relative rank	0.1433	0.1068	1.3407	NS	
	Sex immature	-1.8453	0.1327	-13.9108	0.05	
	TroopL	-0.1898	0.0706	-2.6903	0.05	
	TroopM	0.4584	0.1452	3.1572	0.05	

Table A1.17: Odds ratio (OR), lower and upper 97.5% confidence intervals (LCI and UCI, respectively) and percentage increase or decrease in odds for each variable of MP2c.1–3, for the proximity and grooming (Groom.) networks. Variables include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring and relative rank; troop. The values reported for sex refer to males.

Model	Variable	OR	LCI	UCI	Percentage change
P2c.1 Proximity	Age immature	1.00	1.00	1.00	0.07
	Age:Sex	1.00	1.00	1.01	0.21
	Nb. offspring	1.00	0.98	1.03	0.25
	Relative rank	1.09	1.00	1.19	8.79
	Sex immature	0.91	0.80	1.03	-8.81
	TroopL	0.89	0.85	0.94	-10.59
	TroopM	1.05	0.88	1.25	4.52
P2c.1 Groom. Given	Age immature	1.04	1.03	1.04	3.52
	Age:Sex	1.01	1.00	1.01	0.60
	Nb. offspring	1.01	0.93	1.09	0.81
	Relative rank	1.13	0.82	1.56	13.15
	Sex immature	0.31	0.21	0.44	-69.32
	TroopL	0.70	0.56	0.87	-29.95
	TroopM	1.92	1.28	2.87	91.68
P2c.1 Groom. Received	Age immature	1.01	1.01	1.02	1.20
	Age:Sex	1.00	1.00	1.01	0.23
	Nb. offspring	1.06	0.99	1.13	5.62
	Relative rank	1.06	0.81	1.40	6.25
	Sex immature	0.89	0.69	1.16	-10.74
	TroopL	0.67	0.55	0.80	-33.28
	TroopM	2.02	1.44	2.83	101.71
P2c.1 Groom. Total	Age immature	1.02	1.02	1.03	2.29
	Age:Sex	1.00	0.99	1.01	-0.10
	Nb. offspring	1.02	0.97	1.08	2.46
	Relative rank	1.08	0.85	1.36	7.53
	Sex immature	0.65	0.51	0.82	-35.12
	TroopL	0.68	0.58	0.79	-32.49
	TroopM	1.96	1.46	2.63	96.09
P2c.2 Proximity	Age immature	1.00	0.99	1.00	-0.01
	Age:Sex	1.00	0.99	1.01	0.18
	Nb. offspring	0.99	0.95	1.04	-0.59
	Relative rank	1.05	0.89	1.25	5.46
	Sex immature	0.96	0.73	1.27	-3.56
	TroopL	0.93	0.83	1.03	-7.26
	TroopM	1.09	0.75	1.59	9.16
P2c.2 Groom. Given	Age immature	1.03	1.02	1.04	3.08
	Age:Sex	1.01	1.00	1.03	1.38
	Nb. offspring	0.97	0.87	1.08	-3.10
	Relative rank	1.09	0.70	1.71	9.39
	Sex immature	0.33	0.18	0.60	-66.78
	TroopL	0.81	0.60	1.07	-19.40
	TroopM	1.43	0.75	2.72	42.57
P2c.2	Age immature	1.03	1.02	1.04	2.65

Model	Variable	OR	LCI	UCI	Percentage change
Groom. Received	Age:Sex	1.01	0.99	1.02	0.68
	Nb. offspring	1.04	0.93	1.15	3.64
	Relative rank	1.05	0.69	1.59	4.90
	Sex immature	0.92	0.53	1.59	-8.49
	TroopL	0.75	0.58	0.98	-24.83
	TroopM	1.65	0.89	3.06	65.49
P2c.2 Groom. Total	Age immature	1.03	1.02	1.04	2.79
	Age:Sex	1.01	1.00	1.02	0.90
	Nb. offspring	1.01	0.93	1.11	1.43
	Relative rank	1.05	0.75	1.48	5.20
	Sex immature	0.58	0.37	0.91	-42.02
	TroopL	0.73	0.59	0.91	-27.08
	TroopM	1.31	0.77	2.23	31.34
P2c.3 Proximity	Age immature	1.00	1.00	1.00	0.10
	Age:Sex	1.00	1.00	1.01	0.32
	Nb. offspring	1.00	0.98	1.02	0.22
	Relative rank	1.09	1.00	1.19	9.12
	Sex immature	0.86	0.76	0.97	-14.17
	TroopL	0.90	0.86	0.95	-9.57
	TroopM	1.06	0.89	1.26	6.15
P2c.3 Groom. Given	Age immature	1.04	1.03	1.04	3.71
	Age:Sex	1.01	1.00	1.02	0.79
	Nb. offspring	1.03	0.95	1.11	2.95
	Relative rank	1.21	0.86	1.68	20.61
	Sex immature	0.21	0.14	0.30	-79.27
	TroopL	0.91	0.72	1.15	-8.67
	TroopM	1.73	1.12	2.66	72.53
P2c.3 Groom. Received	Age immature	0.14	1.00	1.01	-85.79
	Age:Sex	0.07	1.01	1.03	-93.23
	Nb. offspring	0.75	1.01	1.13	-24.62
	Relative rank	1.07	0.88	1.40	6.70
	Sex immature	1.11	0.11	0.19	11.25
	TroopL	1.51	0.65	0.87	51.06
	TroopM	1.02	1.10	2.08	2.13
P2c.3 Groom. Total	Age immature	1.02	1.02	1.02	1.99
	Age:Sex	1.02	1.01	1.02	1.59
	Nb. offspring	1.04	0.99	1.10	4.50
	Relative rank	1.15	0.94	1.42	15.40
	Sex immature	0.16	0.12	0.20	-84.20
	TroopL	0.83	0.72	0.95	-17.29
	TroopM	1.58	1.19	2.10	58.15

1.6 MODELS' STANDARDISED ESTIMATES

In order to compare the effects of different independent variables within each model, we derived standardised (i.e., all the variables are on the same scale) estimates using the package *semEff* (Murphy 2022) and the function *stdEff*. For the proximity network (Table A1.18), a mother's social rank and social network integration had greater effects compared to immatures' age and sex (and their interaction), and a mother's number of offspring. The effect of the number of siblings compared to the effect of age was variable but tended to be greater for the models on the inheritance of maternal proximity networks (hypothesis H1) than for those on the changes in the proximity network integration and social partners' characteristics (hypothesis H2). For the grooming network (Table A1.19), on the one hand, a mother's number of offspring had generally greater effects compared to age, sex (and their interaction), and maternal rank for the H1 models; on the other hand, age and sex were more important determinants of the immatures' grooming network characteristics for H2 models. The effect of a mother's grooming network integration was variable depending on the model, being greater than the effect of age only in half of the cases. Finally, for both for the proximity and the grooming networks (Tables A1.18 and A1.19), sex had a strong effect overall, almost always greater than that of age, and the interaction between age and sex had generally a lower weight compared to its main effects.

Table A1.18: Significant variables' standardised estimates (absolute values) for models on the proximity network. The variables of interest include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring, relative rank, and social network strength and centrality. The values reported for sex refer to males. The colour scale represents a range from lower (red) to higher (green) values. Only models with more than one significant variable (for which between-variables comparisons could be made) were included.

Model	Age immature	Age:Sex	Centrality mother	Nb. offspring	Relative rank	Sex immature	Strength mother
P1a	0.0113	0.0039	-	-	0.0175	-	-
P1b	0.0648	0.0162	-	0.0657	0.1775	-	-
P1c.3	-	-	-	0.0196	0.0283	-	-
P1c.4	0.0021	-	-	0.0086	-	-	-
P2a	0.101	-	-	0.0856	-	-	0.2047
P2b.1	0.1078	-	0.3462	0.0651	-	-	-
P2b.2	-	-	-	-	-0.0427	-	-
P2c.1	-	0.0194	-	-	0.092	0.0301	-
P2c.3	0.0517	0.0295	-	-	0.0929	0.0662	-

Table A1.19: Significant variables' standardised estimates (absolute values) for models on the grooming network. The variables of interest include immatures' age, sex, and the age-sex interaction (':'); a mother's number (Nb.) of offspring, relative rank, and social network strength and centrality. The values reported for sex refer to males. The colour scale represents a range from lower (red) to higher (green) values. Only models with more than one significant variable (for which between-variables comparisons could be made) were included.

Model	Grooming	Age immature	Age:Sex	Centrality mother	Nb. offspring	Relative rank	Sex immature	Strength mother
P1a	Total	0.0442	0.0122	-	0.0488	-	0.0461	-
P1b	Given	0.0149	0.0252	-	-	-	-	-
	Received	0.0722	-	-	0.2288	0.1255	-	-
	Total	0.0346	0.013	-	0.0907	-	-	-
P1c.1	Received	-	-	-	0.0197	0.0139	-	-
P1c.2	Given	0.0035	-	-	-	-	0.0263	-
	Received	-	-	-	0.0297	0.0105	-	-
	Total	0.0032	-	-	0.017	-	-	-
P1c.3	Received	0.0071	-	-	0.0459	0.0152	-	-
P1c.4	Given	0.0028	0.0058	-	0.0111	0.0164	-	-
	Received	-	-	-	0.023	0.0142	-	-

Model	Grooming	Age immature	Age:Sex	Centrality mother	Nb. offspring	Relative rank	Sex immature	Strength mother
	Total	0.004	0.0028	-	0.0303	-	-	-
P2a	Given	0.1936	0.0563	-	-	-	0.4684	0.0247
	Total	0.1438	0.0825	-	-	-	-	0.1517
P2b.1	Total	0.0376	-	0.5629	-	-	-	-
P2b.2	Total	0.1568	0.0346	-	0.0805	-	-	-
P2c.1	Given	0.0283	-	-	-	-	0.0545	-
	Received	0.0095	-	-	0.0089	-	-	-
	Total	0.0206	-	-	-	-	0.0357	-
P2c.2	Given	0.0246	-	-	-	-	0.034	-
	Total	0.0209	-	-	-	-	0.0139	-
P2c.3	Given	0.0301	-	-	-	-	0.0721	-
	Received	0.0152	0.0078	-	0.0099	-	0.0776	-
	Total	0.0266	0.0072	-	0.0081	-	0.0977	-

1.7 CHANGES IN MOTHERS' GROOMING NETWORK INTEGRATION

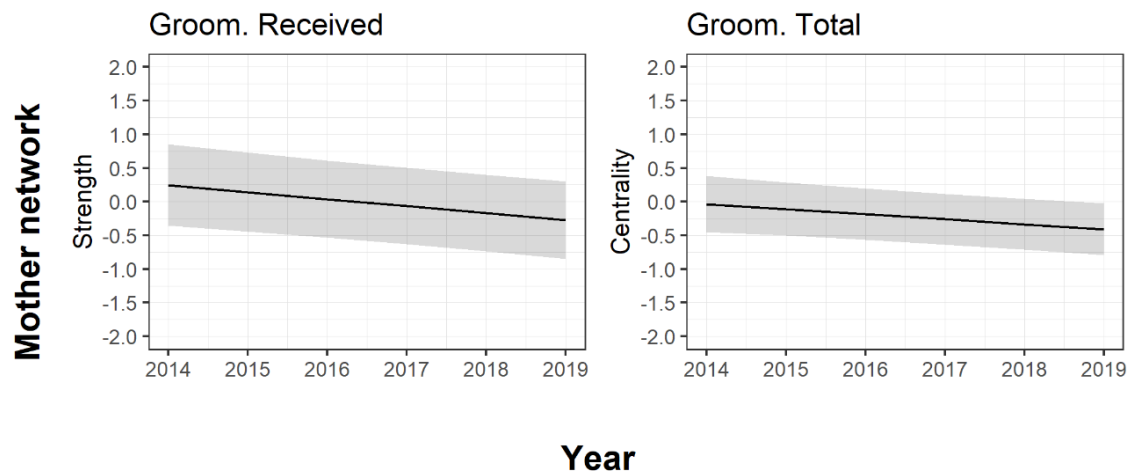
We modelled changes in mothers' grooming network integration across the six study years (from 2014 to 2019). We ran five LMMs with different social network metrics (see Chapter 2, §2.3 for definitions) as dependent variables: strength (all grooming components), centrality and betweenness (grooming total). The independent variable of interest was the year of the record, while we controlled for a mother's number of offspring, social rank, and troop as fixed factors. Finally, we inserted the mothers' identity as a random factor. Node-based permutations were performed to obtain *p*-values (see Chapter 2, §2.3). The mothers' grooming received strength and (total) centrality changed significantly across the study years (Table A1.20). There was no significant year variation in the mothers' grooming given and total strength, and (total) betweenness. Grooming received strength and (total) centrality decreased, respectively, of 1.68% and 1.48% between the study years (Figure A1.6).

Table A1.20: Changes in the mothers' grooming (Groom.) network metrics across the study years (2014–2019). Variables include a mother's number (Nb.) of offspring and relative rank; year and troop. The estimate, standard (Std.) error, degrees of freedom (df), test statistic (t value), *p*-value ('NS' = not significant), and conditional *R*² are reported for each variable/ model.

Model	Variable	Estimate	Std. Error	df	t value	<i>p</i> -value	<i>R</i> ²
Strength Groom. Given	(Intercept)	-43.4964	24.5158	382.0108	-1.7742	-	0.51
	Nb. offspring	-0.0276	0.0228	243.9270	-1.2085	NS	
	Relative rank	0.4463	0.1144	154.7304	3.9022	0.05	
	TroopL	0.2128	0.1100	30.2970	1.9336	0.05	
	TroopM	0.1561	0.1050	512.0843	1.4864	NS	
	Year	0.0219	0.0122	381.0222	1.7991	NS	
Strength Groom. Received	(Intercept)	208.9042	55.0928	699.9277	3.7919	-	0.77
	Nb. offspring	0.4477	0.0529	587.2155	8.4695	0.05	
	Relative rank	0.5878	0.2750	449.9136	2.1374	0.05	
	TroopL	0.9964	0.3702	31.9783	2.6918	0.05	

Model	Variable	Estimate	Std. Error	df	t value	p-value	R ²
	TroopM	1.4041	0.2308	779.7157	6.0836	0.05	
	Year	-0.1045	0.0274	699.4002	-3.8188	0.05	
Strength Groom. Total	(Intercept)	-41.2396	44.3834	522.6991	-0.9292	-	0.66
	Nb. offspring	0.0826	0.0418	377.7754	1.9738	0.05	
	Relative rank	1.3315	0.2129	257.1015	6.2541	0.05	
	TroopL	0.7233	0.2263	37.5542	3.1957	0.05	
	TroopM	0.8406	0.1885	649.3840	4.4590	0.05	
	Year	0.0202	0.0220	521.7992	0.9161	NS	
Centrality Groom. Total	(Intercept)	149.9823	48.2807	478.9856	3.1065	-	0.64
	Nb. offspring	0.1226	0.0454	333.1648	2.6989	0.05	
	Relative rank	0.8789	0.2306	220.5784	3.8111	0.05	
	TroopL	0.9437	0.2409	33.0197	3.9179	0.05	
	TroopM	1.1242	0.2054	613.1496	5.4746	0.05	
	Year	-0.0749	0.0240	478.0405	-3.1240	0.05	
Betweenness Groom. Total	(Intercept)	-61.1655	36.2010	485.2658	-1.6896	-	0.72
	Nb. offspring	-0.1678	0.0339	338.9178	-4.9505	0.05	
	Relative rank	0.2834	0.1710	226.9326	1.6570	NS	
	TroopL	1.2861	0.1713	41.0513	7.5096	0.05	
	TroopM	1.0517	0.1545	610.5861	6.8060	0.05	
	Year	0.0304	0.0180	484.3131	1.6895	NS	

Figure A1.6: Changes in the mothers' grooming (Groom.) received strength and (total) centrality across the study years (2014–2019). Ribbons represent 97.5% confidence intervals.



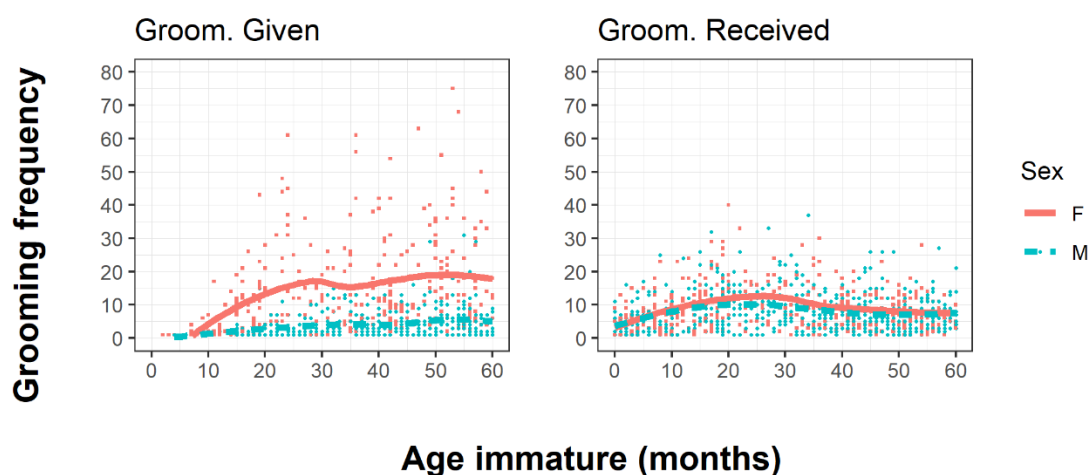
1.8 IMMATURES' GROOMING AMOUNTS

A qualitative exam of the overall amount of grooming shared by immatures (Table A1.21) showed that grooming given was relatively lower for males, while grooming received was similar in the two sexes (Figure A1.7).

Table A1.21: Mean and standard deviation (SD) of the amounts of grooming given and received by immature males and females.

Grooming	Sex	Mean	SD
Given	Males	4.29	4.21
	Females	15.00	13.82
Received	Males	7.81	5.84
	Females	8.94	6.39

Figure A1.7: Changes in the amount of immature's grooming (Groom.) given and received with age (raw data), divided by sex ('F' = female, 'M' = male).

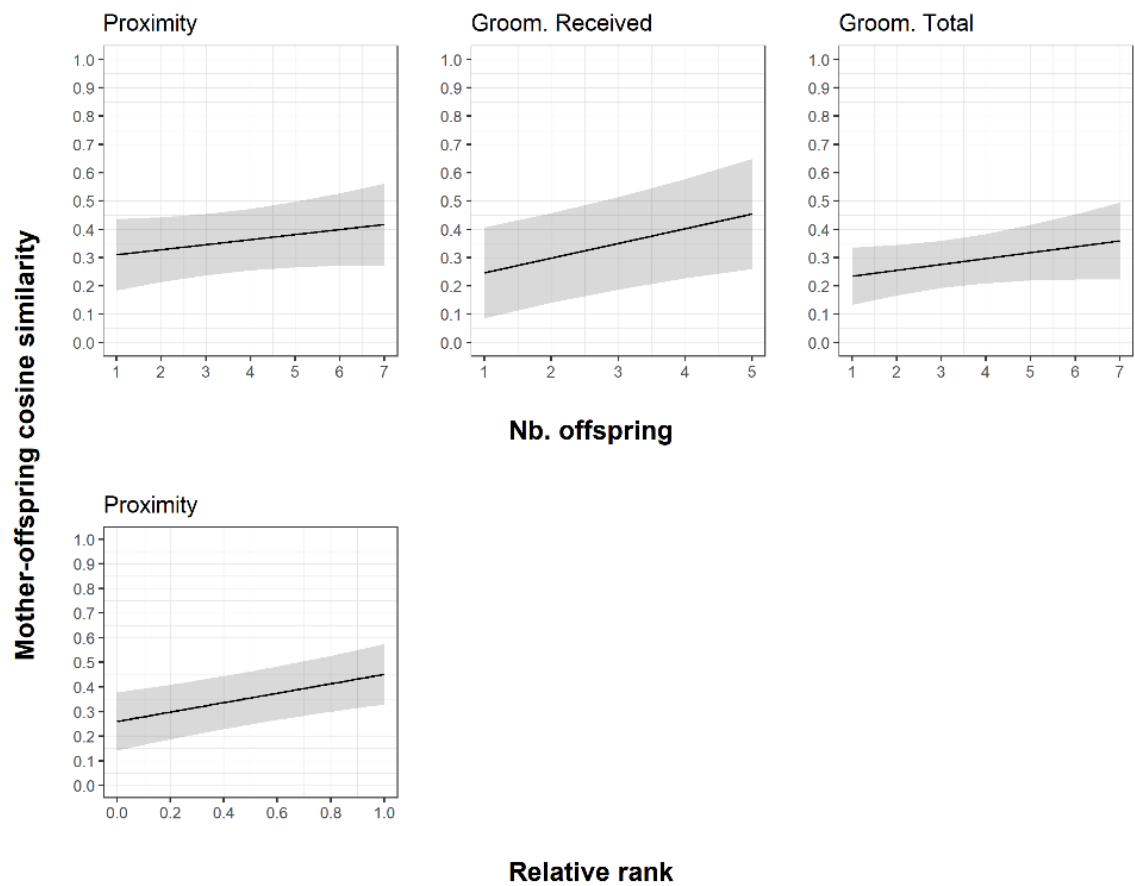


2 APPENDIX 2: MATERNAL INFLUENCES ON SOCIALITY IN WILD BABOONS

2.1 MOTHER-OFFSPRING COSINE SIMILARITY

In order to test whether there was a positive correlation between mothers' and offspring's social networks and how this changed depending on a mother's number of offspring and her dominance rank, we used the Pearson's correlation (MP1b; see Table 3.1 in Chapter 3) and the cosine similarity. Cosine models' structure (LMM) and dependent variables were the same as MP1b (see Chapter 3, §3.3). Cosine (calculated through the package *lsa* (Wild 2022) and the function *cosine*) is the cosine of the angle between two vectors and represents how similar two sets of values are (Jarrett *et al.* 2018). The results of the models in which either the Pearson's correlation or the cosine similarity were used as dependent variables were qualitatively similar (Figure A2.1; see Appendix 1, §1.1).

Figure A2.1: Changes in the mother-offspring social network cosine similarity with a mother's number (Nb.) of offspring (1st row) and relative rank (2nd row) for the proximity and grooming (Groom.) networks. Ribbons represent 97.5% confidence intervals.



2.2 SUPPLEMENTARY RESULTS FOR BINOMIAL MODELS

In this section, we show the odds ratios (Table A2.1) for the significant variables of interest from GLMM binomial models (see Chapter 3, §3.3). The tables including the results from all the independent variables are presented in Appendix 1, §1.5. In addition, we present here the significant (p -value ≤ 0.05 ; see Chapter 3, §3.3) results of part of the models used to test P1c.

Table A2.1: Odds ratio (OR), lower and upper 97.5% confidence intervals (LCI and UCI, respectively) and percentage increase or decrease in odds for each significant variable of interest, for the proximity and grooming (Groom.) networks. Variables include a mother's number (Nb.) of offspring and relative rank.

Model	Variable	OR	LCI	UCI	Percentage change
P1a Proximity	Relative rank	1.59	1.05	2.42	59.48
P1a Groom. Total	Nb. offspring	0.80	0.74	0.88	-19.56
P1c.1 Groom. Received	Nb. offspring	1.39	1.13	1.70	38.79
	Relative rank	2.38	1.01	5.63	138.48
P1c.1 Groom. Total	Nb. offspring	1.40	1.19	1.66	40.48
P1c.2 Groom. Received	Nb. offspring	1.65	1.24	2.18	64.71
	Relative rank	1.90	0.69	5.20	90.01
P1c.2 Groom. Total	Nb. offspring	1.31	1.10	1.57	31.49
P1c.3 Proximity	Nb. offspring	1.27	1.02	1.59	27.46
	Relative rank	4.04	1.66	9.82	303.68
P1c.3 Groom. Received	Nb. offspring	1.94	1.27	2.95	93.53
	Relative rank	2.20	0.44	10.91	120.07
P1c.4 Proximity	Nb. offspring	1.14	0.97	1.33	13.74
P1c.4 Groom. Given	Nb. offspring	1.18	0.96	1.46	18.34
	Relative rank	2.64	1.09	6.37	163.58
P1c.4 Groom. Received	Nb. offspring	1.48	1.16	1.89	48.28
	Relative rank	2.45	1.03	5.82	145.23
P1c.4 Groom. Total	Nb. offspring	1.56	1.29	1.90	56.38
P2c.1 Proximity	Relative rank	1.09	1.00	1.19	8.79
P2c.1 Groom. Received	Nb. offspring	1.06	0.99	1.13	5.62
P2c.3 Proximity	Relative rank	1.09	1.00	1.19	9.12
P2c.3 Groom. Received	Nb. offspring	0.75	1.01	1.13	-24.62
	Nb. offspring	1.04	0.99	1.10	4.50

To test P1c (i.e., that the fact that immatures' networks are more correlated to their mothers' networks than to those of other individuals will increase both with a mother's number of offspring and her dominance rank), we used three approaches, all of which compared the Pearson's correlation coefficient (r) of the mother-immature dyad with combinations of other dyads from the proximity networks or grooming proportions networks (see Chapter 3, §3.3 and §3.4, for the first two approaches: MP1c.1 and MP1c.2). In the third approach, we ranked and standardised the r values of the immature-others' ego-networks (obtaining relative ranks (Huchard and Cowlshaw 2011)). We ran two binomial GLMM with the 1/0 score as the dependent variable, where '1' meant that the rank position of the mother-immature r was: (1) ≥ 0.9 , i.e., the mother-immature's r was in the top 10% of the immatures' r (MP1c.3), and (2) > 0.5 , i.e., the mother-immature's r was above chance (MP1c.4).

The results of MP1c.3 and MP1c.4 generally confirm the ones obtained with the first two approaches (see Chapter 3, §3.4): immatures who had more siblings and a higher rank resembled relatively more their mothers' networks than those of other individuals. For the proximity network, the number of offspring was significant in two models: the addition of one sibling caused an increase of 27.46% and 13.74% (MP1c.3 and MP1c.4, respectively) in the odds that the immatures' networks were relatively more correlated to their mothers'. Relative rank was significant in one case: a rise in one position of relative rank produced an increase of 303.68% in the odds that the immatures' networks were relatively more correlated to their mothers' (MP1c.3). For the grooming network, the number of offspring had a significant effect on grooming given (MP1c.4), received (both models), and total (MP1c.4): the addition of one sibling caused an increase between (hereafter – range of values) 18.34–93.53% (MP1c.4 given and MP1c.3

received, respectively) in the odds that the immatures' networks were relatively more correlated to their mothers'. Relative rank had a significant effect on grooming given (MP1c.4) and received (both models): an increase in one position of relative rank produced an increase between 120.07–163.58% (MP1c.3 received and MP1c.4 given, respectively) in the odds that the immatures' networks were relatively more correlated to their mothers' (Figures A2.2 and A2.3). Maternal features had no significant effect in MP1c.3 for grooming given and total.

Figure A2.2: Changes in the odds that the rank of the mother-offspring social network correlation was ≥ 0.9 (MP1c.3) or > 0.5 (MP1c.4). These changes are related to a mother's number (Nb.) of offspring for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.

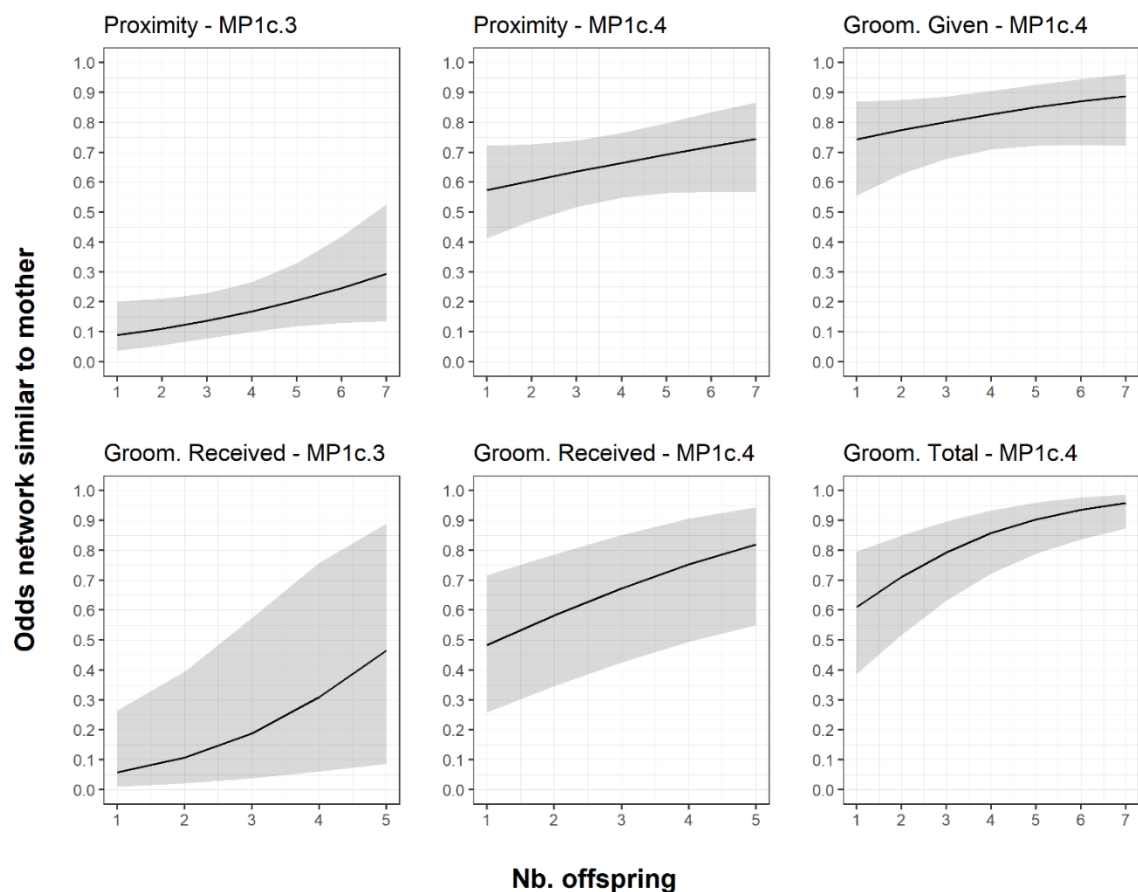
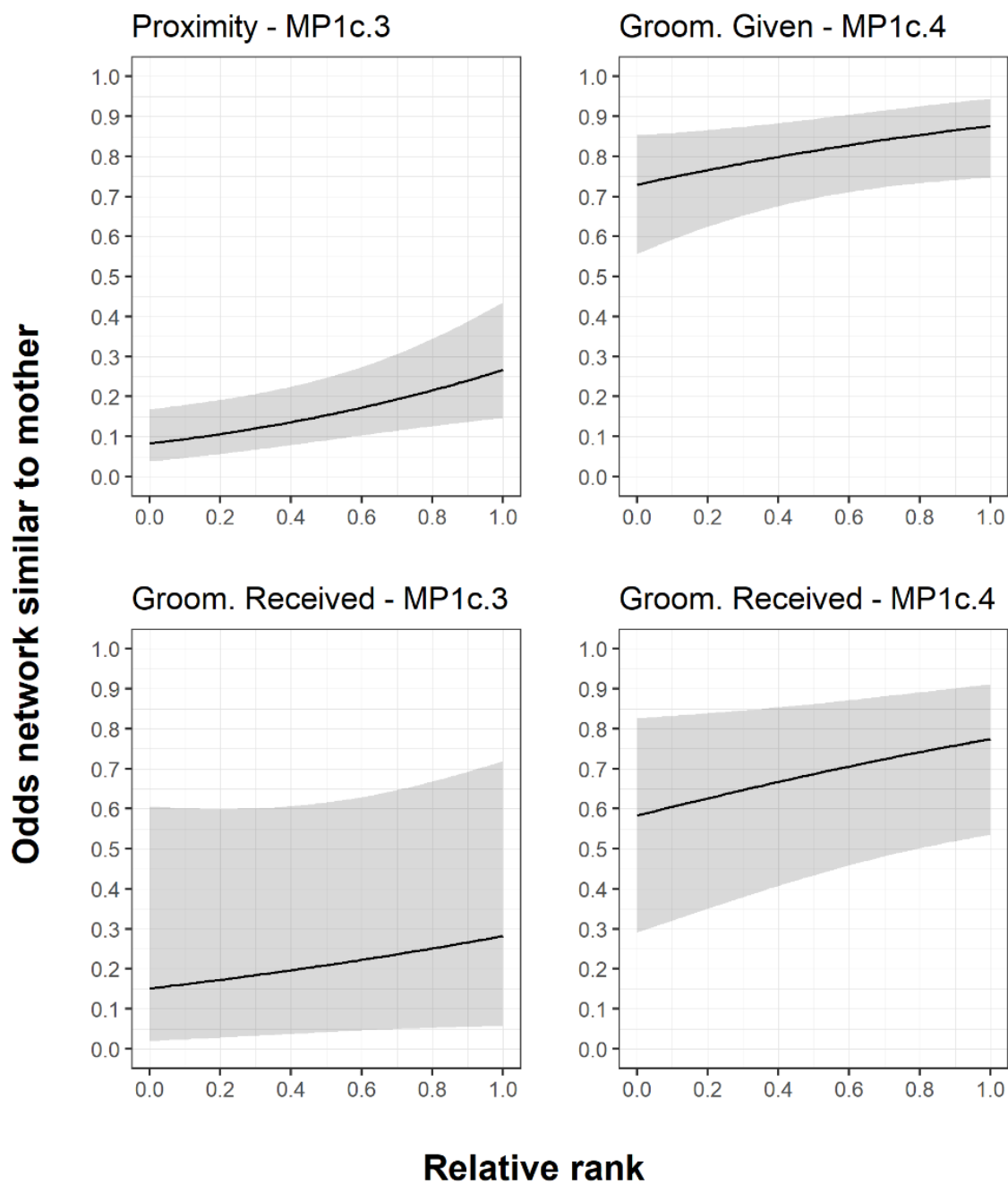


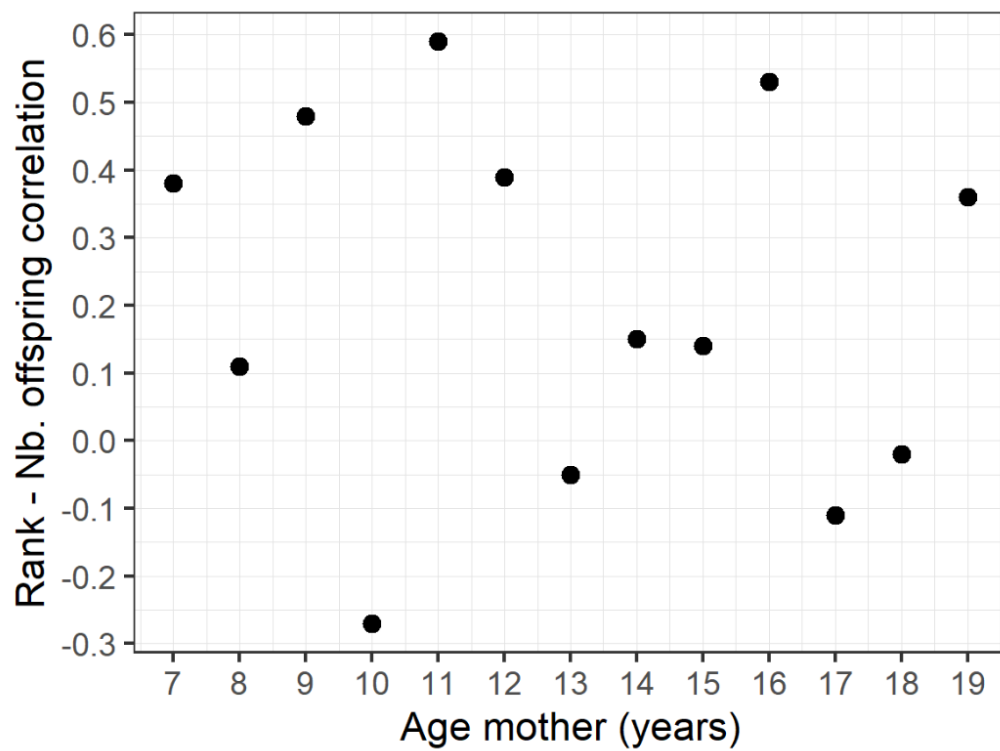
Figure A2.3: Changes in the odds that the rank of the mother-offspring social network correlation was ≥ 0.9 (MP1c.3) or > 0.5 (MP1c.4). These changes are related to a mother's relative rank for the proximity and grooming (Groom.) networks. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.



2.3 RANK – MATRILINE SIZE CORRELATION

Dominant individuals have priority of access to resources and lower stress levels, which could positively affect their fecundity and survival (Majolo *et al.* 2012). However, because individuals of different rank are equally susceptible to causes of mortality independent from their health conditions (e.g., infanticide, predation), higher-ranking matriline (i.e., units formed by a mother and her offspring) may not be larger than lower-ranking ones (Cheney *et al.* 2004). We calculated the Pearson's correlation values between the relative ranks of a sample of mothers and their number of offspring in the troop. Data on mothers who had at least one infant from 2014–2022 were divided into 13 sub-samples (7–26 females in each sub-sample, median of 19 females/ sub-sample) of same-aged females (7–19 years old). Adult females' relative ranks were calculated as in (Roatti *et al.* 2023a) for 2014–2019 (see Chapter 3, §3.3). For 2021–2022, ordinal ranks were calculated on the whole troop through the 'I & SI' method for linear dominance hierarchies (Schmid and de Vries 2013) using the package *compete* and the function *isi13* (500 iterations) (Curley 2023). Absolute ranks were standardised to obtain relative ranks (ranging from 0 – lowest to 1 – highest) (Huchard and Cowlshaw 2011). The number of offspring per mother included individuals of any age who were part of the troop in each year (0–6 offspring/ mother, mean of 3 offspring/ mother). There was no qualitative indication of a relationship between a mother's relative rank and her number of offspring (Figure A2.4).

Figure A2.4: Pearson's correlation values between mothers' relative rank and number (Nb.) of offspring in the troop within each age category (years 7–19).



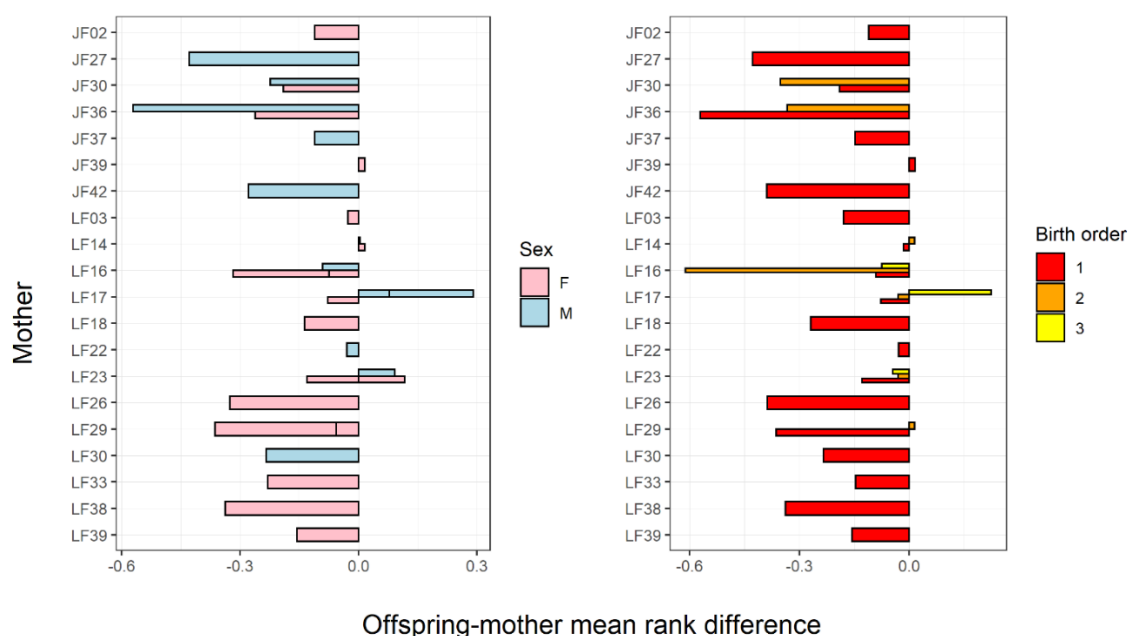
2.4 RANK INHERITANCE BY SEX

In Cercopithecine primates (e.g., baboons, macaques) and spotted hyenas (*Crocuta crocuta*), offspring of both sexes inherit their mothers' dominance ranks through a 'youngest ascendancy' rule, i.e., the offspring born latest inherits a rank just below the mother and above the older siblings (Holekamp and Smale 1991). Kin support in agonistic interactions may be the main determinant of rank inheritance (Holekamp and Smale 1991) and some studies suggest that philopatric females may aid related juvenile females more than males (Pereira 1989, Range 2006). We plotted the raw offspring-mother relative rank differences to check for different inheritance patterns by sex. We used a sample of mothers and their immature (0–5 years old) offspring ≥ 12 months old (when they start to be involved in dominance interactions) from 2021 and 2022 (three time periods). Relative ranks were calculated as described above (Appendix 2, §2.3). We then calculated the offspring-mother mean relative rank difference (absolute values) across the three time periods (60 observations; 20 mothers; 30 offspring: 18 females and 12 males). We did not detect any between-sexes qualitative difference in rank inheritance (Table A2.2 and Figure A2.5). Because baboon females give birth to an infant approx. every two years in our wild population (Dezeure, Baniel, *et al.* 2021), most mothers have one immature offspring (13 mothers), and only a few have two (four) or three (three) (Figure A2.5). Therefore, birth order may have a limited effect on rank inheritance among a mother's immature offspring.

Table A2.2: Offspring-mother mean relative rank difference (absolute values across three time periods) by sex ('F' = female, 'M' = male) and overall.

Time period	Sex	Rank difference by sex	Overall rank difference
1	F	0.21	0.19
	M	0.17	
2	F	0.13	0.11
	M	0.10	
3	F	0.17	0.21
	M	0.26	

Figure A2.5: Offspring-mother mean relative rank difference (absolute values across three time periods) by sex (left; 'F' = female, 'M' = male; bars stacked mong same-sex offspring) and birth order (right; from youngest – 1 – to oldest – 3 – offspring).



3 APPENDIX 3: THE DEVELOPMENT OF SOCIAL LEARNING IN WILD IMMATURE BABOONS

3.1 TROOP COMPOSITION

The composition of the two study troops (J, L) during the two study years is presented in Table A3.1. Individuals are divided according to age class and sex: adult females (from onset of menarche), adult males (fully developed secondary sexual characteristics), subadult males (from onset of development of secondary sexual characteristics), juvenile females and males (weaned non sub/adult individuals), infants (non-weaned individuals).

Table A3.1: Troop composition per age/ sex class in each study year.

Year	Troop	Adult females	Adult males	Subadult males	Juvenile females	Juvenile males	Infants	Total
2021	J	20	3	9	8	9	10	59
	L	24	6	13	14	4	11	72
	J, L	44	9	22	22	13	21	131
2022	J	23	4	11	7	8	11	64
	L	23	6	12	16	6	16	79
	J, L	46	10	23	23	14	27	143

3.2 NUMBER OF FOCAL OBSERVATION HOURS

The number of focal observation hours per focal individual, divided per time period, are shown in Table A3.2. Total values per troop are also present.

Table A3.2: Focal observation hours per focal individual in each time period (TP). Total hours per focal individual in each time period (Obs. h) and overall (Obs. h total) are also shown. The colour scale represents a range from lower (red) to higher (green) values. The bottom of the table presents the total observation hours, divided per troop and overall. The same colour scale is applied.

Troop	FocalID	TP	Obs. h	Obs. h total
J	JF59	1	13.30	21.68
		2	8.38	
	JFI211	2	10.57	10.57
	JM69	1	14.97	24.69
		2	9.72	
	JM79	1	13.05	31.85
		2	10.26	
		3	8.54	
	JM85	1	14.02	34.21
		2	11.47	
		3	8.72	
	JF52	1	12.69	24.51
		2	11.82	
	JF66	2	12.21	21.12
		3	8.91	
	JF64	2	10.69	10.69
	JM74	1	13.51	25.42
		2	11.91	
	JM75	1	14.07	32.95
		2	11.07	
		3	7.81	
	JF60	1	14.08	33.70
		2	10.77	
		3	8.85	
	JF53	1	13.41	34.25
		2	11.47	
		3	9.37	
	JM76	1	15.07	35.17
		2	10.44	
		3	9.66	
	JF56	1	13.97	25.06
		2	11.09	
	JM81	1	13.84	35.91
		2	12.92	
		3	9.15	

Troop	FocalID	TP	Obs. h	Obs. h total
	JM78	1	13.28	34.90
		2	12.55	
		3	9.07	
	JF51	1	13.17	32.05
		2	10.58	
		3	8.30	
	JF58	1	12.84	34.73
		2	12.26	
		3	9.63	
	MM01	1	13.40	24.04
		2	10.64	
	JM80	1	12.60	32.86
		2	12.40	
		3	7.86	
	JF57	1	13.43	34.09
		2	12.01	
		3	8.65	
	JM77	1	13.17	33.52
		2	11.35	
		3	9.00	
	JF61	1	13.78	34.34
		2	11.77	
		3	8.79	
	JF50	1	13.50	24.73
		2	11.23	
L	LM68	1	12.78	34.54
		2	12.39	
		3	9.37	
	LF61	1	12.52	33.99
		2	11.67	
		3	9.80	
	LF51	1	12.65	34.05
		2	12.85	
		3	8.55	
	LMI211	2	7.77	7.77
	LM66	1	12.67	33.66
		2	11.94	
		3	9.05	
	LF41	1	12.77	33.23
		2	11.99	
		3	8.47	
	LF1211	2	11.38	11.38
	LF48	1	13.05	34.28
		2	12.46	
		3	8.77	
	LM59	1	13.09	34.49
		2	12.49	

Troop	FocalID	TP	Obs. h	Obs. h total
		3	8.91	
	LF52	1	12.57	34.25
		2	12.32	
		3	9.36	
	LF58	1	13.00	34.49
		2	11.84	
		3	9.65	
	LM65	1	12.58	24.84
		2	12.26	
	LM64	1	13.49	34.91
		2	12.72	
		3	8.70	
	LF54	1	11.93	33.54
		2	12.91	
		3	8.70	
	LM67	1	13.11	33.80
		2	11.79	
		3	8.90	
	LF53	1	8.64	8.64
	LF62	1	11.76	19.34
		2	7.58	
	LF46	1	11.32	32.00
		2	12.25	
		3	8.43	
	LF55	1	12.75	34.44
		2	12.67	
		3	9.02	
	LF60	1	12.16	33.72
		2	12.34	
		3	9.22	
	LF47	1	12.89	34.24
		2	11.71	
		3	9.64	
	LF59	1	12.76	35.73
		2	13.53	
		3	9.44	
	LM60	1	11.80	33.24
		2	12.23	
		3	9.21	
	LF56	1	13.00	32.93
		2	11.38	
		3	8.55	
	LFI212	1	12.60	33.11
		2	11.91	
		3	8.60	
	LF44	1	12.87	12.87
	LF42	1	13.06	32.49

Troop	FocalID	TP	Obs. h	Obs. h total
		2	12.10	
		3	7.33	
	LF50	1	12.76	34.02
		2	12.36	
		3	8.90	
	LMI212	2	11.79	11.79
J	Obs. h total	1-3	687.04	
L			841.78	
J, L			1528.82	

3.3 NUMBER OF OBSERVATIONS AND SAMPLE SIZE PER DATA TYPE

The number of observations (records and/or hours) and sample size (i.e., number of individuals sampled) per each data type are indicated in Table A3.3. The mean values are also shown. Observations are divided per troop and time period. The kind of data collection is indicated as *ad libitum*, focal or scan. Data were collected on immatures only or on all the recognisable individuals in the troops (see Chapter 4, §4.3).

Table A3.3: Number of observations and sample size per data type and troop/ time period (TP): grooming (Groom.) ego- and troop networks, proximity (Prox.) ego- and troop networks, dominance matrix (records), focal observations (records and hours). Mean values per troop/ time period are also shown. The number of individuals sampled (Nb. IDs) are placed in parentheses. Details indicate the kind of data collection and the targeted age class (immatures or all individuals).

Data	Details	Troop (Nb. IDs)			TP (Nb. IDs)			Mean per troop and TP (Nb. IDs)					
		J-L	J	L	1	2	3	J1	J2	J3	L1	L2	L3
Dominance matrix (records)	<i>ad libitum</i> + focal (all individuals)	8260 (122)	4336 (55)	3924 (68)	3740 (106)	2775 (107)	1745 (115)	46 (49)	27 (49)	14 (53)	26 (57)	25 (58)	16 (63)
Focal observations (hours)	focal (immatures)	1529 (53)	687 (24)	842 (29)	610 (48)	590 (51)	329 (37)	14 (21)	11 (24)	9 (15)	12 (26)	12 (27)	9 (22)
Focal observations (records)	focal (immatures)	4511 (53)	2034 (24)	2477 (29)	1800 (48)	1764 (51)	947 (37)	40 (21)	34 (24)	25 (15)	37 (26)	35 (27)	26 (22)
Groom. ego-network (records)	<i>ad libitum</i> + focal (immatures)	8770 (53)	3722 (24)	5048 (29)	3444 (48)	2889 (51)	2437 (37)	95 (21)	63 (24)	60 (15)	85 (26)	69 (27)	89 (22)
Groom. troop network (records)	<i>ad libitum</i> (all individuals)	14186 (150)	6136 (67)	8050 (84)	5631 (123)	4290 (127)	4265 (140)	49 (55)	32 (58)	25 (63)	43 (68)	36 (69)	34 (78)
Prox. ego-network (records)	focal (immatures)	2824 (53)	1170 (24)	1654 (29)	955 (48)	1059 (51)	810 (37)	18 (21)	21 (24)	21 (15)	22 (26)	25 (27)	22 (22)

Data	Details	Troop (Nb. IDs)			TP (Nb. IDs)			Mean per troop and TP (Nb. IDs)					
		J-L	J	L	1	2	3	J1	J2	J3	L1	L2	L3
Prox. troop network (records)	scan (all individuals)	7985 (151)	3757 (70)	4228 (84)	2926 (123)	2802 (127)	2257 (141)	30 (57)	22 (59)	15 (64)	19 (68)	23 (69)	22 (78)

3.4 VARIABLE CORRELATIONS

The Pearson's correlation coefficients (r) between the independent variables considered in hypothesis H1 and H2 models are presented in Table A3.4 (H1) and Table A3.5 (H2). Variables with $r \geq 0.5$ were not included in the same model (see Chapter 4, §4.3).

Table A3.4: Pearson's correlation coefficients (absolute values) between hypothesis H1 models' independent variables, including immatures' age, grooming (Groom.) and proximity (Prox.) centrality, (relative) rank, sex, and orphan status (binary 0/1); observation (Obs.) length, time period, and troop. The colour scale represents a range from lower (red) to higher (green) correlation values.

Variable	Age immature	Groom. centrality	Obs. length	Orphan	Prox. centrality	Rank immature	Sex immature	Time period	Troop
Age immature	1.0	0.1	0.0	0.6	0.6	0.0	0.1	0.1	0.1
Groom. centrality	0.1	1.0	0.0	0.3	0.4	0.5	0.1	0.1	0.0
Obs. length	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.1	0.0
Orphan	0.6	0.3	0.0	1.0	0.4	0.2	0.0	0.0	0.3
Prox. centrality	0.6	0.4	0.0	0.4	1.0	0.4	0.1	0.2	0.0
Rank immature	0.0	0.5	0.0	0.2	0.4	1.0	0.2	0.1	0.1
Sex immature	0.1	0.1	0.0	0.0	0.1	0.2	1.0	0.0	0.2
Time period	0.1	0.1	0.1	0.0	0.2	0.1	0.0	1.0	0.0
Troop	0.1	0.0	0.0	0.3	0.0	0.1	0.2	0.0	1.0

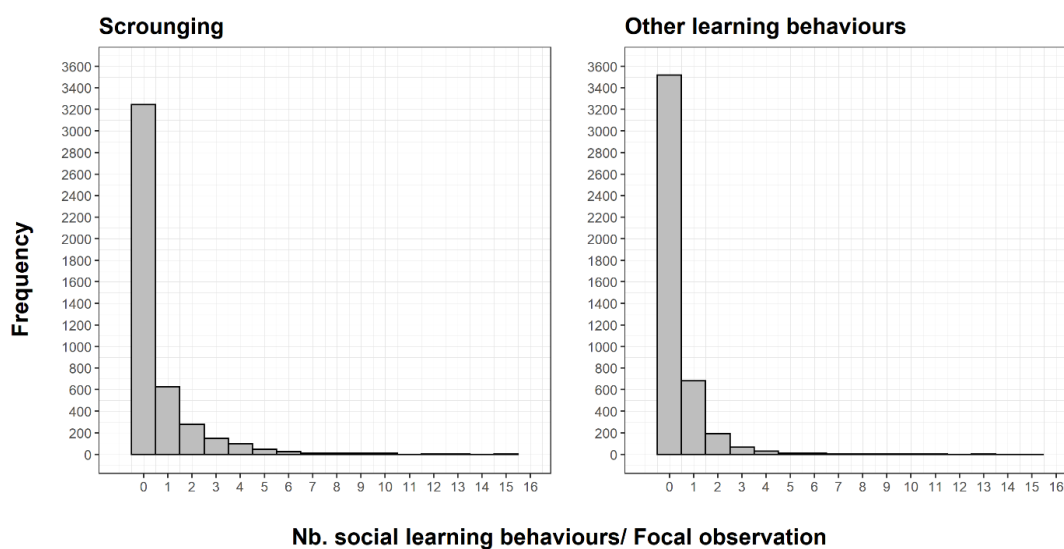
Table A3.5: Pearson's correlation coefficients (absolute values) between hypothesis H2 models' independent variables, including immatures' age, sex, (relative) rank, proximity (prox.) degree, number (Nb.) of matriline members, orphan status (binary 0/1), and total grooming (Groom.) amount; demonstrators' age, sex, and their age availability (avail.); a (immature-demonstrator) dyad's grooming allocation, maternal relatedness (related.), proximity in the foraging network, and (relative) rank difference; time period and troop. The colour scale represents a range from lower (red) to higher (green) correlation values.

Variable	Age demonstrator	Age immature	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Maternal related.	Nb. matriline	Orphan	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Sex immature	Time period	Troop
Age demonstrator	1.0	0.0	0.0	0.3	0.1	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.0	0.0
Age immature	0.0	1.0	0.1	0.0	0.0	0.3	0.0	0.0	0.6	0.1	0.0	0.0	0.0	0.1	0.2	0.1
Degree prox.	0.0	0.1	1.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.1	0.0
Demonstrator avail. (age)	0.3	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.1
Groom. allocation	0.1	0.0	0.0	0.0	1.0	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.1	0.0	0.0	0.0
Groom. amount	0.0	0.3	0.1	0.0	0.0	1.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.5	0.1	0.1
Maternal related.	0.1	0.0	0.0	0.0	0.7	0.0	1.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Nb. matriline	0.0	0.0	0.1	0.0	0.0	0.0	0.1	1.0	0.4	0.0	0.1	0.1	0.0	0.2	0.1	0.1
Orphan	0.0	0.6	0.1	0.0	0.0	0.2	0.0	0.4	1.0	0.1	0.1	0.1	0.0	0.0	0.0	0.3
Prox. foraging	0.1	0.1	0.0	0.0	0.3	0.0	0.2	0.0	0.1	1.0	0.0	0.1	0.0	0.0	0.1	0.1
Rank difference	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	1.0	0.6	0.4	0.1	0.0	0.1
Rank immature	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.6	1.0	0.0	0.2	0.1	0.1
Sex demonstrator	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.4	0.0	1.0	0.0	0.0	0.0
Sex immature	0.0	0.1	0.1	0.0	0.0	0.5	0.0	0.2	0.0	0.0	0.1	0.2	0.0	1.0	0.0	0.2
Time period	0.0	0.2	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.0	1.0	0.0
Troop	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.3	0.1	0.1	0.1	0.0	0.2	0.0	1.0

3.5 FREQUENCY OF SOCIAL LEARNING BEHAVIOURS

The number of scrounging (Figure A3.1, left) and other social learning behaviours (Figure A3.1, right) in each focal observation was none or one behaviour in most cases (see Chapter 4, §4.3).

Figure A3.1: Frequency of different numbers (Nb.) of scrounging (left) and other learning behaviours (right) in each focal observation.



3.6 H2 MODELS BY SEX

The sets of candidate models (32 each) evaluated for the sex-separated hypothesis H2 models is shown in Table A3.6. The models had the same variables as the overall (i.e., applied to immatures of both sexes) models (see Chapter 4, §4.3) but were applied to females (Models 3.1 and 4.1 for scrounging and other social learning behaviours, respectively) and males (Models 3.2 and 4.2 for scrounging and other social learning behaviours, respectively) separately. These models undertook the same selection procedure as the overall models (see Chapter 4, §4.3) and had qualitatively similar results (Table A3.7 and Figure A3.2) as the overall models (see Chapter 4, §4.4). However, three differences were present in the averaged (final) males' models compared to the averaged females' and overall models. First, a (immature-demonstrator) dyad's grooming allocation (significant) had a stronger effect for females (second and first variable with the greatest effect for the scrounging and other learning behaviours models, respectively) compared to male peers (third variable with the greatest effect, following proximity foraging and the age-proximity interaction for the scrounging and the other learning behaviours model, respectively). Second, a dyad's rank difference was included in the males' scrounging model with a non-significant effect. Third, the interaction between immatures' age and a dyad's proximity during foraging had a significant effect for the males' other learning behaviours model (second variable with the greatest effect): the odds of performing other learning behaviours towards demonstrators in proximity decreased with males' age (see Chapter 4, §4.5). On the other hand, the interaction between immatures' age and a dyad's proximity during foraging was not included in all females' best models (compared to males' and the overall best models – despite the sample size for females being larger). Table A3.8 shows the Akaike model parameters of

the best models, derived with the package *AICcmodavg* (Mazerolle 2023) and the function *aictab*. Table A3.9 shows the relative variable importance based on the sum of Akaike weights (see Chapter 4, §4.3). Figure A3.3 includes trends for H2 models' significant variables of interest, divided by sex. Demonstrators' age was not significant in the sex-separated scrounging models and the trend was similar in the two sexes. Because the same variable was marginally significant in the scrounging model for both sexes, the absence of overall significance may be due to lack of statistical power. The distributions of demonstrator-immature age differences (Figure A3.4) and immature-demonstrator rank differences (Figure A3.5) were qualitatively similar for males and females and all peaked around zero (individuals with similar age/ rank).

Table A3.6: Full model sets for hypothesis H2 models by sex (scrounging: 3.1 – females – and 3.2 – males; other social learning behaviours: 4.1 – females – and 4.2 – males), showing all possible combinations of biologically plausible models (on rows; green = variable included; NA = variable excluded). In all models were included the following variables: immatures' age, number (Nb.) of matriline members, proximity (prox.) degree; a (immature-demonstrator) dyad's proximity during foraging; time period and troop. In addition, either immatures' (relative) rank or a dyad's (relative) rank difference was added in all models, but they were not present together. A dyad's grooming (Groom.) allocation was present together with immatures' total grooming amount, while the availability (avail.) of demonstrators of a certain age was present together with demonstrators' age. The values reported for sex refer to males. The models' parameters shown are the degrees of freedom (df), the log-likelihood, the AICc value, the difference (delta) in AICc from the top model (lowest AICc), and the Akaike weight. The best models are indicated by the $\Delta AICc < 7$ in bold, including models with a sum of AICc weights < 0.95 .

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
3.1	-2.2203	-0.1403	0.5934	-0.5021	0.0965	-0.0466	0.5502	-0.0671	-0.0723	0.4488	NA	-0.3087	NA	+	-0.2555	17	-1387.0345	2808.7342	0.0000	0.4242
	-2.2278	NA	0.5986	-0.4773	0.0962	NA	0.4981	-0.0646	-0.0859	0.4797	NA	-0.3108	NA	+	-0.2398	15	-1389.5372	2809.5950	0.8609	0.2758
	-2.2194	-0.1368	0.5949	-0.4991	0.0963	-0.0425	0.5537	-0.0657	-0.0735	0.4505	NA	-0.3104	0.0294	+	-0.2517	18	-1386.9390	2810.6223	1.8881	0.1650
	-2.2260	NA	0.6009	-0.4739	0.0960	NA	0.5059	-0.0622	-0.0872	0.4809	NA	-0.3137	0.0506	+	-0.2344	16	-1389.2524	2811.0955	2.3613	0.1302
	-2.1892	NA	0.6636	NA	0.0895	NA	0.5209	-0.1038	-0.0981	0.6135	NA	-0.3203	NA	+	-0.2190	14	-1395.7280	2819.9110	11.1768	0.0016
	-2.1808	-0.1276	0.6615	NA	0.0893	-0.0321	0.5681	-0.1070	-0.0870	0.5923	NA	-0.3186	NA	+	-0.2307	16	-1393.8305	2820.2517	11.5175	0.0013
	-2.1878	NA	0.6654	NA	0.0895	NA	0.5295	-0.1005	-0.0995	0.6138	NA	-0.3232	0.0604	+	-0.2132	15	-1395.3530	2821.2266	12.4924	0.0008
	-2.1802	-0.1224	0.6629	NA	0.0894	-0.0264	0.5728	-0.1046	-0.0884	0.5936	NA	-0.3206	0.0433	+	-0.2258	17	-1393.6415	2821.9482	13.2140	0.0006
	-2.2426	-0.1569	0.5387	-0.4867	0.0857	-0.0466	0.5550	-0.0698	-0.1061	0.4286	-0.0571	NA	NA	+	-0.2401	17	-1394.5487	2823.7626	15.0285	0.0002
	-2.2524	NA	0.5364	-0.4506	0.0829	NA	0.4971	-0.0628	-0.1231	0.4668	-0.0265	NA	NA	+	-0.2255	15	-1397.4539	2825.4284	16.6942	0.0001
	-2.2426	-0.1564	0.5386	-0.4862	0.0856	-0.0463	0.5552	-0.0695	-0.1062	0.4289	-0.0563	NA	0.0023	+	-0.2399	18	-1394.5482	2825.8407	17.1065	0.0001
	-2.2514	NA	0.5338	-0.4438	0.0819	NA	0.5029	-0.0575	-0.1253	0.4707	-0.0131	NA	0.0399	+	-0.2229	16	-1397.3002	2827.1912	18.4570	0.0000
	-2.2058	-0.1377	0.5855	NA	0.0742	-0.0341	0.5701	-0.0786	-0.1230	0.5747	-0.0273	NA	NA	+	-0.2276	16	-1400.6313	2833.8532	25.1190	0.0000
	-2.2163	NA	0.5796	NA	0.0722	NA	0.5186	-0.0710	-0.1362	0.5992	-0.0007	NA	NA	+	-0.2175	14	-1402.7423	2833.9396	25.2055	0.0000
	-2.2157	NA	0.5735	NA	0.0711	NA	0.5266	-0.0617	-0.1385	0.6021	0.0199	NA	0.0618	+	-0.2143	15	-1402.3942	2835.3089	26.5748	0.0000
	-2.2059	-0.1317	0.5824	NA	0.0737	-0.0303	0.5724	-0.0739	-0.1247	0.5771	-0.0161	NA	0.0316	+	-0.2253	17	-1400.5447	2835.7545	27.0204	0.0000
	-2.2145	0.1377	0.5390	-0.5956	0.1108	-0.0370	NA	NA	-0.1277	0.6661	NA	-0.3193	NA	+	-0.2404	15	-1438.1763	2906.8733	98.1391	0.0000
	-2.2155	0.1250	0.5335	-0.6011	0.1107	-0.0467	NA	NA	-0.1261	0.6606	NA	-0.3154	-0.0726	+	-0.2489	16	-1437.6890	2907.9686	99.2345	0.0000
	-2.2056	NA	0.5334	-0.6167	0.1113	NA	NA	NA	-0.1170	0.6530	NA	-0.3177	NA	+	-0.2453	13	-1441.0096	2908.4132	99.6790	0.0000
	-2.2079	NA	0.5274	-0.6195	0.1112	NA	NA	NA	-0.1158	0.6486	NA	-0.3130	-0.0957	+	-0.2546	14	-1440.1839	2908.8229	100.0888	0.0000
	-2.2385	0.1331	0.4765	-0.5659	0.0914	-0.0379	NA	NA	-0.1612	0.6599	-0.0043	NA	NA	+	-0.2320	15	-1445.6956	2921.9118	113.1776	0.0000
	-2.2336	NA	0.4735	-0.6101	0.0975	NA	NA	NA	-0.1467	0.6319	-0.0767	NA	-0.1281	+	-0.2437	14	-1446.9365	2922.3280	113.5939	0.0000
	-2.2397	0.1110	0.4742	-0.5841	0.0938	-0.0497	NA	NA	-0.1583	0.6471	-0.0378	NA	-0.0952	+	-0.2405	16	-1444.9745	2922.5397	113.8056	0.0000

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
	-2.2305	NA	0.4755	-0.5960	0.0950	NA	NA	NA	-0.1490	0.6432	-0.0386	NA	NA	+	-0.2344	13	-1448.2670	2922.9280	114.1938	0.0000
	-2.1675	0.1657	0.5813	NA	0.1015	-0.0180	NA	NA	-0.1591	0.8636	NA	-0.3264	NA	+	-0.2130	14	-1447.9905	2924.4360	115.7019	0.0000
	-2.1678	0.1552	0.5773	NA	0.1010	-0.0259	NA	NA	-0.1582	0.8606	NA	-0.3238	-0.0608	+	-0.2195	15	-1447.6696	2925.8597	117.1256	0.0000
	-2.1549	NA	0.5761	NA	0.1016	NA	NA	NA	-0.1489	0.8571	NA	-0.3237	NA	+	-0.2176	12	-1451.4887	2927.3147	118.5805	0.0000
	-2.1565	NA	0.5708	NA	0.1010	NA	NA	NA	-0.1481	0.8536	NA	-0.3202	-0.0935	+	-0.2261	13	-1450.7617	2927.9174	119.1832	0.0000
	-2.1896	0.1669	0.5158	NA	0.0761	-0.0232	NA	NA	-0.1810	0.8510	0.0393	NA	NA	+	-0.2197	14	-1454.1075	2936.6700	127.9359	0.0000
	-2.1895	0.1532	0.5158	NA	0.0771	-0.0302	NA	NA	-0.1809	0.8468	0.0182	NA	-0.0608	+	-0.2242	15	-1453.8255	2938.1717	129.4375	0.0000
	-2.1766	NA	0.5174	NA	0.0799	NA	NA	NA	-0.1709	0.8432	-0.0010	NA	NA	+	-0.2201	12	-1457.6251	2939.5874	130.8533	0.0000
	-2.1783	NA	0.5173	NA	0.0814	NA	NA	NA	-0.1710	0.8376	-0.0337	NA	-0.1100	+	-0.2268	13	-1456.7149	2939.8237	131.0896	0.0000
3.2	-2.0410	-0.1537	0.8586	-0.5719	0.1473	0.0794	0.4649	0.0957	0.0351	0.5156	NA	-0.2538	NA	+	0.0991	17	-828.5834	1692.2755	0.0000	0.4199
	-2.0388	-0.1509	0.8669	-0.5703	0.1521	0.0886	0.4812	0.0972	0.0359	0.5195	NA	-0.2553	0.0966	+	0.1217	18	-827.8168	1692.8749	0.5994	0.3111
	-2.0388	NA	0.8801	-0.5587	0.1464	NA	0.3980	0.1087	0.0214	0.5476	NA	-0.2749	NA	+	0.0921	15	-831.8569	1694.5803	2.3048	0.1326
	-2.0370	NA	0.8874	-0.5557	0.1502	NA	0.4123	0.1102	0.0215	0.5512	NA	-0.2774	0.0853	+	0.1108	16	-831.2575	1695.4988	3.2233	0.0838
	-2.0080	-0.2183	0.8332	-0.5758	0.1772	0.0789	0.4897	0.0157	-0.0249	0.4573	-0.1708	NA	NA	+	0.1737	17	-831.2262	1697.5611	5.2856	0.0299
	-2.0060	-0.2144	0.8340	-0.5738	0.1799	0.0834	0.4958	0.0127	-0.0263	0.4600	-0.1582	NA	0.0410	+	0.1842	18	-831.1046	1699.4505	7.1750	0.0116
	-1.9964	-0.1423	0.8810	NA	0.0952	0.0862	0.4828	0.0722	0.0414	0.7662	NA	-0.2475	NA	+	0.1427	16	-834.4189	1701.8215	9.5460	0.0035
	-1.9945	-0.1378	0.8888	NA	0.0999	0.0955	0.4987	0.0738	0.0411	0.7690	NA	-0.2491	0.0998	+	0.1664	17	-833.6326	1702.3738	10.0983	0.0027
	-2.0019	NA	0.8732	-0.5338	0.1955	NA	0.3995	0.0354	-0.0370	0.5205	-0.0886	NA	NA	+	0.1823	15	-836.3608	1703.5881	11.3126	0.0015
	-1.9957	NA	0.9008	NA	0.0945	NA	0.4216	0.0843	0.0295	0.7928	NA	-0.2666	NA	+	0.1351	14	-837.4521	1703.6610	11.3856	0.0014
	-1.9941	NA	0.9077	NA	0.0983	NA	0.4364	0.0857	0.0288	0.7948	NA	-0.2689	0.0902	+	0.1551	15	-836.8030	1704.4723	12.1969	0.0009
	-2.0004	NA	0.8792	-0.5268	0.2014	NA	0.4095	0.0374	-0.0350	0.5283	-0.0645	NA	0.0587	+	0.1972	16	-836.1211	1705.2259	12.9504	0.0006
	-1.9621	-0.1922	0.8714	NA	0.1305	0.0855	0.5024	0.0005	-0.0098	0.7193	-0.1388	NA	NA	+	0.2178	16	-837.0656	1707.1149	14.8394	0.0003
	-1.9597	-0.1809	0.8788	NA	0.1384	0.0916	0.5091	0.0001	-0.0094	0.7255	-0.1099	NA	0.0605	+	0.2341	17	-836.8267	1708.7621	16.4866	0.0001
	-1.9559	NA	0.9056	NA	0.1518	NA	0.4226	0.0140	-0.0188	0.7611	-0.0607	NA	NA	+	0.2215	14	-841.2189	1711.1945	18.9190	0.0000
	-1.9538	NA	0.9101	NA	0.1590	NA	0.4348	0.0134	-0.0184	0.7657	-0.0327	NA	0.0744	+	0.2392	15	-840.8337	1712.5337	20.2583	0.0000
	-2.0112	NA	0.8258	-0.6758	0.1726	NA	NA	NA	-0.0159	0.5856	NA	-0.2248	NA	+	0.1314	13	-855.7304	1738.1154	45.8399	0.0000
	-2.0175	0.0817	0.8364	-0.6645	0.1772	0.1304	NA	NA	-0.0160	0.5939	NA	-0.2237	NA	+	0.1479	15	-854.0196	1738.9057	46.6302	0.0000
	-2.0117	NA	0.8232	-0.6750	0.1706	NA	NA	NA	-0.0153	0.5840	NA	-0.2237	-0.0415	+	0.1226	14	-855.6083	1739.9733	47.6979	0.0000
	-2.0177	0.0795	0.8350	-0.6645	0.1763	0.1285	NA	NA	-0.0157	0.5929	NA	-0.2232	-0.0183	+	0.1437	16	-853.9963	1740.9764	48.7009	0.0000
	-1.9950	NA	0.8434	-0.6740	0.2197	NA	NA	NA	-0.0744	0.5615	-0.1025	NA	NA	+	0.1915	13	-859.2180	1745.0907	52.8152	0.0000

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
	-1.9976	NA	0.8327	-0.6777	0.2068	NA	NA	NA	-0.0737	0.5505	-0.1453	NA	-0.0958	+	0.1624	14	-858.6660	1746.0888	53.8134	0.0000
	-2.0018	0.0536	0.8501	-0.6660	0.2262	0.1339	NA	NA	-0.0745	0.5673	-0.0890	NA	NA	+	0.2089	15	-857.6818	1746.2299	53.9545	0.0000
	-2.0044	0.0326	0.8373	-0.6738	0.2131	0.1261	NA	NA	-0.0745	0.5540	-0.1340	NA	-0.0749	+	0.1809	16	-857.3873	1747.7584	55.4829	0.0000
	-1.9617	NA	0.8642	NA	0.1104	NA	NA	NA	-0.0043	0.9008	NA	-0.2260	NA	+	0.1692	12	-863.7762	1752.1125	59.8370	0.0000
	-1.9686	0.0996	0.8762	NA	0.1166	0.1367	NA	NA	-0.0042	0.9026	NA	-0.2256	NA	+	0.1865	14	-861.7812	1752.3192	60.0437	0.0000
	-1.9623	NA	0.8618	NA	0.1087	NA	NA	NA	-0.0034	0.8988	NA	-0.2248	-0.0444	+	0.1600	13	-863.6439	1753.9425	61.6670	0.0000
	-1.9688	0.0973	0.8750	NA	0.1158	0.1349	NA	NA	-0.0038	0.9017	NA	-0.2251	-0.0178	+	0.1825	15	-861.7599	1754.3861	62.1107	0.0000
	-1.9415	NA	0.8878	NA	0.1612	NA	NA	NA	-0.0505	0.8829	-0.0625	NA	NA	+	0.2232	12	-866.8330	1758.2262	65.9508	0.0000
	-1.9471	0.0888	0.8974	NA	0.1721	0.1389	NA	NA	-0.0495	0.8856	-0.0368	NA	NA	+	0.2421	14	-864.9735	1758.7038	66.4284	0.0000
	-1.9434	NA	0.8849	NA	0.1543	NA	NA	NA	-0.0494	0.8767	-0.0923	NA	-0.0797	+	0.2067	13	-866.4604	1759.5755	67.3000	0.0000
	-1.9483	0.0787	0.8950	NA	0.1673	0.1342	NA	NA	-0.0490	0.8815	-0.0562	NA	-0.0439	+	0.2317	15	-864.8663	1760.5989	68.3235	0.0000
4.1	-2.1619	NA	0.6789	-0.3672	0.0319	NA	0.8099	-0.0041	0.0020	0.0556	NA	-0.1341	NA	+	-0.0275	15	-839.1049	1708.9889	0.0000	0.2552
	-2.1482	NA	0.7530	NA	0.0288	NA	0.8136	-0.0546	-0.0073	0.2655	NA	-0.1248	NA	+	-0.0253	14	-840.8523	1710.3853	1.3964	0.1270
	-2.1774	NA	0.6943	-0.3677	0.0238	NA	0.8180	-0.0191	-0.0075	0.0398	-0.0792	NA	NA	+	-0.0231	15	-839.8776	1710.5343	1.5454	0.1178
	-2.1618	NA	0.6788	-0.3677	0.0324	NA	0.8086	-0.0043	0.0020	0.0558	NA	-0.1344	-0.0084	+	-0.0275	16	-839.1012	1711.0870	2.0981	0.0894
	-2.1560	-0.1154	0.6849	-0.3762	0.0332	-0.0276	0.8479	-0.0085	0.0188	0.0367	NA	-0.1340	NA	+	-0.0362	17	-838.1959	1711.3886	2.3996	0.0769
	-2.1630	NA	0.7675	NA	0.0209	NA	0.8207	-0.0695	-0.0161	0.2511	-0.0645	NA	NA	+	-0.0213	14	-841.6301	1711.9408	2.9519	0.0583
	-2.1481	NA	0.7530	NA	0.0290	NA	0.8131	-0.0547	-0.0074	0.2657	NA	-0.1250	-0.0032	+	-0.0253	15	-840.8518	1712.4828	3.4938	0.0445
	-2.1763	NA	0.6942	-0.3725	0.0262	NA	0.8122	-0.0197	-0.0080	0.0392	-0.0898	NA	-0.0386	+	-0.0231	16	-839.8098	1712.5042	3.5152	0.0440
	-2.1701	-0.1285	0.7023	-0.3804	0.0253	-0.0252	0.8606	-0.0238	0.0108	0.0177	-0.0958	NA	NA	+	-0.0324	17	-838.7700	1712.5367	3.5478	0.0433
	-2.1423	-0.1096	0.7615	NA	0.0294	-0.0259	0.8500	-0.0608	0.0091	0.2523	NA	-0.1242	NA	+	-0.0335	16	-840.0242	1712.9330	3.9441	0.0355
	-2.1551	-0.1198	0.6848	-0.3786	0.0350	-0.0322	0.8443	-0.0095	0.0195	0.0366	NA	-0.1353	-0.0315	+	-0.0369	18	-838.1474	1713.4106	4.4217	0.0280
	-2.1620	NA	0.7678	NA	0.0225	NA	0.8167	-0.0702	-0.0166	0.2525	-0.0715	NA	-0.0263	+	-0.0213	15	-841.5983	1713.9759	4.9870	0.0211
	-2.1557	-0.1211	0.7786	NA	0.0217	-0.0237	0.8612	-0.0767	0.0016	0.2369	-0.0799	NA	NA	+	-0.0300	16	-840.6383	1714.1612	5.1723	0.0192
	-2.1669	-0.1420	0.7033	-0.3911	0.0302	-0.0363	0.8535	-0.0260	0.0123	0.0141	-0.1178	NA	-0.0757	+	-0.0343	18	-838.5231	1714.1619	5.1730	0.0192
	-2.1416	-0.1130	0.7615	NA	0.0309	-0.0295	0.8471	-0.0618	0.0096	0.2532	NA	-0.1251	-0.0247	+	-0.0340	17	-839.9942	1714.9852	5.9963	0.0127
	-2.1527	-0.1316	0.7805	NA	0.0256	-0.0325	0.8555	-0.0792	0.0025	0.2388	-0.0969	NA	-0.0600	+	-0.0315	17	-840.4817	1715.9602	6.9712	0.0078
	-2.1529	NA	0.5528	-0.5698	0.0585	NA	NA	NA	-0.0618	0.4266	NA	-0.2060	-0.2381	+	-0.0254	14	-901.9867	1832.6540	123.6651	0.0000
	-2.1601	0.1816	0.5552	-0.5385	0.0568	0.0335	NA	NA	-0.0746	0.4361	NA	-0.2029	-0.1956	+	-0.0192	16	-900.1092	1833.1029	124.1139	0.0000
	-2.1691	0.2161	0.5564	-0.5327	0.0490	0.0669	NA	NA	-0.0794	0.4436	NA	-0.1991	NA	+	-0.0165	15	-901.6209	1834.0210	125.0321	0.0000

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
	-2.1709	NA	0.5568	-0.5730	0.0502	NA	NA	NA	-0.0813	0.4145	-0.1314	NA	-0.2877	+	-0.0174	14	-903.2479	1835.1766	126.1876	0.0000
	-2.1620	NA	0.5542	-0.5686	0.0494	NA	NA	NA	-0.0644	0.4338	NA	-0.2024	NA	+	-0.0267	13	-904.2998	1835.1886	126.1997	0.0000
	-2.1790	0.1652	0.5569	-0.5391	0.0473	0.0325	NA	NA	-0.0931	0.4260	-0.0980	NA	-0.2361	+	-0.0107	16	-901.7679	1836.4203	127.4313	0.0000
	-2.1428	0.1986	0.5912	NA	0.0593	0.0380	NA	NA	-0.1032	0.7430	NA	-0.1874	-0.1904	+	-0.0097	15	-903.6659	1838.1111	129.1222	0.0000
	-2.1911	0.2143	0.5537	-0.5170	0.0363	0.0713	NA	NA	-0.0994	0.4421	-0.0315	NA	NA	+	-0.0055	15	-903.6876	1838.1543	129.1654	0.0000
	-2.1336	NA	0.5906	NA	0.0608	NA	NA	NA	-0.0901	0.7518	NA	-0.1890	-0.2373	+	-0.0159	13	-905.9424	1838.4738	129.4848	0.0000
	-2.1520	0.2322	0.5926	NA	0.0516	0.0705	NA	NA	-0.1076	0.7475	NA	-0.1840	NA	+	-0.0074	14	-905.1066	1838.8939	129.9050	0.0000
	-2.1837	NA	0.5534	-0.5558	0.0373	NA	NA	NA	-0.0845	0.4309	-0.0569	NA	NA	+	-0.0169	13	-906.2730	1839.1350	130.1461	0.0000
	-2.1432	NA	0.5927	NA	0.0517	NA	NA	NA	-0.0926	0.7587	NA	-0.1856	NA	+	-0.0175	12	-908.2417	1840.9875	131.9985	0.0000
	-2.1506	NA	0.5932	NA	0.0523	NA	NA	NA	-0.1085	0.7420	-0.1037	NA	-0.2760	+	-0.0080	13	-907.2249	1841.0388	132.0499	0.0000
	-2.1612	0.1874	0.5911	NA	0.0492	0.0383	NA	NA	-0.1208	0.7334	-0.0672	NA	-0.2178	+	-0.0010	15	-905.2932	1841.3656	132.3767	0.0000
	-2.1732	0.2322	0.5873	NA	0.0391	0.0740	NA	NA	-0.1258	0.7368	-0.0071	NA	NA	+	0.0032	14	-906.9441	1842.5689	133.5800	0.0000
	-2.1639	NA	0.5896	NA	0.0399	NA	NA	NA	-0.1107	0.7484	-0.0337	NA	NA	+	-0.0081	12	-910.0210	1844.5461	135.5571	0.0000
4.2	-2.0934	NA	0.8058	-0.7964	-0.0326	NA	0.3733	0.0282	-0.1999	0.2782	NA	0.0854	NA	+	-0.0946	15	-438.1481	907.6955	0.0000	0.2620
	-2.0874	NA	0.8017	-0.7977	-0.0122	NA	0.3996	0.0206	-0.2020	0.2680	NA	0.0824	0.1495	+	-0.0764	16	-437.2342	908.0590	0.3635	0.2184
	-2.1009	NA	0.8040	-0.8071	-0.0492	NA	0.3705	0.0505	-0.1627	0.2931	-0.0088	NA	NA	+	-0.1188	15	-438.4655	908.3305	0.6350	0.1907
	-2.0937	NA	0.7929	-0.8125	-0.0284	NA	0.3972	0.0350	-0.1726	0.2772	0.0402	NA	0.1653	+	-0.0975	16	-437.4634	908.5175	0.8220	0.1737
	-2.0913	0.0594	0.8056	-0.7815	-0.0302	-0.0553	0.3426	0.0267	-0.2105	0.2987	NA	0.0794	NA	+	-0.0953	17	-437.7240	911.2427	3.5472	0.0445
	-2.0982	0.0672	0.8030	-0.7888	-0.0458	-0.0542	0.3359	0.0460	-0.1783	0.3144	0.0049	NA	NA	+	-0.1168	17	-437.9958	911.7863	4.0908	0.0339
	-2.0857	0.0642	0.8036	-0.7763	-0.0105	-0.0353	0.3675	0.0200	-0.2109	0.2915	NA	0.0763	0.1430	+	-0.0763	18	-436.9047	911.8211	4.1256	0.0333
	-2.0909	0.0815	0.7944	-0.7829	-0.0244	-0.0304	0.3583	0.0307	-0.1877	0.3045	0.0562	NA	0.1652	+	-0.0928	18	-437.0262	912.0642	4.3687	0.0295
	-2.0373	NA	0.9063	NA	-0.0762	NA	0.3714	-0.0288	-0.2032	0.7580	NA	0.1049	NA	+	-0.0213	14	-443.6968	916.6145	8.9190	0.0030
	-2.0313	NA	0.9026	NA	-0.0573	NA	0.3976	-0.0362	-0.2048	0.7492	NA	0.1009	0.1491	+	-0.0031	15	-442.7878	916.9750	9.2795	0.0025
	-2.0451	NA	0.9075	NA	-0.0974	NA	0.3690	-0.0010	-0.1553	0.7840	-0.0263	NA	NA	+	-0.0515	14	-444.1526	917.5262	9.8307	0.0019
	-2.0381	NA	0.8972	NA	-0.0783	NA	0.3948	-0.0159	-0.1647	0.7719	0.0204	NA	0.1590	+	-0.0303	15	-443.2211	917.8416	10.1461	0.0016
	-2.0392	0.1267	0.9067	NA	-0.0696	-0.0067	0.3152	-0.0251	-0.2134	0.7748	NA	0.0920	NA	+	-0.0175	16	-442.8130	919.2166	11.5211	0.0008
	-2.0337	0.1311	0.9043	NA	-0.0499	0.0133	0.3417	-0.0313	-0.2135	0.7641	NA	0.0877	0.1495	+	0.0013	17	-441.9162	919.6271	11.9316	0.0007
	-2.0700	0.2258	0.8160	-0.7067	-0.0420	-0.0407	NA	NA	-0.2141	0.5318	0.0593	NA	NA	+	-0.0928	15	-444.2073	919.8141	12.1185	0.0006
	-2.0653	0.2146	0.8280	-0.6993	-0.0265	-0.0415	NA	NA	-0.2308	0.5287	NA	0.0602	NA	+	-0.0746	15	-444.2139	919.8272	12.1317	0.0006
	-2.0465	0.1350	0.9054	NA	-0.0884	-0.0052	0.3082	-0.0029	-0.1748	0.7979	-0.0003	NA	NA	+	-0.0432	16	-443.1822	919.9551	12.2596	0.0006

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
	-2.0398	0.1489	0.8953	NA	-0.0665	0.0184	0.3320	-0.0177	-0.1847	0.7837	0.0527	NA	0.1712	+	-0.0189	17	-442.1375	920.0697	12.3741	0.0005
	-2.0661	0.2403	0.8139	-0.7053	-0.0274	-0.0255	NA	NA	-0.2195	0.5318	0.0911	NA	0.0974	+	-0.0755	16	-443.8535	921.2977	13.6021	0.0003
	-2.0625	0.2212	0.8289	-0.6967	-0.0177	-0.0324	NA	NA	-0.2308	0.5317	NA	0.0572	0.0595	+	-0.0660	16	-444.0631	921.7168	14.0212	0.0002
	-2.0616	NA	0.8295	-0.7886	-0.0273	NA	NA	NA	-0.2190	0.5052	NA	0.0824	NA	+	-0.0800	13	-447.4986	922.0524	14.3568	0.0002
	-2.0661	NA	0.8189	-0.7982	-0.0479	NA	NA	NA	-0.1897	0.5148	0.0242	NA	NA	+	-0.1079	13	-447.7885	922.6322	14.9366	0.0001
	-2.0595	NA	0.8294	-0.7904	-0.0210	NA	NA	NA	-0.2193	0.5062	NA	0.0807	0.0441	+	-0.0738	14	-447.4130	924.0469	16.3514	0.0001
	-2.0634	NA	0.8168	-0.8034	-0.0388	NA	NA	NA	-0.1930	0.5130	0.0427	NA	0.0622	+	-0.0976	14	-447.6358	924.4926	16.7971	0.0001
	-2.0265	0.2648	0.9241	NA	-0.0612	0.0032	NA	NA	-0.2209	0.9472	NA	0.0639	NA	+	-0.0005	14	-448.4206	926.0620	18.3665	0.0000
	-2.0311	0.2751	0.9138	NA	-0.0775	0.0041	NA	NA	-0.2011	0.9560	0.0465	NA	NA	+	-0.0204	14	-448.5032	926.2273	18.5318	0.0000
	-2.0272	0.2898	0.9111	NA	-0.0629	0.0193	NA	NA	-0.2068	0.9552	0.0792	NA	0.1003	+	-0.0030	15	-448.1271	927.6537	19.9581	0.0000
	-2.0236	0.2720	0.9247	NA	-0.0518	0.0129	NA	NA	-0.2209	0.9489	NA	0.0602	0.0666	+	0.0086	15	-448.2310	927.8615	20.1660	0.0000
	-2.0121	NA	0.9349	NA	-0.0676	NA	NA	NA	-0.2111	0.9824	NA	0.0923	NA	+	-0.0007	12	-453.0327	930.9671	23.2716	0.0000
	-2.0159	NA	0.9271	NA	-0.0907	NA	NA	NA	-0.1750	1.0004	0.0002	NA	NA	+	-0.0330	12	-453.4343	931.7703	24.0748	0.0000
	-2.0100	NA	0.9350	NA	-0.0624	NA	NA	NA	-0.2114	0.9843	NA	0.0906	0.0394	+	0.0049	13	-452.9643	932.9837	25.2881	0.0000
	-2.0135	NA	0.9258	NA	-0.0840	NA	NA	NA	-0.1777	1.0015	0.0144	NA	0.0486	+	-0.0246	13	-453.3404	933.7360	26.0404	0.0000

Table A3.7: Hypothesis H2 averaged models' results by sex. Variables include immatures' age, (relative) rank, proximity (prox.) degree, number (Nb.) of matriline members, and total grooming (Groom.) amount; demonstrators' age, sex (male), and their age availability (avail.); a (immature-demonstrator) dyad's grooming allocation, proximity in the foraging network, and (relative) rank difference; time period and troop. For each variable/ model are shown the estimate, the standard (Std.) error, the z value, the *p*-value, the odds ratio (OR), the lower (LCI) and upper (UCI) 97.5% confidence intervals, and the percentage change in the odds of scrounging (Models 3.1 and 3.2) or of performing other social learning behaviours (Models 4.1 and 4.2) at the increase of one unit in the independent variable.

Model	Variable	Estimate	Std. Error	z value	<i>p</i> -value	OR	LCI	UCI	Percentage change
3.1	(Intercept)	-2.2230	0.0724	30.6469	0.0000	0.11	0.09	0.12	-89.17
	Age demonstrator	-0.0825	0.0844	0.9771	0.3285	0.92	0.77	0.99	-7.92
	Age immature	0.5961	0.1068	5.5751	0.0000	1.82	1.47	2.24	81.50
	Age:Proximity	-0.4910	0.1361	3.6022	0.0003	0.61	0.47	0.80	-38.80
	Degree prox.	0.0963	0.0665	1.4455	0.1483	1.10	0.97	1.25	10.11
	Demonstrator avail. (age)	-0.0269	0.0522	0.5150	0.6065	0.97	0.85	1.08	-2.65
	Groom. allocation	0.5305	0.0564	9.4022	0.0000	1.70	1.52	1.90	69.99
	Groom. amount	-0.0656	0.0950	0.6892	0.4907	0.94	0.78	1.13	-6.35
	Nb. matriline	-0.0782	0.0766	1.0204	0.3075	0.92	0.80	1.07	-7.52
	Prox. foraging	0.4619	0.0813	5.6758	0.0000	1.59	1.35	1.86	58.70
	Rank immature	-0.3102	0.0762	4.0668	0.0000	0.73	0.63	0.85	-26.67
	Sex demonstrator	0.0115	0.0409	0.2805	0.7791	1.01	0.91	1.19	1.16
	Time period 2	-0.4808	0.0755	6.3587	0.0000	0.62	0.53	0.72	-38.17
	Time period 3	-0.6188	0.0852	7.2508	0.0000	0.54	0.46	0.64	-46.14
	Troop	-0.2478	0.0879	2.8149	0.0049	0.78	0.66	0.93	-21.94
3.2	(Intercept)	-2.0386	0.1006	20.2202	0.0000	0.13	0.11	0.16	-86.98
	Age demonstrator	-0.1207	0.0945	1.2757	0.2020	0.89	0.73	1.00	-11.37
	Age immature	0.8659	0.1024	8.4350	0.0000	2.38	1.94	2.91	137.71
	Age:Proximity	-0.5683	0.1696	3.3441	0.0008	0.57	0.41	0.79	-43.35
	Degree prox.	0.1499	0.0870	1.7193	0.0856	1.16	0.98	1.38	16.17
	Demonstrator avail. (age)	0.0647	0.0725	0.8915	0.3727	1.07	0.94	1.25	6.69
	Groom. allocation	0.4573	0.0674	6.7720	0.0000	1.58	1.38	1.80	57.98
	Groom. amount	0.0967	0.0875	1.1027	0.2702	1.10	0.93	1.31	10.16
	Nb. matriline	0.0305	0.0801	0.3796	0.7042	1.03	0.88	1.21	3.09
	Prox. foraging	0.5225	0.1049	4.9722	0.0000	1.69	1.37	2.07	68.62
	Rank difference	-0.0052	0.0323	0.1618	0.8714	0.99	0.73	0.98	-0.52
	Rank immature	-0.2514	0.0902	2.7814	0.0054	0.78	0.66	0.90	-22.23
	Sex demonstrator	0.0381	0.0674	0.5642	0.5726	1.04	0.94	1.28	3.88
	Time period 2	-0.5518	0.1143	4.8171	0.0000	0.58	0.46	0.72	-42.41
	Time period 3	-1.0166	0.1109	9.1474	0.0000	0.36	0.29	0.45	-63.82
	Troop	0.1086	0.0893	1.2143	0.2246	1.11	0.94	1.33	11.48
4.1	(Intercept)	-2.1607	0.0694	31.0764	0.0000	0.12	0.10	0.13	-88.48
	Age demonstrator	-0.0292	0.0671	0.4348	0.6637	0.97	0.75	1.05	-2.88
	Age immature	0.7099	0.1517	4.6703	0.0000	2.03	1.51	2.74	103.39
	Age:Proximity	-0.2498	0.2384	1.0470	0.2951	0.78	0.47	1.02	-22.11
	Degree prox.	0.0289	0.0837	0.3447	0.7303	1.03	0.87	1.21	2.93
	Demonstrator avail. (age)	-0.0068	0.0435	0.1564	0.8757	0.99	0.82	1.15	-0.68

Model	Variable	Estimate	Std. Error	z value	p-value	OR	LCI	UCI	Percentage change
	Groom. allocation	0.8224	0.0692	11.8671	0.0000	2.28	1.99	2.61	127.59
	Groom. amount	-0.0269	0.1375	0.1955	0.8450	0.97	0.74	1.27	-2.66
	Nb. matriline	0.0001	0.0853	0.0009	0.9993	1.00	0.85	1.18	0.01
	Prox. foraging	0.1146	0.1555	0.7358	0.4619	1.12	0.83	1.52	12.14
	Rank difference	-0.0273	0.0627	0.4342	0.6642	0.97	0.78	1.09	-2.69
	Rank immature	-0.0878	0.0946	0.9261	0.3544	0.92	0.74	1.04	-8.40
	Sex demonstrator	-0.0063	0.0545	0.1147	0.9087	0.99	0.80	1.20	-0.62
	Time period 2	-0.0596	0.0881	0.6759	0.4991	0.94	0.79	1.12	-5.79
	Time period 3	0.1691	0.1116	1.5121	0.1305	1.18	0.95	1.47	18.43
	Troop	-0.0276	0.0955	0.2879	0.7734	0.97	0.81	1.17	-2.72
4.2	(Intercept)	-2.0933	0.0867	24.0645	0.0000	0.12	0.10	0.15	-87.67
	Age demonstrator	0.0096	0.0458	0.2087	0.8347	1.01	0.87	1.31	0.96
	Age immature	0.8018	0.1289	6.1960	0.0000	2.23	1.73	2.87	122.95
	Age:Proximity	-0.7996	0.2466	3.2311	0.0012	0.45	0.28	0.73	-55.05
	Degree prox.	-0.0299	0.1193	0.2497	0.8028	0.97	0.77	1.23	-2.94
	Demonstrator avail. (age)	-0.0065	0.0429	0.1501	0.8807	0.99	0.78	1.18	-0.64
	Groom. allocation	0.3795	0.0869	4.3542	0.0000	1.46	1.23	1.73	46.15
	Groom. amount	0.0324	0.1128	0.2857	0.7751	1.03	0.83	1.29	3.29
	Nb. matriline	-0.1881	0.1050	1.7850	0.0743	0.83	0.67	1.02	-17.15
	Prox. foraging	0.2821	0.1745	1.6103	0.1073	1.33	0.94	1.87	32.59
	Rank difference	0.0072	0.0718	0.1005	0.9200	1.01	0.82	1.26	0.73
	Rank immature	0.0471	0.0902	0.5211	0.6023	1.05	0.88	1.34	4.82
	Sex demonstrator	0.0720	0.1095	0.6567	0.5114	1.07	0.94	1.46	7.47
	Time period 2	-0.0847	0.1176	0.7180	0.4727	0.92	0.73	1.16	-8.12
	Time period 3	0.0715	0.1320	0.5398	0.5893	1.07	0.83	1.39	7.41
	Troop	-0.0959	0.1173	0.8146	0.4153	0.91	0.72	1.14	-9.14

Table A3.8: The characteristics of each hypothesis H2 best model by sex (scrounging: 3.1 – females – and 3.2 – males; other social learning behaviours: 4.1 – females – and 4.2 – males), including the number (Nb.) of parameters, the AICc value, the difference (delta) in AICc from the top model (lowest AICc), the likelihood, the log-likelihood, the Akaike weight, and the cumulative weight (sum).

Model	Nb. parameters	AICc	Delta	Likelihood	log-Likelihood	Weight	Cumulative weight
3.1	17	2808.7342	0.0000	1.0000	-1387.0345	0.4262	0.4262
	15	2809.5950	0.8609	0.6502	-1389.5372	0.2771	0.7033
	18	2810.6223	1.8881	0.3890	-1386.9390	0.1658	0.8691
	16	2811.0955	2.3613	0.3071	-1389.2524	0.1309	1.0000
3.2	17	1692.2755	0.0000	1.0000	-828.5834	0.4296	0.4296
	18	1692.8749	0.5994	0.7410	-827.8168	0.3184	0.7480
	15	1694.5803	2.3048	0.3159	-831.8569	0.1357	0.8837
	16	1695.4988	3.2233	0.1996	-831.2575	0.0857	0.9694
	17	1697.5611	5.2856	0.0712	-831.2262	0.0306	1.0000
4.1	15	1708.9889	0.0000	1.0000	-839.1049	0.2552	0.2552
	14	1710.3853	1.3964	0.4975	-840.8523	0.1270	0.3822
	15	1710.5343	1.5454	0.4618	-839.8776	0.1178	0.5000
	16	1711.0870	2.0981	0.3503	-839.1012	0.0894	0.5894

Model	Nb. parameters	AICc	Delta	Likelihood	log-Likelihood	Weight	Cumulative weight
	17	1711.3886	2.3996	0.3013	-838.1959	0.0769	0.6663
	14	1711.9408	2.9519	0.2286	-841.6301	0.0583	0.7246
	15	1712.4828	3.4938	0.1743	-840.8518	0.0445	0.7691
	16	1712.5042	3.5152	0.1725	-839.8098	0.0440	0.8131
	17	1712.5367	3.5478	0.1697	-838.7700	0.0433	0.8564
	16	1712.9330	3.9441	0.1392	-840.0242	0.0355	0.8920
	18	1713.4106	4.4217	0.1096	-838.1474	0.0280	0.9199
	15	1713.9759	4.9870	0.0826	-841.5983	0.0211	0.9410
	16	1714.1612	5.1723	0.0753	-840.6383	0.0192	0.9602
	18	1714.1619	5.1730	0.0753	-838.5231	0.0192	0.9795
	17	1714.9852	5.9963	0.0499	-839.9942	0.0127	0.9922
	17	1715.9602	6.9712	0.0306	-840.4817	0.0078	1.0000
4.2	15	907.6955	0.0000	1.0000	-438.1481	0.2657	0.2657
	16	908.0590	0.3635	0.8338	-437.2342	0.2216	0.4873
	15	908.3305	0.6350	0.7280	-438.4655	0.1934	0.6807
	16	908.5175	0.8220	0.6630	-437.4634	0.1762	0.8569
	17	911.2427	3.5472	0.1697	-437.7240	0.0451	0.9020
	17	911.7863	4.0908	0.1293	-437.9958	0.0344	0.9363
	18	911.8211	4.1256	0.1271	-436.9047	0.0338	0.9701
	18	912.0642	4.3687	0.1126	-437.0262	0.0299	1.0000

Table A3.9: Variables' relative importance (RVI; 1 = highest) for hypothesis H2 averaged models by sex (scrounging: 3.1 – females – and 3.2 – males; other social learning behaviours: 4.1 – females – and 4.2 – males), including immatures' age, (relative) rank, proximity (prox.) degree, number (Nb.) of matriline members, and total grooming (Groom.) amount; demonstrators' age, sex (male), and their age availability (avail.); a (immature-demonstrator) dyad's grooming allocation, proximity in the foraging network, and (relative) rank difference; time period and troop.

Model	Variable	RVI	Model	Variable	RVI
3.1	Age demonstrator	0.59	4.1	Age demonstrator	0.24
	Age immature	1.00		Age immature	1.00
	Age:Proximity	1.00		Age:Proximity	0.67
	Degree prox.	1.00		Degree prox.	1.00
	Demonstrator avail. (age)	0.59		Demonstrator avail. (age)	0.24
	Groom. allocation	1.00		Groom. allocation	1.00
	Groom. amount	1.00		Groom. amount	1.00
	Nb. matriline	1.00		Nb. matriline	1.00
	Prox. foraging	1.00		Prox. foraging	1.00
	Rank immature	1.00		Rank difference	0.33
	Sex demonstrator	0.30		Rank immature	0.67
	Time period	1.00		Sex demonstrator	0.27
	Troop	1.00		Time period	1.00
3.2	Age demonstrator	0.78	4.2	Troop	1.00
	Age immature	1.00		Age demonstrator	0.14
	Age:Proximity	1.00		Age immature	1.00
	Degree prox.	1.00		Age:Proximity	1.00
	Demonstrator avail. (age)	0.78		Degree prox.	1.00
	Groom. allocation	1.00		Demonstrator avail. (age)	0.14

Model	Variable	RVI	Model	Variable	RVI
	Groom. amount	1.00		Groom. allocation	1.00
	Nb. matriline	1.00		Groom. amount	1.00
	Prox. foraging	1.00		Nb. matriline	1.00
	Rank difference	0.03		Prox. foraging	1.00
	Rank immature	0.97		Rank difference	0.43
	Sex demonstrator	0.40		Rank immature	0.57
	Time period	1.00		Sex demonstrator	0.46
	Troop	1.00		Time period	1.00
				Troop	1.00

Figure A3.2: Hypothesis H2 averaged models' results for scrounging (top) and the other social learning behaviours (bottom) divided by sex: females (left, red), males (right, blue). The variables of interest include immatures' age and (relative) rank; demonstrators' age and sex (male); a (immature-demonstrator) dyad's grooming (Groom.) allocation, proximity (Prox.) in the foraging network, and (relative) rank difference. Independent variables' points represent odds ratios and whiskers are 97.5% confidence intervals (CIs). Points have different shapes depending on whether their CIs overlap with 1 (the odds of learning from a certain model – response – does not change at the increase in the independent variable), they are < 1 (the response decreases at the increase in the independent variable), or they are > 1 (the response increases at the increase in the independent variable). Variables are ordered based on effect size and significance (** = significant).

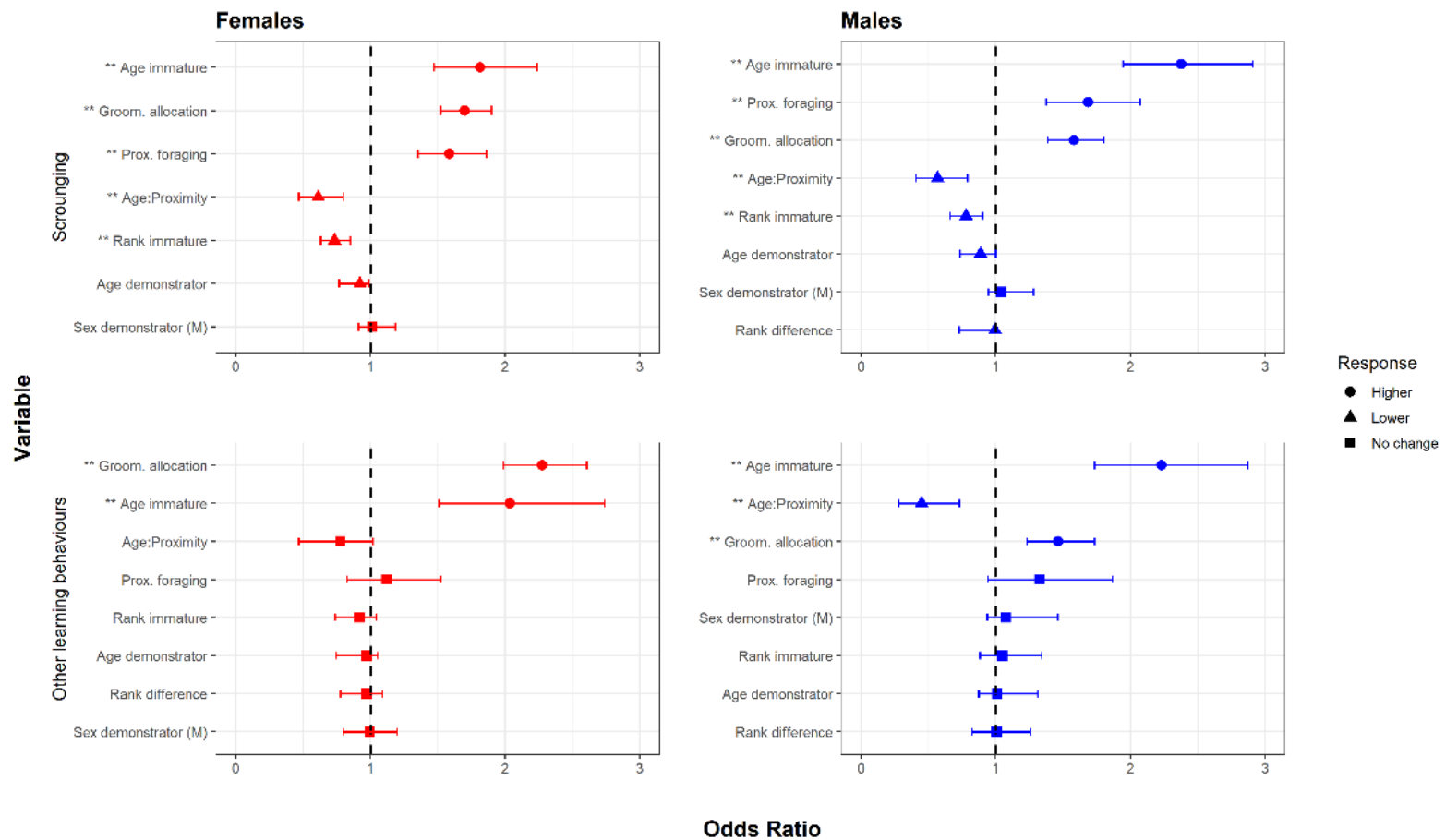


Figure A3.3: Hypothesis H2 averaged models' significant results (plus demonstrators' age – marginally significant in both-sexes model) for scrounging (left – first two columns) and the other social learning behaviours (right – last two columns), divided by sex (females: 1st and 3rd column; males: 2nd and 4th column). The plots in different rows show the changes in the odds of learning from a certain demonstrator with (1st) immatures' age (at different immature-demonstrator proximity association levels during foraging), (2nd) a (immature-demonstrator) dyad's grooming allocation, (3rd) proximity during foraging (at different immatures' age stages), (4th) demonstrators' age, and (5th) immatures' (relative) rank. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.

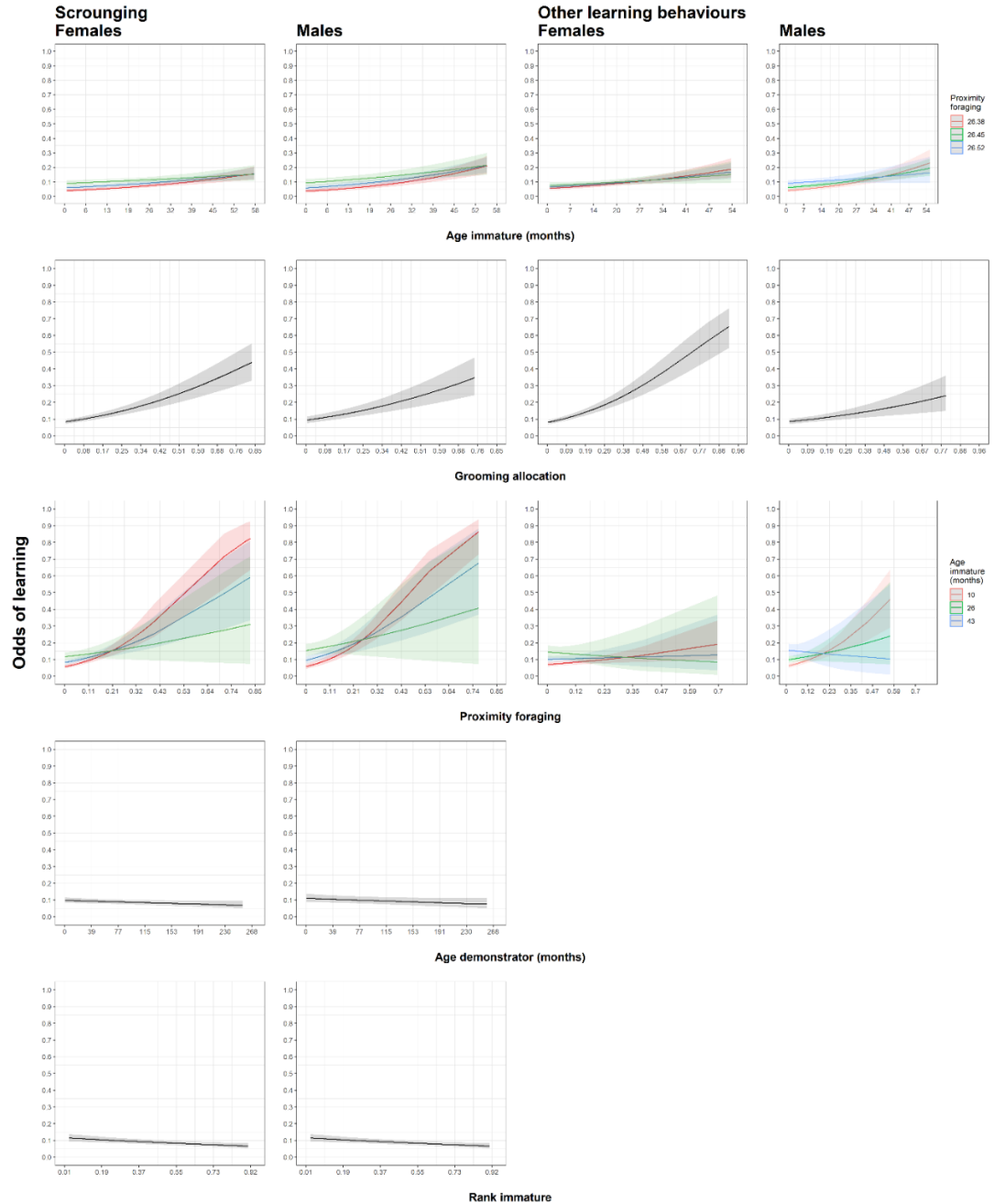


Figure A3.4: Distribution of demonstrator-immature age differences for scrounging (top) and the other social learning behaviours (bottom), for females (left, red) and males (right, blue).

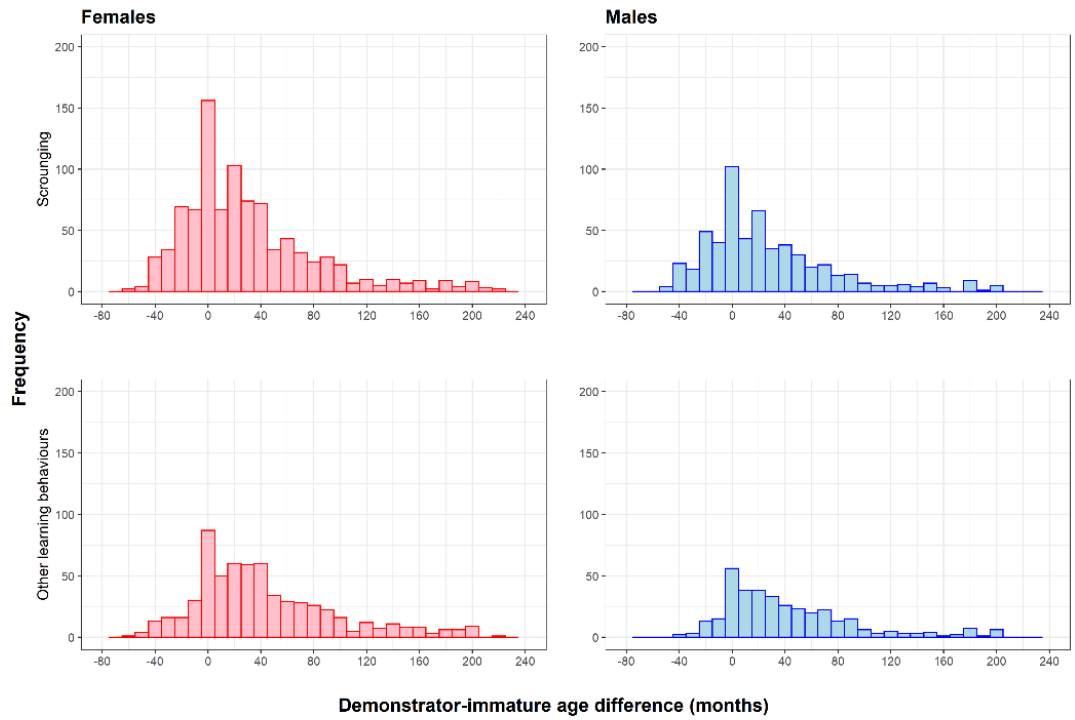
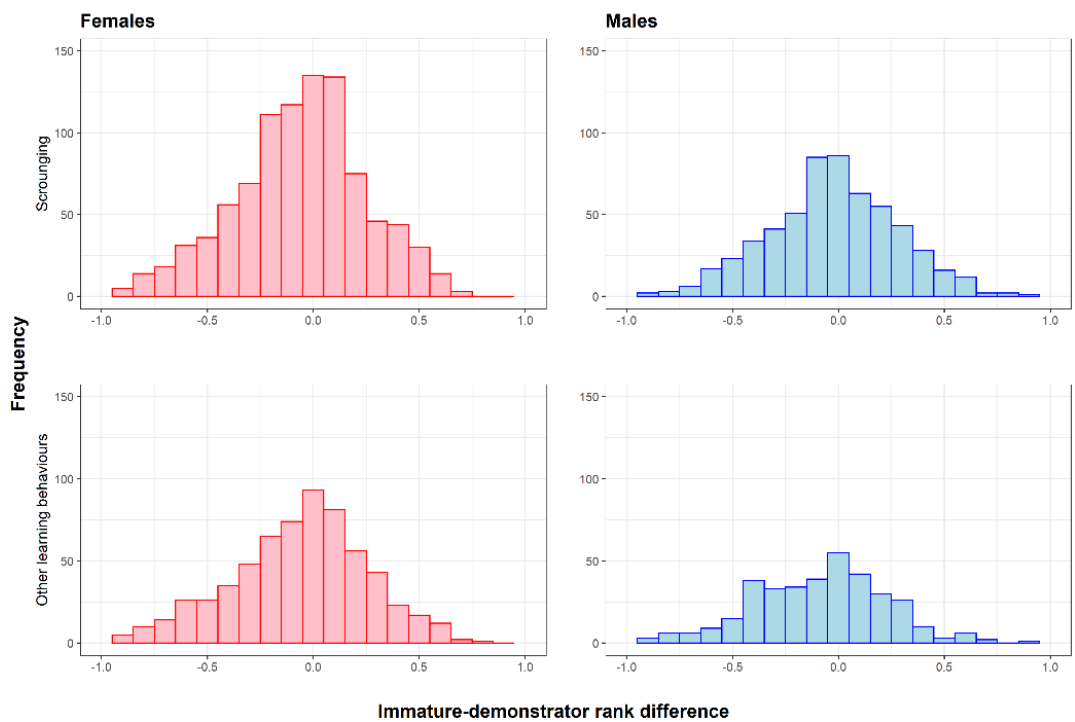


Figure 3.5: Distribution of immature-demonstrator (relative) rank differences for scrounging (top) and the other social learning behaviours (bottom), for females (left, red) and males (right, blue).



3.7 H2 MODELS' SETS AND SELECTION

Here we present hypothesis H2 models' sets, and the characteristics of the best models and the averaged models. Table A3.10 shows the sets of biologically plausible candidate models (32 each). Table A3.11 presents the characteristics of the best models (see Appendix 3, §3.6 for details on parameters' calculation) and Table A3.12 indicates the relative variable importance of each averaged model (see Chapter 4, §4.3).

Table A3.10: Full model sets for hypothesis H2 models (scrounging: 3; other social learning behaviours: 4), showing all possible combinations of biologically plausible models (on rows; green = variable included; NA = variable excluded). In all models were included the following variables: immatures' age, number (Nb.) of matriline members, proximity (prox.) degree, a (immature-demonstrator) dyad's proximity during foraging, time period and troop. In addition, either immatures' (relative) rank or a dyad's (relative) rank difference was added in all models, but they were not present together. A dyad's grooming (Groom.) allocation was present together with immatures' total grooming amount, while the availability (avail.) of demonstrators of a certain age was present together with demonstrators' age. The values reported for sex refer to males. The models' parameters shown are the degrees of freedom (df), the log-likelihood, the AICc value, the difference (delta) in AICc from the top model (lowest AICc), and the Akaike weight. The best models are indicated by the $\Delta AICc < 7$ in bold, including models with a sum of AICc weights < 0.95 .

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
3	-2.1831	-0.1410	0.5953	-0.5573	0.0496	0.0020	0.5082	0.0256	-0.0554	0.4740	NA	-0.2736	NA	+	-0.1496	17	-2235.0528	4504.5162	0.0000	0.5621
	-2.1813	-0.1367	0.5976	-0.5534	0.0501	0.0080	0.5144	0.0267	-0.0564	0.4771	NA	-0.2759	0.0505	+	-0.1416	18	-2234.5782	4505.6158	1.0995	0.3244
	-2.1906	NA	0.6069	-0.5430	0.0509	NA	0.4570	0.0231	-0.0657	0.4969	NA	-0.2796	NA	+	-0.1410	15	-2239.2289	4508.7796	4.2633	0.0667
	-2.1885	NA	0.6092	-0.5395	0.0513	NA	0.4650	0.0247	-0.0668	0.4991	NA	-0.2821	0.0590	+	-0.1329	16	-2238.6028	4509.5705	5.0542	0.0449
	-2.1893	-0.1614	0.5441	-0.5249	0.0919	0.0006	0.5141	0.0365	-0.0929	0.4713	-0.0605	NA	NA	+	-0.1788	17	-2241.0814	4516.5736	12.0574	0.0014
	-2.1881	-0.1566	0.5435	-0.5197	0.0931	0.0041	0.5168	0.0375	-0.0934	0.4754	-0.0497	NA	0.0295	+	-0.1755	18	-2240.9413	4518.3420	13.8257	0.0006
	-2.1958	NA	0.5509	-0.4980	0.0976	NA	0.4548	0.0348	-0.1061	0.5038	-0.0241	NA	NA	+	-0.1726	15	-2246.2332	4522.7881	18.2719	0.0001
	-2.1933	NA	0.5496	-0.4899	0.0996	NA	0.4617	0.0373	-0.1062	0.5097	-0.0055	NA	0.0536	+	-0.1679	16	-2245.7762	4523.9172	19.4010	0.0000
	-2.1369	-0.1268	0.6429	NA	0.0426	0.0161	0.5236	-0.0125	-0.0767	0.6818	NA	-0.2498	NA	+	-0.1157	16	-2249.2378	4530.8405	26.3242	0.0000
	-2.1355	-0.1213	0.6450	NA	0.0431	0.0231	0.5308	-0.0102	-0.0781	0.6838	NA	-0.2521	0.0623	+	-0.1065	17	-2248.5505	4531.5118	26.9955	0.0000

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
	-2.1439	NA	0.6528	NA	0.0435	NA	0.4769	-0.0131	-0.0851	0.6988	NA	-0.2564	NA	+	-0.1091	14	-2252.7340	4533.7493	29.2331	0.0000
	-2.1422	NA	0.6549	NA	0.0439	NA	0.4858	-0.0105	-0.0864	0.7000	NA	-0.2587	0.0679	+	-0.1003	15	-2251.9277	4534.1771	29.6609	0.0000
	-2.1409	-0.1396	0.5848	NA	0.0814	0.0134	0.5262	0.0055	-0.1036	0.6720	-0.0299	NA	NA	+	-0.1518	16	-2253.5738	4539.5125	34.9962	0.0000
	-2.1399	-0.1303	0.5820	NA	0.0836	0.0196	0.5307	0.0091	-0.1039	0.6760	-0.0096	NA	0.0556	+	-0.1471	17	-2253.0916	4540.5939	36.0776	0.0000
	-2.1479	NA	0.5879	NA	0.0861	NA	0.4736	0.0084	-0.1135	0.6929	0.0030	NA	NA	+	-0.1495	14	-2257.5323	4543.3459	38.8296	0.0000
	-2.1459	NA	0.5841	NA	0.0886	NA	0.4828	0.0136	-0.1131	0.6964	0.0282	NA	0.0742	+	-0.1444	15	-2256.6614	4543.6445	39.1283	0.0000
	-2.1648	0.1242	0.6133	-0.6578	0.0776	0.0268	NA	NA	-0.0922	0.6420	NA	-0.2827	NA	+	-0.1310	15	-2313.9376	4658.1969	153.6807	0.0000
	-2.1653	0.1155	0.6105	-0.6601	0.0768	0.0203	NA	NA	-0.0910	0.6383	NA	-0.2805	-0.0560	+	-0.1393	16	-2313.4455	4659.2558	154.7396	0.0000
	-2.1572	NA	0.6055	-0.6816	0.0789	NA	NA	NA	-0.0872	0.6278	NA	-0.2792	NA	+	-0.1395	13	-2317.1701	4660.5838	156.0675	0.0000
	-2.1585	NA	0.6023	-0.6820	0.0778	NA	NA	NA	-0.0858	0.6243	NA	-0.2765	-0.0809	+	-0.1497	14	-2316.1717	4660.6248	156.1085	0.0000
	-2.1683	0.1206	0.5658	-0.6060	0.1270	0.0253	NA	NA	-0.1241	0.6530	0.0029	NA	NA	+	-0.1592	15	-2320.6423	4671.6064	167.0901	0.0000
	-2.1695	0.1054	0.5666	-0.6157	0.1237	0.0176	NA	NA	-0.1236	0.6443	-0.0225	NA	-0.0689	+	-0.1662	16	-2320.0036	4672.3720	167.8558	0.0000
	-2.1647	NA	0.5656	-0.6439	0.1205	NA	NA	NA	-0.1184	0.6263	-0.0591	NA	-0.1040	+	-0.1722	14	-2322.0878	4672.4568	167.9406	0.0000
	-2.1620	NA	0.5638	-0.6360	0.1251	NA	NA	NA	-0.1186	0.6352	-0.0265	NA	NA	+	-0.1635	13	-2323.5669	4673.3774	168.8611	0.0000
	-2.1117	0.1520	0.6512	NA	0.0660	0.0423	NA	NA	-0.1188	0.9028	NA	-0.2439	NA	+	-0.1061	14	-2333.8802	4696.0417	191.5255	0.0000
	-2.1119	0.1447	0.6489	NA	0.0654	0.0369	NA	NA	-0.1177	0.9004	NA	-0.2422	-0.0477	+	-0.1131	15	-2333.5358	4697.3933	192.8770	0.0000
	-2.0999	NA	0.6433	NA	0.0665	NA	NA	NA	-0.1140	0.8977	NA	-0.2370	NA	+	-0.1163	12	-2338.5657	4701.3402	196.8239	0.0000
	-2.1008	NA	0.6402	NA	0.0657	NA	NA	NA	-0.1126	0.8944	NA	-0.2349	-0.0808	+	-0.1264	13	-2337.6331	4701.5098	196.9936	0.0000
	-2.1125	0.1554	0.5938	NA	0.1104	0.0385	NA	NA	-0.1333	0.8967	0.0447	NA	NA	+	-0.1428	14	-2337.4966	4703.2745	198.7583	0.0000
	-2.1128	0.1468	0.5948	NA	0.1085	0.0343	NA	NA	-0.1335	0.8940	0.0303	NA	-0.0396	+	-0.1465	15	-2337.2890	4704.8997	200.3834	0.0000
	-2.1029	NA	0.5964	NA	0.1034	NA	NA	NA	-0.1296	0.8852	-0.0189	NA	-0.0895	+	-0.1541	13	-2341.2036	4708.6509	204.1346	0.0000
	-2.1012	NA	0.5939	NA	0.1069	NA	NA	NA	-0.1291	0.8899	0.0087	NA	NA	+	-0.1471	12	-2342.2332	4708.6751	204.1588	0.0000
4	-2.1396	NA	0.7514	-0.5330	-0.0170	NA	0.6535	-0.0427	-0.0864	0.1595	-0.0628	NA	NA	+	-0.0589	15	-1298.7528	2627.9979	0.0000	0.3309
	-2.1367	NA	0.7474	-0.5310	-0.0182	NA	0.6494	-0.0414	-0.0795	0.1659	NA	-0.0484	NA	+	-0.0624	15	-1298.9610	2628.4143	0.4164	0.2687
	-2.1408	NA	0.7494	-0.5306	-0.0173	NA	0.6591	-0.0414	-0.0868	0.1590	-0.0517	NA	0.0395	+	-0.0573	16	-1298.6334	2629.8254	1.8275	0.1327
	-2.1378	NA	0.7450	-0.5294	-0.0183	NA	0.6583	-0.0386	-0.0798	0.1640	NA	-0.0478	0.0589	+	-0.0601	16	-1298.6650	2629.8886	1.8907	0.1286
	-2.1378	-0.0503	0.7506	-0.5450	-0.0176	-0.0144	0.6700	-0.0405	-0.0811	0.1479	-0.0699	NA	NA	+	-0.0624	17	-1298.4850	2631.5989	3.6010	0.0547
	-2.1357	-0.0386	0.7467	-0.5399	-0.0189	-0.0141	0.6618	-0.0400	-0.0758	0.1572	NA	-0.0475	NA	+	-0.0652	17	-1298.7979	2632.2248	4.2270	0.0400
	-2.1389	-0.0457	0.7492	-0.5418	-0.0178	-0.0101	0.6729	-0.0398	-0.0819	0.1486	-0.0610	NA	0.0299	+	-0.0606	18	-1298.4203	2633.5443	5.5464	0.0207
	-2.1370	-0.0325	0.7446	-0.5365	-0.0188	-0.0063	0.6684	-0.0377	-0.0766	0.1569	NA	-0.0471	0.0546	+	-0.0622	18	-1298.5522	2633.8082	5.8103	0.0181

Model	(Intercept)	Age demonstrator	Age immature	Age:Proximity	Degree prox.	Demonstrator avail. (age)	Groom. allocation	Groom. amount	Nb. matriline	Prox. foraging	Rank difference	Rank immature	Sex demonstrator	Time period	Troop	df	log-Likelihood	AICc	Delta	Weight
	-2.1157	NA	0.8290	NA	-0.0304	NA	0.6544	-0.0884	-0.0963	0.4733	-0.0519	NA	NA	+	-0.0307	14	-1304.9682	2638.3668	10.3689	0.0019
	-2.1138	NA	0.8253	NA	-0.0313	NA	0.6512	-0.0872	-0.0909	0.4774	NA	-0.0379	NA	+	-0.0332	14	-1305.1242	2638.6786	10.6808	0.0016
	-2.1173	NA	0.8263	NA	-0.0309	NA	0.6610	-0.0866	-0.0968	0.4711	-0.0390	NA	0.0466	+	-0.0289	15	-1304.8004	2640.0931	12.0952	0.0008
	-2.1151	NA	0.8227	NA	-0.0315	NA	0.6605	-0.0841	-0.0912	0.4746	NA	-0.0376	0.0610	+	-0.0311	15	-1304.8033	2640.0989	12.1010	0.0008
	-2.1146	-0.0249	0.8295	NA	-0.0309	0.0010	0.6630	-0.0879	-0.0937	0.4706	-0.0557	NA	NA	+	-0.0315	16	-1304.8955	2642.3495	14.3516	0.0003
	-2.1133	-0.0156	0.8256	NA	-0.0317	0.0012	0.6566	-0.0870	-0.0894	0.4756	NA	-0.0374	NA	+	-0.0336	16	-1305.0942	2642.7470	14.7491	0.0002
	-2.1166	-0.0181	0.8269	NA	-0.0312	0.0074	0.6674	-0.0864	-0.0947	0.4690	-0.0425	NA	0.0447	+	-0.0291	17	-1304.7488	2644.1265	16.1286	0.0001
	-2.1150	-0.0089	0.8228	NA	-0.0317	0.0099	0.6641	-0.0841	-0.0902	0.4731	NA	-0.0373	0.0617	+	-0.0306	17	-1304.7772	2644.1833	16.1854	0.0001
	-2.1346	0.2290	0.6701	-0.5831	-0.0107	0.0322	NA	NA	-0.1224	0.5051	NA	-0.1086	NA	+	-0.0719	15	-1363.8013	2758.0950	130.0971	0.0000
	-2.1318	0.2159	0.6723	-0.5865	-0.0118	0.0194	NA	NA	-0.1205	0.5019	NA	-0.1078	-0.0811	+	-0.0763	16	-1363.3509	2759.2603	131.2624	0.0000
	-2.1436	0.2263	0.6691	-0.5767	-0.0095	0.0316	NA	NA	-0.1391	0.5015	-0.0141	NA	NA	+	-0.0628	15	-1364.8223	2760.1369	132.1391	0.0000
	-2.1393	0.2063	0.6735	-0.5845	-0.0103	0.0160	NA	NA	-0.1356	0.4964	-0.0437	NA	-0.1018	+	-0.0692	16	-1364.2011	2760.9607	132.9628	0.0000
	-2.1304	NA	0.6665	-0.6302	-0.0134	NA	NA	NA	-0.1140	0.4898	NA	-0.1087	NA	+	-0.0826	13	-1368.7051	2763.7829	135.7850	0.0000
	-2.1266	NA	0.6701	-0.6311	-0.0149	NA	NA	NA	-0.1120	0.4865	NA	-0.1078	-0.1210	+	-0.0868	14	-1367.7244	2763.8791	135.8812	0.0000
	-2.1324	NA	0.6739	-0.6304	-0.0121	NA	NA	NA	-0.1255	0.4804	-0.0878	NA	-0.1561	+	-0.0810	14	-1368.0434	2764.5171	136.5192	0.0000
	-2.1386	NA	0.6674	-0.6254	-0.0112	NA	NA	NA	-0.1295	0.4859	-0.0470	NA	NA	+	-0.0744	13	-1369.5129	2765.3984	137.4006	0.0000
	-2.1111	0.2538	0.7215	NA	-0.0226	0.0465	NA	NA	-0.1361	0.8456	NA	-0.0978	NA	+	-0.0430	14	-1370.9772	2770.3847	142.3868	0.0000
	-2.1083	0.2421	0.7236	NA	-0.0236	0.0350	NA	NA	-0.1346	0.8443	NA	-0.0969	-0.0738	+	-0.0467	15	-1370.6032	2771.6987	143.7009	0.0000
	-2.1197	0.2527	0.7193	NA	-0.0220	0.0457	NA	NA	-0.1525	0.8382	0.0006	NA	NA	+	-0.0346	14	-1371.8339	2772.0980	144.1002	0.0000
	-2.1156	0.2360	0.7232	NA	-0.0224	0.0327	NA	NA	-0.1487	0.8376	-0.0242	NA	-0.0862	+	-0.0396	15	-1371.3843	2773.2608	145.2630	0.0000
	-2.1038	NA	0.7212	NA	-0.0268	NA	NA	NA	-0.1278	0.8594	NA	-0.0959	NA	+	-0.0540	12	-1377.0193	2778.3577	150.3598	0.0000
	-2.0997	NA	0.7246	NA	-0.0281	NA	NA	NA	-0.1259	0.8564	NA	-0.0948	-0.1202	+	-0.0580	13	-1376.0625	2778.4976	150.4997	0.0000
	-2.1048	NA	0.7275	NA	-0.0259	NA	NA	NA	-0.1378	0.8505	-0.0737	NA	-0.1496	+	-0.0529	13	-1376.3679	2779.1083	151.1104	0.0000
	-2.1113	NA	0.7212	NA	-0.0252	NA	NA	NA	-0.1419	0.8531	-0.0354	NA	NA	+	-0.0468	12	-1377.7075	2779.7341	151.7362	0.0000

Table A3.11: The characteristics of each hypothesis H2 best model (scrounging: 3; other social learning behaviours: 4), including the number (Nb.) of parameters, the AICc value, the difference (delta) in AICc from the top model (lowest AICc), the likelihood, the log-likelihood, the Akaike weight, and the cumulative weight (sum).

Model	Nb. parameters	AICc	Delta	Likelihood	log-Likelihood	Weight	Cumulative weight
3	17	4504.5162	0.0000	1.0000	-2235.0528	0.5632	0.5632
	18	4505.6158	1.0995	0.5771	-2234.5782	0.3250	0.8882
	15	4508.7796	4.2633	0.1186	-2239.2289	0.0668	0.9550
	16	4509.5705	5.0542	0.0799	-2238.6028	0.0450	1.0000
4	15	2627.9979	0.0000	1.0000	-1298.7528	0.3328	0.3328
	15	2628.4143	0.4164	0.8120	-1298.9610	0.2702	0.6030
	16	2629.8254	1.8275	0.4010	-1298.6334	0.1335	0.7365
	16	2629.8886	1.8907	0.3885	-1298.6650	0.1293	0.8658
	17	2631.5989	3.6010	0.1652	-1298.4850	0.0550	0.9208
	17	2632.2248	4.2270	0.1208	-1298.7979	0.0402	0.9610
	18	2633.5443	5.5464	0.0625	-1298.4203	0.0208	0.9818
	18	2633.8082	5.8103	0.0547	-1298.5522	0.0182	1.0000

Table A3.12: Variables' relative importance (RVI; 1 = highest) for hypothesis H2 averaged models (scrounging: 3; other social learning behaviours: 4), including immatures' age, (relative) rank, proximity (prox.) degree, number (Nb.) of matriline members, and total grooming (Groom.) amount; demonstrators' age, sex (male), and their age availability (avail.); a (immature-demonstrator) dyad's grooming allocation, proximity in the foraging network, and (relative) rank difference; time period and troop.

Model	Variable	RVI	Model	Variable	RVI
3	Age demonstrator	0.89	4	Age demonstrator	0.13
	Age immature	1.00		Age immature	1.00
	Age:Proximity	1.00		Age:Proximity	1.00
	Degree prox.	1.00		Degree prox.	1.00
	Demonstrator avail. (age)	0.89		Demonstrator avail. (age)	0.13
	Groom. allocation	1.00		Groom. allocation	1.00
	Groom. amount	1.00		Groom. amount	1.00
	Nb. matriline	1.00		Nb. matriline	1.00
	Prox. foraging	1.00		Prox. foraging	1.00
	Rank immature	1.00		Rank difference	0.54
	Sex demonstrator	0.37		Rank immature	0.46
	Time period	1.00		Sex demonstrator	0.30
	Troop	1.00		Time period	1.00
				Troop	1.00

3.8 MODELS' NUMBER OF OBSERVATIONS AND SAMPLE SIZE

The number of observations and the sample size for each hypothesis H1 and H2 model are shown in Table A3.13. Individuals include the immatures, their mothers, and, for H2 models, the demonstrators (see Chapter 4, §4.3).

Table A3.13: Number (Nb.) of observations and individuals sampled for each hypothesis H1 (Models 1 and 2) and H2 (overall: Models 3 and 4; and by sex: Models 3.1 and 4.1 for females, and 3.2 and 4.2 for males) model.

Model	Immatures	Mothers	Demonstrators	Nb. observations
1	53	38	-	4511
2				
3	52	37	142	1508
3.1	33	29	139	938
3.2	19	17	132	570
4	53	38	137	991
4.1	34	30	130	632
4.2	19	17	118	359

3.9 FULL MODEL RESULTS' TABLES

Here we present the full tables (i.e., with all the independent variables) for hypothesis H1 and H2 averaged models' results. Table A3.14 shows H1 models' (1 and 2) results and Table A3.15 their predicted values divided by sex during two age stages (see Chapter 4, §4.3). Table A3.16 displays H2 models' (3 and 4) results. Figure A3.6 includes trends for H2 models' significant variables of interest. Figures A3.7 and A3.8 show the distributions of demonstrator-immature age differences and immature-demonstrator relative rank differences, respectively. These distributions both peaked around zero, indicating a preference for demonstrators of similar age and rank. Finally, Table A3.17 and Figure A3.9 present the results of an alternative scrounging model to check for circularity because scrounging (foraging within 1 m) was predicted by a dyad's proximity during foraging. The model featured a dyad's proximity outside of a foraging context as a fixed factor instead of proximity during foraging (the two ego-networks were positively correlated; Spearman's rank correlation: 0.33, p -value = < 0.001). The results of this additional scrounging model were qualitatively similar to those of the main model (see Chapter 4, §4.4.2).

Table A3.14: Hypothesis H1 averaged models' results. Variables include immatures' linear and quadratic age, sex, age-sex interactions ('·'), and (relative) rank; observation (Obs.) length, time period, and troop. The values reported for sex refer to males. For each variable/ model are shown the estimate, the standard (Std.) error, the z value, the p -value, the coefficient of determination (conditional, delta R^2), the odds ratio (OR), the lower (LCI) and upper (UCI) 97.5% confidence intervals, and the percentage change in the odds of scrounging (Model 1) or performing other social learning behaviours (Model 2) at the increase of one unit in the independent variable.

Model	Variable	Estimate	Std. Error	z value	p -value	R^2	OR	LCI	UCI	Percentage change
1	(Intercept)	-3.2961	0.3198	10.3059	0.0000	0.11	0.04	0.02	0.08	-96.30
	Age immature	-11.3419	4.7092	-2.4085	0.0160		0.00	0.00	0.46	-100.00
	Age:Sex	1.1684	7.4901	0.1560	0.8760		3.22	0.00	6.29E+07	221.69
	Age ² immature	-18.6803	3.9576	-4.7201	0.0000		0.00	0.00	0.00	-100.00
	Age ² :Sex	6.3010	6.2056	1.0154	0.3099		545.09	0.00	5.99E+08	5.44E+04
	Obs. length	0.0009	0.0002	3.7938	0.0001		1.00	1.00	1.00	0.09

Model	Variable	Estimate	Std. Error	z value	p-value	R ²	OR	LCI	UCI	Percentage change
	Rank immature	0.7648	0.2262	3.3805	0.0007		2.15	1.29	3.57	114.85
	Sex immature	0.0116	0.1176	0.0987	0.9214		1.01	0.78	1.32	1.17
	Time period 2	0.8902	0.0865	10.2925	0.0000		2.44	2.01	2.96	143.55
	Time period 3	1.7779	0.1028	17.2865	0.0000		5.92	4.70	7.45	491.71
	Troop	0.2387	0.1166	2.0461	0.0407		1.27	0.98	1.65	26.96
2	(Intercept)	-3.0928	0.3400	-9.0964	0.0000	0.04	0.05	0.02	0.10	-95.46
	Age immature	-16.1940	3.7098	-4.3652	0.0000		0.00	0.00	0.00	-100.00
	Age:Sex	-11.8188	6.0851	-1.9422	0.0521		0.00	0.00	6.17	-100.00
	Age ² immature	-3.9443	3.4911	-1.1298	0.2586		0.02	0.00	48.46	-98.06
	Age ² :Sex	1.6544	5.7195	0.2893	0.7724		5.23	0.00	1.93E+06	423.00
	Obs. length	0.0013	0.0003	4.9942	0.0000		1.00	1.00	1.00	0.13
	Rank immature	0.1907	0.1877	1.0159	0.3097		1.21	0.79	1.84	21.01
	Sex immature	-0.0601	0.0932	-0.6456	0.5186		0.94	0.76	1.16	-5.84
	Time period 2	-0.0456	0.0844	-0.5404	0.5889		0.96	0.79	1.15	-4.46
	Time period 3	0.2805	0.1003	2.7958	0.0052		1.32	1.06	1.66	32.37
	Troop	0.2100	0.0922	2.2781	0.0227		1.23	1.00	1.52	23.36

Table A3.15: Hypothesis H1 predicted odds ratio (OR) values for scrounging (Model 1) and the other social learning behaviours (Model 2) during two age periods (1 and 4 years old), divided by sex. For each model and sex, the percentage change in odds between 1–4 years old is shown.

Model	Year	Sex	OR	Percentage change
1	1	Female	0.18	-41.83
	4		0.10	
	1	Male	0.17	-35.63
	4		0.11	
2	1	Female	0.30	-41.56
	4		0.17	
	1	Male	0.33	-58.61
	4		0.14	

Table A3.16: Hypothesis H2 averaged models' results. Variables include immatures' age, (relative) rank, proximity (prox.) degree, number (Nb.) of matriline members, and total grooming (Groom.) amount; demonstrators' age, sex, and their age availability (avail.); a (immature-demonstrator) dyad's grooming allocation, proximity in the foraging network, and (relative) rank difference; time period and troop. The values reported for sex refer to males. For each variable/model are shown the estimate, the standard (Std.) error, the z value, the *p*-value, the odds ratio (OR), the lower (LCI) and upper (UCI) 97.5% confidence intervals, and the percentage change in the odds of scrounging (Model 3) or performing other social learning behaviours (Model 4) at the increase of one standard deviation in the independent variable.

Model	Variable	Estimate	Std. Error	z value	<i>p</i> -value	OR	LCI	UCI	Percentage change
3	(Intercept)	-2.1833	0.0606	36.0024	0.0000	0.11	0.10	0.13	-88.73
	Age demonstrator	-0.1238	0.0642	1.9275	0.0539	0.88	0.79	0.96	-11.65
	Age immature	0.5975	0.0652	9.1520	0.0000	1.82	1.60	2.07	81.75
	Age:Proximity	-0.5542	0.1050	5.2755	0.0000	0.57	0.47	0.71	-42.55
	Degree prox.	0.0499	0.0490	1.0195	0.3080	1.05	0.96	1.16	5.12
	Demonstrator avail. (age)	0.0037	0.0446	0.0836	0.9334	1.00	0.92	1.10	0.37
	Groom. allocation	0.5049	0.0417	12.1068	0.0000	1.66	1.53	1.80	65.68
	Groom. amount	0.0257	0.0593	0.4339	0.6643	1.03	0.91	1.15	2.61
	Nb. matriline	-0.0569	0.0631	0.9010	0.3676	0.94	0.83	1.07	-5.53
	Prox. foraging	0.4776	0.0634	7.5235	0.0000	1.61	1.42	1.83	61.22
	Rank immature	-0.2752	0.0661	4.1609	0.0000	0.76	0.67	0.86	-24.06
	Sex demonstrator	0.0191	0.0400	0.4759	0.6342	1.02	0.95	1.16	1.92
	Time period 2	-0.4848	0.0621	7.8051	0.0000	0.62	0.55	0.70	-38.42
	Time period 3	-0.7322	0.0685	10.6730	0.0000	0.48	0.42	0.55	-51.92
	Troop	-0.1457	0.0711	2.0475	0.0406	0.86	0.75	0.99	-13.56
4	(Intercept)	-2.1384	0.0547	39.0289	0.0000	0.12	0.11	0.13	-88.22
	Age demonstrator	-0.0059	0.0294	0.1992	0.8421	0.99	0.84	1.10	-0.58
	Age immature	0.7488	0.0852	8.7773	0.0000	2.11	1.79	2.50	111.45
	Age:Proximity	-0.5329	0.1539	3.4580	0.0005	0.59	0.43	0.79	-41.31
	Degree prox.	-0.0177	0.0642	0.2750	0.7833	0.98	0.87	1.11	-1.75
	Demonstrator avail. (age)	-0.0017	0.0252	0.0668	0.9467	1.00	0.86	1.13	-0.17
	Groom. allocation	0.6557	0.0519	12.6292	0.0000	1.93	1.74	2.13	92.64
	Groom. amount	-0.0413	0.0768	0.5362	0.5918	0.96	0.83	1.12	-4.04
	Nb. matriline	-0.0827	0.0654	1.2636	0.2064	0.92	0.81	1.05	-7.94
	Prox. foraging	0.1608	0.1067	1.5049	0.1323	1.17	0.95	1.45	17.44
	Rank difference	-0.0329	0.0580	0.5669	0.5708	0.97	0.82	1.07	-3.24
	Rank immature	-0.0220	0.0527	0.4171	0.6766	0.98	0.83	1.09	-2.18
	Sex demonstrator	0.0145	0.0489	0.2962	0.7671	1.01	0.90	1.23	1.46
	Time period 2	-0.0625	0.0683	0.9135	0.3610	0.94	0.82	1.07	-6.06
	Time period 3	0.1122	0.0836	1.3402	0.1802	1.12	0.95	1.32	11.88
	Troop	-0.0603	0.0742	0.8118	0.4169	0.94	0.81	1.09	-5.85

Figure A3.6: Hypothesis H2 averaged models' significant results (plus demonstrators' age – marginally significant) for scrounging (left) and the other social learning behaviours (right). The plots in different rows show the changes in the odds of learning from a certain demonstrator with (1st) immatures' age (at different immature-demonstrator proximity association levels during foraging), (2nd) a (immature-demonstrator) dyad's grooming allocation, (3rd) proximity during foraging (at different immatures' age stages), (4th) demonstrators' age, and (5th) immatures' (relative) rank. Higher odds ratios mean a relatively higher likelihood of an event (y-axis variable) to occur. Ribbons represent 97.5% confidence intervals.

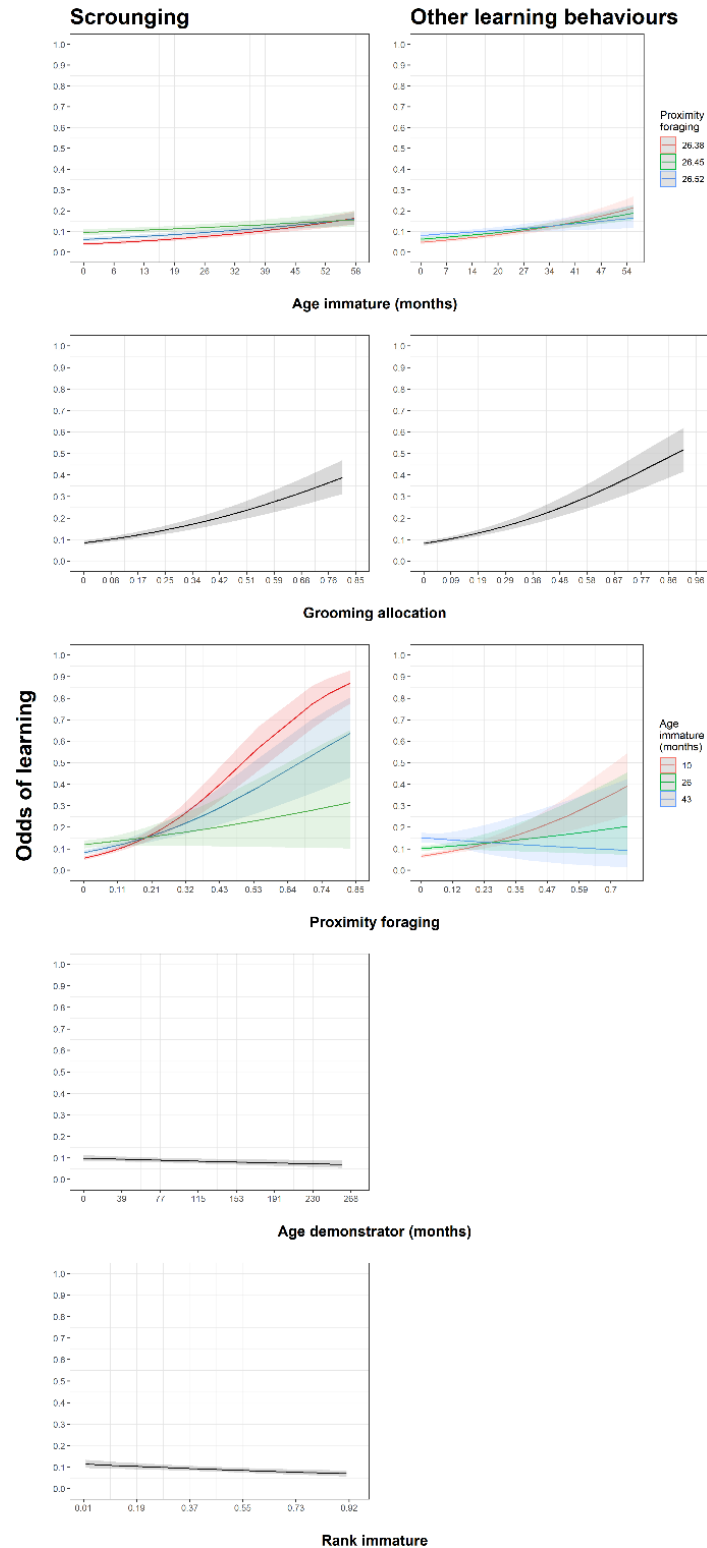


Figure A3.7: Distribution of demonstrator-immature age differences for scrounging (left) and the other social learning behaviours (right).

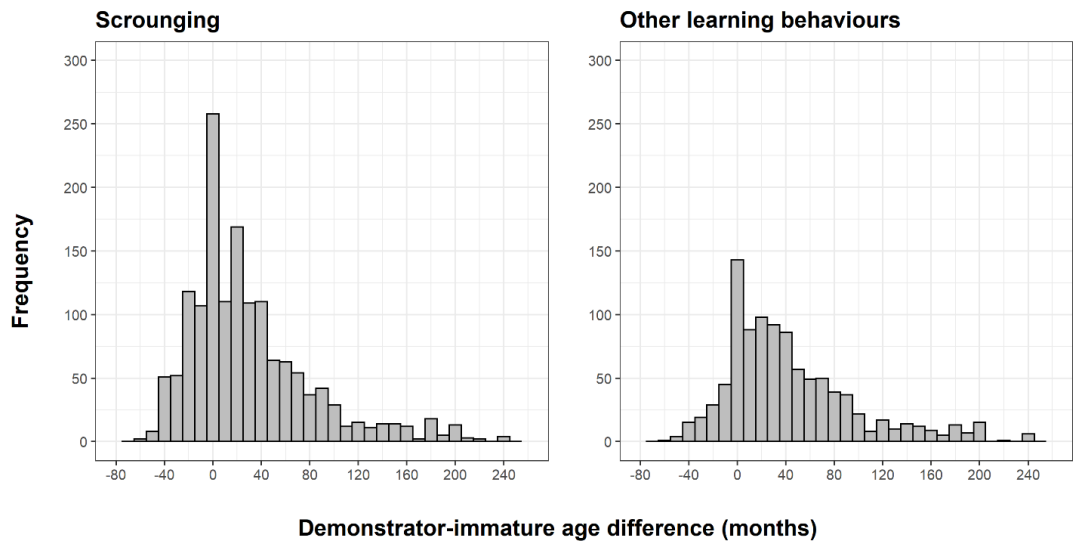


Figure A3.8: Distribution of immature-demonstrator (relative) rank differences for scrounging (left) and the other social learning behaviours (right).

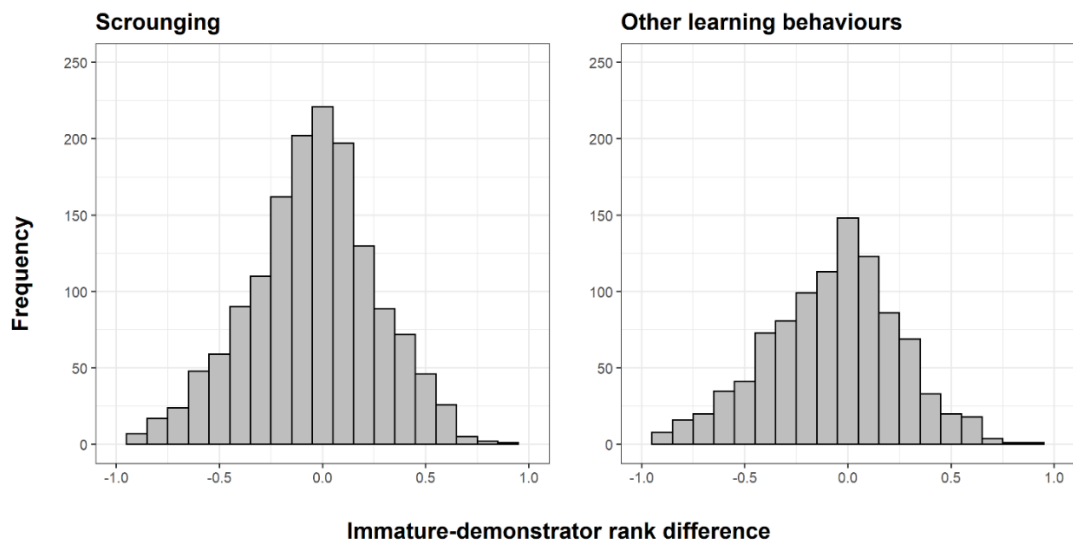
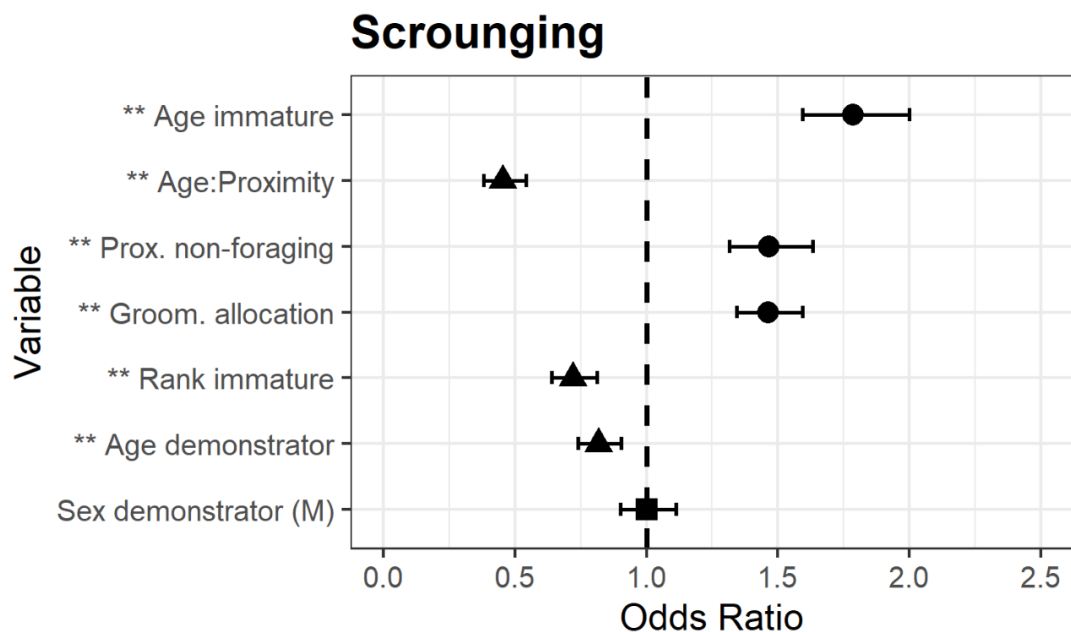


Table A3.17: Alternative scrounging averaged model's results. Variables include immatures' age, (relative) rank, proximity (prox.) degree, number (Nb.) of matriline members, and total grooming (Groom.) amount; demonstrators' age, sex, and their age availability (avail.); a (immature-demonstrator) dyad's grooming allocation, proximity in the non-foraging network, and (relative) rank difference; time period and troop. The values reported for Sex refer to males. For each variable/ model are shown the estimate, the standard (Std.) error, the z value, the *p*-value, the odds ratio (OR), the lower (LCI) and upper (UCI) 97.5% confidence intervals, and the percentage change in the odds of scrounging at the increase of one standard deviation in the independent variable.

Variable	Estimate	Std. Error	z value	<i>p</i> -value	OR	LCI	UCI	Percentage change
(Intercept)	-2.2197	0.0593	37.3787	< 0.001	0.11	0.10	0.12	-89.14
Age demonstrator	-0.2004	0.0507	3.9485	< 0.001	0.82	0.74	0.90	-18.16

Variable	Estimate	Std. Error	z value	p-value	OR	LCI	UCI	Percentage change
Age immature	0.5798	0.0576	10.0646	< 0.001	1.79	1.60	2.00	78.57
Age:Proximity	-0.7898	0.0914	8.6379	< 0.001	0.45	0.38	0.54	-54.61
Degree prox.	0.1013	0.0461	2.1943	< 0.05	1.11	1.01	1.21	10.66
Demonstrator avail. (age)	-0.0015	0.0490	0.0315	NS	1.00	0.91	1.10	-0.15
Groom. allocation	0.3798	0.0437	8.6918	< 0.001	1.46	1.34	1.59	46.20
Groom. amount	0.0383	0.0547	0.6996	NS	1.04	0.93	1.16	3.91
Nb. matriline	-0.0218	0.0617	0.3525	NS	0.98	0.87	1.10	-2.15
Prox. non-foraging	0.3827	0.0552	6.9292	< 0.001	1.47	1.32	1.63	46.63
Rank immature	-0.3276	0.0601	5.4445	< 0.001	0.72	0.64	0.81	-27.94
Sex demonstrator	0.0005	0.0277	0.0179	NS	1.00	0.90	1.11	0.05
Time period 2	-0.4514	0.0618	7.3009	< 0.001	0.64	0.56	0.72	-36.33
Time period 3	-0.7583	0.0653	11.6049	< 0.001	0.47	0.41	0.53	-53.15
Troop	-0.2504	0.0690	3.6261	< 0.001	0.78	0.68	0.89	-22.15

Figure A3.9: Alternative scrounging averaged model's results. The variables of interest include immatures' age and (relative) rank; demonstrators' age and sex (male); a (immature-demonstrator) dyad's grooming (Groom.) allocation, proximity (Prox.) in the non-foraging network, and (relative) rank difference. Independent variables' points represent odds ratios and whiskers are 97.5% confidence intervals (CIs). Points have different shapes depending on whether their CIs overlap with 1 (the odds of learning from a certain model – response – does not change at the increase in the independent variable), they are < 1 (the response decreases at the increase in the independent variable), or they are > 1 (the response increases at the increase in the independent variable). Variables are ordered based on effect size and significance ('***' = significant).



3.10 H1 MODELS' STANDARDISED ESTIMATES

For hypothesis H1, we derived standardised variables' estimates (i.e., all variables on the same scale) within each model in order to compare the effect sizes of immatures' characteristics on the presence of social learning behaviours (see Chapter 4, §4.4.1 and §4.5). We used the package *SemEff* (Murphy 2022) and the function *StdEff* to calculate standardised estimates. Among the significant effects for scrounging, the effect of (relative) rank was the strongest, followed by age. The quadratic effect of age and especially its interaction with sex were greater than the linear counterparts. For the other social learning behaviours, linear age had the strongest effect. The interaction between linear age and sex (marginally significant) had a slightly lower effect than rank (not significant), whose effect followed in size that of linear age (Table A3.18).

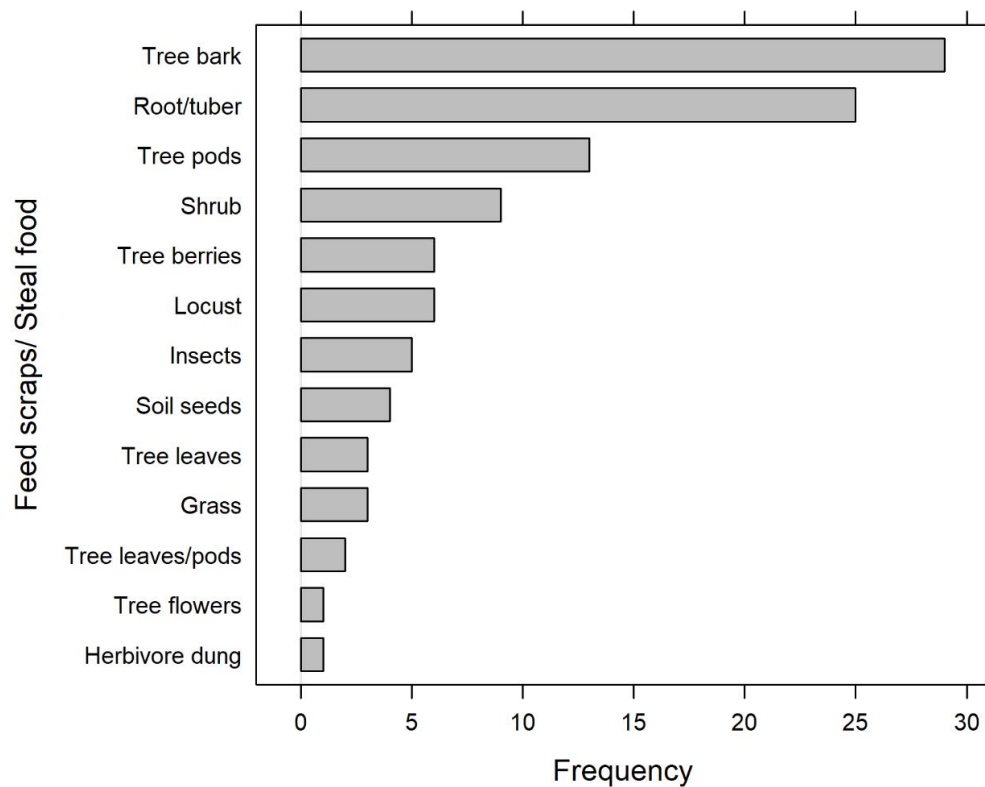
Table A3.18: Standardised estimates (absolute values) of hypothesis H1 models' variables of interest ('***' = significant; '**' = marginally significant), for scrounging (Model 1) and the other social learning behaviours (Model 2). Variables include immatures' linear and quadratic age, sex, age-sex interactions ('.'), and (relative) rank. The values reported for sex refer to males. The colour scale ranges from lower (red) to higher (green) values.

Model	Age immature	Age:Sex	Age ² immature	Age ² :Sex	Rank immature	Sex immature
1	0.0030**	0.0002	0.0045**	0.0025	0.0093**	0.0003
2	0.0063**	0.0017*	0.0010	0.0007	0.0025	0.0017

3.11 SOCIAL LEARNING ON DIFFERENT FOOD TYPES

The food types involved in social learning through feeding on others' scraps and stealing food from others are shown in Figure A3.10. The most frequent food types gained from others during focal observations were tree bark, roots, and tubers. These may be difficult to access for infants and young juveniles due to the strength required in extracting them.

Figure A3.10: Feed scraps and steal food social learning behaviours directed at different food types during focal observations.

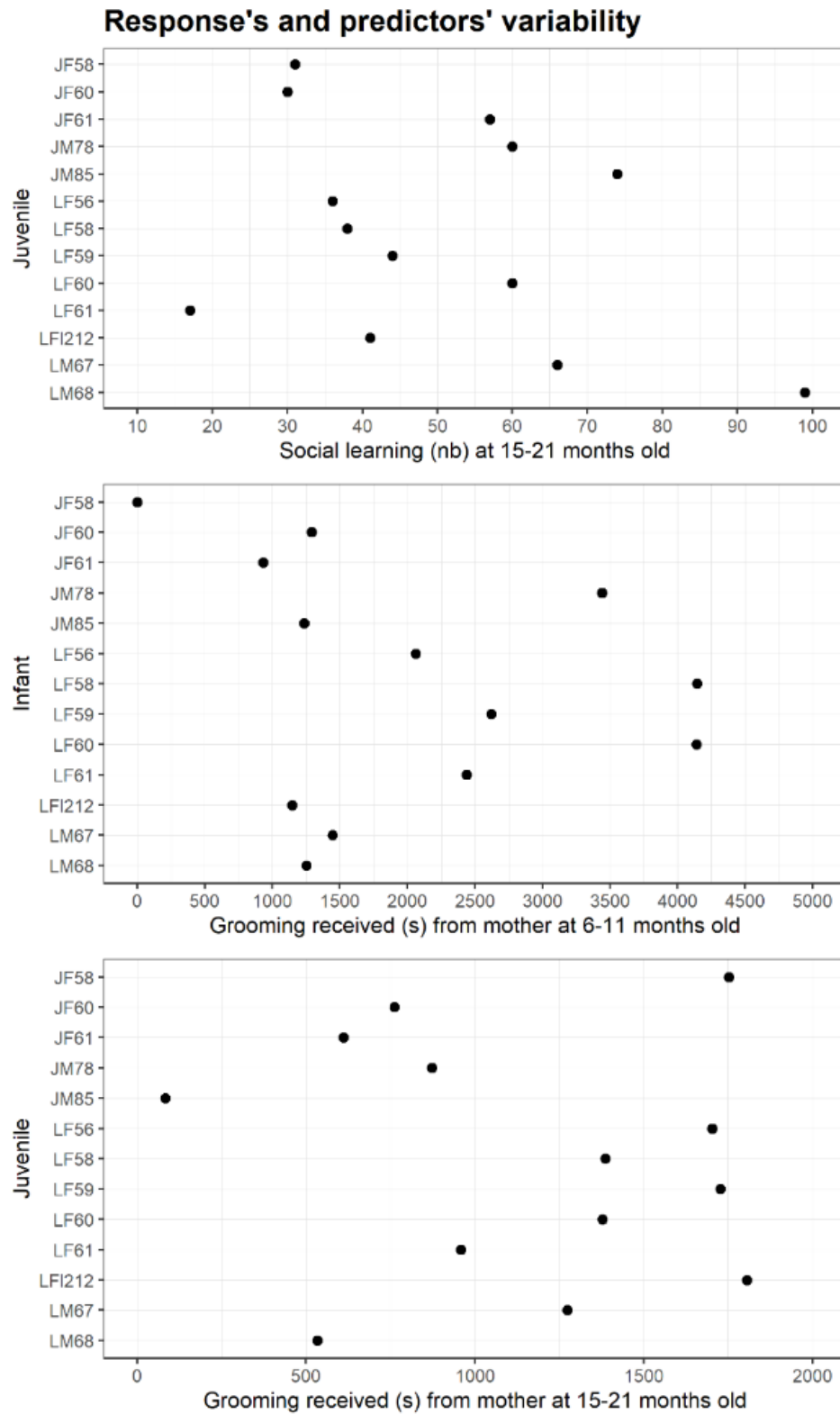


4 APPENDIX 4: THE ROLE OF MATERNAL WARMTH ON SOCIAL INFORMATION ACQUISITION IN WILD BABOONS

4.1 RESPONSE AND PREDICTORS

The between-immature variability in the raw number of juveniles' (15–21 months of age) social learning behaviours (response – dependent – variable; modelled as social learning rate) and the raw duration of grooming received from the mother (modelled as the proportion of grooming over the total focal observation time) during infancy (6–11 months of age) and juvenescence (predictor variables) are shown in Figure A4.1. The number of social learning behaviours during juvenescence ranged between 17–99 with a mean of 50.23. The duration of grooming received from the mother during infancy ranged between 0–4144 s with a mean of 2011.69 s, while the duration of grooming during juvenescence ranged between 83–1806 s with a mean of 1142.23 s. While maternal grooming received during juvenescence was mostly recorded during winter 2022 (all immatures but one individual sampled in summer 2021), grooming received during infancy was collected both in winter 2021 (8 individuals) and in summer 2021 (5 individuals). The mean proportion of time immatures were groomed by their mothers (over the total observation time) did not differ significantly between winter and summer 2021 in our dataset ($N = 13$; two-sided t -test: $t = 0.37$, degrees of freedom = 8.08, p -value = 0.72).

Figure A4.1: Between-immature variability in the number (nb) of juveniles' (15–21 months of age) social learning behaviours and the grooming received (in seconds) from the mother during infancy (6–11 months of age) and juvenescence. The y-axis represents the different immature study subjects by individual code (troop – sex ('F' = female; 'M' = male) – sequential number ('I' plus '21' and number for unmarked infants born in 2021)).



4.2 VARIABLE CORRELATIONS

The Pearson's correlation coefficients (r) between the models' independent variables are presented in Table A4.1. Variables with $r \geq 0.5$ were not included in the same model (see Chapter 5, §5.3). Specifically, juveniles' grooming network centrality was not inserted together with their relative dominance rank; the proportion of grooming received by the mother during juvenescence (duration over the total focal observation time) was not inserted together with juveniles' rank and troop; juveniles' number of maternal siblings was not inserted together with their proportion of time spent in proximity (5 m) to the mother; and the latter was also not inserted together with troop.

Table A4.1: Pearson's correlation coefficients (absolute values) between the models' independent variables, including immatures' grooming (Groom.) and proximity (Prox.) centrality during juvenescence (15–21 months of age), proportion of grooming (duration over total focal observation time) received from the mother during infancy (#1; 6–11 months of age) and juvenescence (#2), number (Nb.) of siblings (juvenescence), proportion (Prop.) of time spent in proximity (5 m) to the mother (juvenescence), and (relative) rank (juvenescence); troop. The colour scale represents a range from lower (red) to higher (green) correlation values.

Variable	Groom. centrality	Groom. received #1	Groom. received #2	Nb. siblings	Prop. time with mother	Prox. centrality	Rank immature	Troop
Groom. centrality	1.0	0.2	0.2	0.1	0.4	0.3	0.9	0.2
Groom. received #1	0.2	1.0	0.1	0.0	0.1	0.0	0.2	0.4
Groom. received #2	0.2	0.1	1.0	0.4	0.4	0.3	0.5	0.5
Nb. siblings	0.1	0.0	0.4	1.0	0.5	0.1	0.2	0.2
Prop. time with mother	0.4	0.1	0.4	0.5	1.0	0.1	0.2	0.7
Prox. centrality	0.3	0.0	0.3	0.1	0.1	1.0	0.4	0.4
Rank immature	0.9	0.2	0.5	0.2	0.2	0.4	1.0	0.0
Troop	0.2	0.4	0.5	0.2	0.7	0.4	0.0	1.0

4.3 MODEL SET

Here we present the model set and the characteristics of the best models. Table A4.2 shows the set of biologically plausible candidate models (31). Table A4.3 presents the characteristics of the best models (six) derived with the package *AICcmodavg* (Mazerolle 2023) and the function *aictab* (see Chapter 5, §5.3).

Table A4.2: Full model set showing all possible combinations of models (on rows; green = variable included; NA = variable excluded) including up to two of the following variables: immatures' grooming (Groom.) and proximity (Prox.) centrality during juvenescence (15–21 months of age), proportion of grooming (duration over total focal observation time) received from the mother during infancy (#1; 6–11 months of age) and juvenescence (#2), proportion (Prop.) of time spent in proximity (5 m) to the mother (juvenescence), number (Nb.) of siblings (juvenescence), and (relative) rank (juvenescence); troop. The models' parameters shown are the degrees of freedom (df), the log-likelihood, the AICc value, the difference (delta) in AICc from the top model (lowest AICc), and the Akaike weight. The best models are indicated by the AICc weights (sum < 0.95) in bold (1–6), including models with $\Delta\text{AICc} < 7$ (1–4).

Model	(Intercept)	Groom. centrality	Groom. received #1	Groom. received #2	Nb. siblings	Prop. time with mother	Prox. centrality	Rank immature	Troop	Offset	df	log-Likelihood	AICc	Delta	Weight
1	-7.6631	NA	NA	NA	0.1871	NA	NA	1.0643	NA	+	4	-49.9216	112.8432	0.0000	0.5708
2	-7.7000	0.2140	NA	NA	0.2399	NA	NA	NA	NA	+	4	-50.6457	114.2915	1.4483	0.2767
3	-7.4974	NA	NA	NA	0.2155	NA	NA	NA	NA	+	3	-54.6295	117.9257	5.0825	0.0450
4	-6.8394	NA	NA	NA	NA	NA	NA	1.2355	NA	+	3	-54.8820	118.4307	5.5876	0.0349
5	-7.5495	NA	NA	NA	0.2113	NA	0.1442	NA	NA	+	4	-53.9273	120.8545	8.0114	0.0104
6	-7.1754	NA	NA	-5.4828	0.1841	NA	NA	NA	NA	+	4	-54.2882	121.5765	8.7333	0.0072
7	-6.4755	NA	NA	NA	NA	-1.8870	NA	1.3048	NA	+	4	-54.3949	121.7897	8.9466	0.0065
8	-6.0767	NA	NA	-13.0043	NA	NA	NA	NA	NA	+	3	-56.6765	122.0197	9.1765	0.0058
9	-6.7251	NA	-2.9090	NA	NA	NA	NA	1.2884	NA	+	4	-54.5456	122.0911	9.2479	0.0056
10	-7.6169	NA	NA	NA	0.2201	NA	NA	NA	0.0612	+	4	-54.5826	122.1652	9.3221	0.0054
11	-7.4938	NA	-0.0651	NA	0.2154	NA	NA	NA	NA	+	4	-54.6294	122.2587	9.4155	0.0052
12	-6.8485	NA	NA	NA	NA	NA	0.0586	1.1614	NA	+	4	-54.7883	122.5766	9.7335	0.0044
13	-6.5681	0.1809	NA	NA	NA	NA	NA	NA	NA	+	3	-56.9694	122.6054	9.7622	0.0043
14	-6.7621	NA	NA	NA	NA	NA	NA	1.2285	-0.0469	+	4	-54.8541	122.7081	9.8649	0.0041
15	-6.5834	NA	NA	NA	NA	NA	0.1809	NA	NA	+	3	-57.6394	123.9454	11.1023	0.0022

Model	(Intercept)	Groom. centrality	Groom. received #1	Groom. received #2	Nb. siblings	Prop. time with mother	Prox. centrality	Rank immature	Troop	Offset	df	log-Likelihood	AICc	Delta	Weight
16	-6.2104	0.1348	NA	-10.6001	NA	NA	NA	NA	NA	+	4	-55.8090	124.6181	11.7749	0.0016
17	-6.4361	NA	-1.2853	NA	NA	NA	NA	NA	NA	+	3	-58.2162	125.0991	12.2559	0.0012
18	-6.3850	NA	NA	NA	NA	-0.5305	NA	NA	NA	+	3	-58.2314	125.1295	12.2863	0.0012
19	-6.4046	NA	NA	NA	NA	NA	NA	NA	-0.0549	+	3	-58.2328	125.1322	12.2890	0.0012
20	-6.0517	0.2327	NA	NA	NA	-2.6427	NA	NA	NA	+	4	-56.3708	125.7417	12.8985	0.0009
21	-6.6324	0.1633	NA	NA	NA	NA	0.1423	NA	NA	+	4	-56.5000	126.0001	13.1569	0.0008
22	-6.1707	NA	NA	-11.4525	NA	NA	0.0884	NA	NA	+	4	-56.5208	126.0416	13.1984	0.0008
23	-6.2376	NA	NA	-14.0163	NA	0.9492	NA	NA	NA	+	4	-56.5928	126.1857	13.3425	0.0007
24	-6.0867	NA	0.2846	-13.0876	NA	NA	NA	NA	NA	+	4	-56.6740	126.3480	13.5048	0.0007
25	-6.4510	0.1913	-2.7463	NA	NA	NA	NA	NA	NA	+	4	-56.7600	126.5200	13.6769	0.0006
26	-6.3475	0.1920	NA	NA	NA	NA	NA	NA	-0.1401	+	4	-56.7900	126.5800	13.7368	0.0006
27	-6.8461	NA	NA	NA	NA	NA	0.2335	NA	0.1468	+	4	-57.5143	128.0287	15.1855	0.0003
28	-6.5143	NA	-1.5964	NA	NA	NA	0.1842	NA	NA	+	4	-57.5722	128.1444	15.3012	0.0003
29	-6.6215	NA	NA	NA	NA	0.1795	0.1841	NA	NA	+	4	-57.6365	128.2731	15.4299	0.0003
30	-6.3493	NA	-1.1729	NA	NA	-0.4504	NA	NA	NA	+	4	-58.1988	129.3976	16.5544	0.0001
31	-6.3864	NA	-1.0863	NA	NA	NA	NA	NA	-0.0363	+	4	-58.2070	129.4140	16.5709	0.0001

Table A4.3: The characteristics of each best model, including the number (Nb.) of parameters, the AICc value, the difference (delta) in AICc from the top model (lowest AICc), the likelihood, the log-likelihood, the Akaike weight, and the cumulative weight (sum).

Model	Nb. parameters	AICc	Delta	Likelihood	log- Likelihood	Weight	Cumulative weight
1	4	112.8432	0.0000	1.0000	-49.9216	0.6040	0.6040
2	4	114.2915	1.4483	0.4847	-50.6457	0.2928	0.8968
3	3	117.9257	5.0825	0.0788	-54.6295	0.0476	0.9444
4	3	118.4307	5.5876	0.0612	-54.8820	0.0370	0.9813
5	4	120.8545	8.0114	0.0182	-53.9273	0.0110	0.9923
6	4	121.5765	8.7333	0.0127	-54.2882	0.0077	1.0000

4.4 MODELS' STANDARDISED ESTIMATES

We derived standardised estimates (i.e., all variables on the same scale) for the variables included in the best models in order to compare the effect sizes of juveniles' (15–21 months of age) characteristics (see below) and the proportion of grooming received from the mother (duration over the total focal observation time) during juvenescence on juveniles' social learning rate (see Chapter 5, §5.4 and §5.5). We used the package *SemEff* (Murphy 2022) and the function *StdEff* to calculate standardised estimates. Because the models have all the same dependent variable and are run on the same dataset, effect sizes could be compared both within and across models (George *et al.* 2020). Among the significant variables, the juveniles' number of maternal siblings in the troop had, in general, the strongest effect and was included in five out of six best models. The number of siblings was followed by juveniles' relative dominance rank (included in two best models), and then by grooming network centrality (included in one best model). Juveniles' centrality in the proximity network and maternal grooming were each included in one best model with non-significant (and weakest) effects (Table A4.4).

Table A4.4: Standardized estimates (absolute values) of the best models' variables ('***' = significant), including juveniles' (15–21 months of age) grooming (Groom.) and proximity (Prox.) centrality, proportion of grooming received from the mother (#2; duration over total focal observation time), number (Nb.) of siblings, and (relative) rank. The colour scale ranges from lower (red) to higher (green) values.

Model	Groom. centrality	Groom. received #2	Nb. siblings	Prox. centrality	Rank immature
1	-	-	0.5390 **	-	0.4918 **
2	0.4664 **	-	0.6959 **	-	-
3	-	-	0.6308 **	-	-
4	-	-	-	-	0.5799 **
5	-	-	0.6153 **	0.2404	-
6	-	0.1600	0.4875 **	-	-

5 APPENDIX 5: A ‘THANK YOU’ TO THE IMMATURE STUDY SUBJECTS

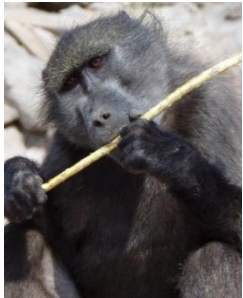
This section serves as a special ‘thank you’ to the main subjects of this study: the immature individuals of troops J and L living at Tsaobis. I collected portrait pictures of all the immatures followed, divided into four tables (Tables A5.1–A5.4) based on troop and sex. Although some individuals grew up a lot during the study period (from pink infants to young juveniles), each picture is taken approx. within the age class they have been observed the most. Individuals are ordered based on their age class and their (secret) field names. At the end of each table are the ‘pink beauties’ (the infants followed only when they were pink). Some of the immatures shown here have sadly disappeared (☹️). Part of the pictures were kindly provided by my fellow field mates (name present below each picture if not my own).

Table A5.1: J troop immature females.

		
JF59 ☹️	JF60	JF66
		

JF58	JF61	JF52 (left)
		
JF53 (Jules Dezeure)	JF56	JF51
		
JF57	JF50	JF64
		
JFI211 		

Table A5.2: J troop immature males.

		
JM85	JM78	JM69
		
JM79	JM74	JM75

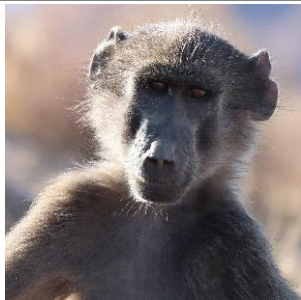
		
JM76	JM81	MM01 (Axelle Delaunay)
		
JM80	JM77	

Table A5.3: L troop immature females.

		
LF61	LF52	LF58 (Axelle Delaunay)
		
LF53 (left)  (Elisa Fernández-Fueyo)	LF60 (Axelle Delaunay)	LF59

		
LF56	LF1212 (Axelle Delaunay)	LF51 (Axelle Delaunay)
		
LF41 (Axelle Delaunay)	LF48	LF54
		
LF62  (Ben Kawam)	LF46 (Jules Dezeure)	LF55
		
LF47	LF44	LF42 (Ben Kawam)
		
LF50 (Axelle Delaunay)	LF1211	

Table A5.4: L troop immature males.

		
LM68 (Axelle Delaunay)	LM66 (Axelle Delaunay)	LM67 (Axelle Delaunay)
		
LM59	LM65	LM64
		
LM60 (Axelle Delaunay)	LMI211	LMI212