Kinship and sociality in wild Assamese macaques (*Macaca assamensis*): are they related?

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When I reached the sleep tree, the time was 5:50 am and our friends had begun moving already up the canopy. All 54 monkeys in the troop slept on the same tree, most of the sleep trees are a fig tree nearby a creek. I prepared the radio, GPS, PDA and binoculars while looking up to see some monkeys jumping out of the sleep tree above my head.

"Which way are you going today, guys?"

- Piya Saisawatdikul, The Assamese Diary

Table of Contents

General Introduction

The *New York Times* weekly publishes “the best advice on living a better, smarter, more fulfilling life.” In a recent article from the series entitled “How to Have Closer Friendships (and Why You Need Them)” by Pattee (2019), close friendships are said to be “necessary for optimal health and well-being” and to be characterized by “consistency, availability, reliability, responsiveness and predictability.” Readers are encouraged to take their friends out for a “test drive”: “Ask for help even when you don’t need it so that when you truly need them, you’ll feel more comfortable reaching out and you’ll have a better sense of how they will respond [. . .]. Not only is this a low-risk way of testing how reliable a friend is, it also builds closeness.”

The parallels from these statements with what I will discuss in this thesis are striking: they serve as testimony for the importance of close bonds and the universal characteristics of them. The effects that forming strong social relationships have on human longevity are similar in size to those from well-established risk factors such as frequent smoking and heavy drinking (Holt-Lunstad et al., 2010). Similarly, overwhelming support for links between social bonding and survival and reproductive success has been found in mammals as diverse as bottlenose dolphins (Frère et al., 2010), feral horses (Cameron et al., 2009) and various non-human primates (Ellis et al., 2019; Kalbitzer et al., 2017; Ostner and Schülke, 2018; Silk et al., 2009).

Many of these strong social relationships are formed between closely related individuals. Over fifty years ago, early field researchers studying Japanese and rhesus macaques observed that females tended to form close relationships with maternal kin (Sade, 1972; Yamada, 1963). Since then, kinship has emerged as one of the main factors affecting the development of long-term bonds in animals (Seyfarth and Cheney, 2012; Silk, 2009; Smith, 2014). The bulk of this research, however, has focused on *maternal* kinship in philopatric *females*. In this thesis I took the road less travelled and studied a population of wild Assamese macaques in Thailand to investigate how *paternal* kinship affects sociality in females (Chapter 2), and how kinship influences social bonding in post-dispersal *males* (Chapter 3). In this first chapter, I briefly introduce the fundamental concepts underlying the study of kin biases in social bonding. In the final chapter, I discuss the implications of my findings on our understanding of the impact of kinship on social relationships.

1.1. Evolution of sociality

1.1.1. Group living and social relationships

Although solitary living is the ancestral state for most vertebrate lineages, sociality (i.e. permanent, stable social groups) has arisen independently across most vertebrate orders (Pérez-Barbería et al., 2007). The selective forces that caused and maintained group living act on the individual level: group living evolves only if, for all members, the benefits outweigh the automatic costs of group living, which are increased competition for resources and increased likelihood of disease transmission (Alexander, 1974; Krause and Ruxton, 2002). Different pathways towards sociality across taxa suggest that different selective pressures, and different benefits, have driven the formation of stable groups. In primates, group living likely evolved during the shift from nocturnal to diurnal living, where group living lowered predation risk (Shultz et al., 2011; Van Schaik, 1983). In delphinids too, predation risk is thought to have led to the evolution of sociality (Möller, 2012), while in carnivores the benefits of cooperative hunting or cooperative rearing of young are the likely drivers of group living (Macdonald, 1983).

Gregarious animals repeatedly interact, so that if they can recognize each other they develop a relationship, in which the pattern of previous interactions predicts the content and quality of the next interaction (Hinde, 1976). Social relationships represent shortcuts that help individuals navigate group living. They are a major mechanism at the interface of an individual and its environment, and can have a big impact on its fitness (Alberts, 2018; Kappeler et al., 2013; Silk et al., 2013). Establishing dominance relationships, for example, allows individuals to save energy and to minimize the risk of injury by behaving in accordance with hierarchical ranks (Kaufmann, 1983). The formation of affiliative relationships can have an adaptive value too, which depends on a partner's qualities (strength, skill, experience), tendencies (probability to perform certain behaviour) and availability (Kummer, 1978). Affiliative relationships vary over several dimensions, such as stability, strength, tenor and symmetry (Silk et al., 2013). Strong, stable and, over the long run, equitable affiliative relationships are called social bonds (Box 1; Silk, 2002a), and are found throughout the mammalian kingdom (Seyfarth and Cheney, 2012). Typically, individuals form strong social bonds with only a few of their group mates and weak relationships with the rest of the group (Connor and Krützen, 2015; Silk et al., 2006).

1.1.2. Benefits of social bonding

Within-group sociality is thought to be a product of natural selection that allows individuals to deal with the inevitable costs associated with a gregarious lifestyle (Brent et al., 2014; Silk, 2007). Affiliative tendencies are under genetic control, and are therefore a trait upon which selection may act (Brent et al., 2013; Fowler et al., 2009; Lea et al., 2010). The first evidence for a fitness benefit from sociality was reported in yellow baboons (*Papio cynocephalus*), where the infants of socially well-integrated females had a better chance of surviving to one year of age (Silk et al., 2003). Since then, strong links have been established between social integration and increased survival and/or reproductive success in a diverse range of taxa (Archie et al., 2014; Cameron et al., 2009; Feh, 1999; Frère et al., 2010; Holt-Lunstad et al., 2010; Kalbitzer et al., 2017; Ramp et al., 2010; Schülke et al., 2010; Silk et al., 2009, 2010; Wiszniewski et al., 2012b; Yang et al., 2016). Bond partners can provide agonistic support (Smith et al., 2010), which in turn can lead to rank acquisition (Gilby et al., 2013; Lea et al., 2014; Schülke et al., 2010) or protection from harassment (Cameron et al., 2009; Haunhorst et al., 2017; Nguyen et al., 2009). By forming bonds, individuals can also enhance their access to resources through tolerance and joint defence (Haunhorst et al., 2017; Heesen et al., 2014; Wiszniewski et al., 2012b). In contrast to group living, which evolves only if it leads to net benefits for all individuals, social bonds provide benefits to an individual at the cost of other group members and are therefore formed with only a subset of group mates (Ostner and Schülke, 2018).

1.1.3. Pathways to cooperation

Clearly, individuals can benefit from forming strong, stable bonds; but how do individuals choose which group mates to form social bonds with? To understand partner choice, supportive and tolerant behaviour needs to be framed in the light of the evolution of cooperation (Brent et al., 2014). Cooperation forms an evolutionary paradox, since natural selection should lead to selfish behaviour and competition (West et al., 2007a). There are three main solutions to the paradox, that is, three mechanisms under which it can be evolutionary stable to pay a cost for another individual's benefit: kin selection, direct reciprocity, and mutualism (Table 1 and Box 1; Van Schaik and Kappeler, 2006).

Table 1: The three main pathways to cooperation

	Kin selection	Reciprocity	Mutualism
Rule	$r * b_R > c_A$	$p * b_R > c_A$	$b_A > c_A$
Receiver	Kin	Kin & non-kin	Kin & non-kin
Benefit to actor	Indirect	Delayed direct	Immediate direct
Risk	Mistakes in kin discrimination	Defection	Free-riding & risk-avoidance

A: actor of the behaviour; R: receiver of the behaviour; b: benefit of the behaviour; c: cost of the behaviour
r: pairwise genetic relatedness; p: probability of a next encounter between actor and receiver

For kin selection, the fundamental principle is to focus on the gene rather than on the individual as the unit of selection; cooperating with kin can be beneficial because it still leads to a part of an individual's genes (the more closely related, the larger the part likely is) to be carried over to the next generation (Hamilton, 1964). Cooperation through kin selection is therefore selected for because of the indirect fitness benefits gained from the increased fitness of related individuals (Van Schaik and Kappeler, 2006; West et al., 2007a). Under reciprocity, two individuals alternate between providing and obtaining fitness benefits (Trivers, 1971). A central element to reciprocity is the time delay between incurring a cost of providing support and receiving a benefit when the partner reciprocates, which creates the risk of defection (a partner failing to reciprocate; Van Schaik and Kappeler, 2006). Reciprocity can therefore only be evolutionarily stable when individuals interact repeatedly: only the average consequences of a behaviour are beneficial for both partners, not the consequences of every instance (West et al., 2007a). Contingent reciprocity is short-term and relies on partner control: decisions made in future interactions are based on outcomes from previous interactions, with "tit-for-tat" (start with cooperation, then do what partner did) and "win-stay lose-shift" (repeat previous move if successful, otherwise change) as essential strategies (Nowak, 2006). An alternative framework for the exchange of services is the biological market theory (Noë and Hammerstein, 1995). Here, the focus is on partner choice, which is defined by partner supply (how many partners can provide the required service) and partner demand (how many individuals are competing for them), and allows for the selection of reliable partners. Biological market theory also adds communication to the picture, whereby partners can share information about their willingness to cooperate (Noë, 1992), which is likely to make reciprocity more stable (Van Schaik and Kappeler, 2006). More recent reciprocity definitions include cooperation that is enforced either by partner choice or partner control (Carter, 2014; Schweinfurth and Call, 2019; Box 1), which is, in fact, how it was originally defined (Trivers, 1971). Lastly, mutualism generates immediate benefits shared by the cooperators that exceed the cost of providing support (Clutton-Brock, 2002, 2009). Since there is no time delay, there is no risk of defection, but there is still the risk of free-riding (asymmetric distribution of costs and/or benefits) and risk-avoidance (the possibility that the partner withdraws at the moment of risky cooperation, e.g. during agonistic coalitions; Van Schaik and Kappeler, 2006).

Cooperation usually takes place between kin and/or within long-term relationships, in which both partners have an interest in keeping the beneficial cooperation going, and incentives for large-scale defection, free-riding or risk-avoidance are minimal (Van Schaik and Kappeler, 2006). Strong social bonds can thus be considered as investments for future fitness benefits through secondary exchanges of affiliation, agonistic support and access to food resources (Cords, 1997; Kummer, 1978). Bonded partners are concerned with the costs and benefits of their cooperative behaviour on a much larger time scale than the interaction, allowing for some temporary inequity (Cheney, 2011; Pusey and Packer, 1997; Schino and Aureli, 2009). The balance or tenor of the relationship is believed to be mediated through "emotional bookkeeping", an emotion-based mechanism that allows long-term tracking of interactions without excessive cognitive load (Schino and Aureli, 2009).

1.2. Kinship and sociality

Within research on partner choice, the impact of kinship on sociality (often with the implicit assumption of kin selection; Chapais, 2006) is a key topic of interest. Among social mammals, there is a substantial body of evidence that individuals bias their affiliative and supportive behaviour towards kin (Smith, 2014), and that such biases can be adaptive (Silk, 2007; Widdig, 2007). Animals from a wide variety of taxa, ranging from primates to bats, over marsupials, ungulates, cetaceans and carnivores, tend to maintain spatial associations with kin (84% of 44 tested species; Smith, 2014), a pattern that even affects the distribution of home ranges of solitary species (Arora et al., 2012; Kappeler et al., 2002). The bias towards kin is even more pronounced in agonistic support, a behaviour with a higher cost (94% of 31 tested species; Smith, 2014). While kinship has emerged as one of the main factors structuring social relationships, our understanding of some of the most basic aspects of kin-related behaviour patterns, such as the mechanisms of kin recognition and the categories of kin that are discriminated (e.g. maternal vs. paternal kin), remain elusive (Chapais and Berman, 2004).

1.2.1. Kin discrimination, kin recognition and kin biases

A critical point for the establishment of any relationship is social recognition (Sherman et al., 1997). The ability to recognize individuals has been demonstrated for a wide range of taxa (Yorzinski, 2017). It is expected to evolve when animals interact repeatedly and benefit from discriminating among group members, which is the case when they form a dominance hierarchy or when they engage in cooperative behaviour (Mateo, 2004; West et al., 2007a). A prime example of social recognition is kin recognition, which is thought to have evolved to facilitate directing the appropriate behaviour towards related individuals (e.g. avoid mating with but support kin; Holmes and Sherman, 1983).

Kin discrimination refers to the ability to distinguish (i.e. kin recognition) and the differential treatment (i.e. kin bias) of kin and non-kin (Box 1; Penn and Frommen, 2010). It involves four key components: (1) the expression of cues, (2) the perception of those cues in other individuals, (3) the decision, and (4) the action taken based on the perceived cue (Mateo, 2004; Penn and Frommen, 2010). The decision is almost always based on heuristics – simple rules-of-thumb, allowing efficient classifications that are accurate under most circumstances but can lead to errors (Penn and Frommen, 2010). There are four broad categories of kin recognition, determined by the cues used (Figure 1; Mateo, 2004; Waldman, 1987).

The simplest form of kin recognition is based on contextual cues. Three types of contextual cues can carry information on relatedness. Spatial cues can be a proxy for kinship when kin (and only kin) are reliably encountered in a particular area, for example, a nest or a burrow (Holmes and Sherman, 1982). Mating access carries information on paternity, and can be used by males to estimate the chance of being the sire of an offspring; most accurately when matings are (almost) fully monopolized (Alberts and Fitzpatrick, 2012). Cohort sharing can act as a proxy for paternal kinship when reproductive skew is high, tenure is short and breeding is seasonal, all together leading to distinct age cohorts sired by the same male (Altmann, 1979a; Widdig, 2013). It is debated whether kin recognition based on contextual cues is “real” kin recognition, since the cues are not carried by the individuals themselves, and therefore do not allow for recognition of kin outside of the specific context (Tang-Martinez, 2001). In any case, contextual cues can reliably correlate with kinship and might therefore allow for accurate kin discrimination (Mateo, 2004).

The second category of kin recognition mechanisms, sometimes referred to as "real" kin recognition, is based on phenotypic cues. Within this category fall kin recognition through (1) familiarity, (2) phenotypic matching and (3) recognition alleles. Recognition through familiarity or prior association relies on the associative learning of individually distinctive cues during a learning phase early in development (Berman, 2004), with the assumption that those individuals encountered early on in life are likely to be kin (Penn and Frommen, 2010). Because it is the individual *per se* that is recognised, prior association or familiarization with the individual to be recognized is necessary (Mateo, 2004). Familiarization can occur directly or can be mediated through a shared attraction to a third individual (e.g. mother- and father-mediated familiarity; Holmes and Sherman, 1982; Widdig, 2007). Although powerful in its simplicity, kin recognition through familiarity can lead to the inability to recognize kin when they are only encountered after the learning phase, which can be the case for dispersing individuals (Mateo, 2004).

Recognition through phenotypic matching, on the other hand, is based on the associative learning of kin-distinctive cues (Holmes and Sherman, 1982), with the assumption that individuals who resemble familiar kin (or the individual itself) are likely to be kin (Penn and Frommen, 2010). Here, it is a specific trait that is recognized and then compared to a template (based on familiar kin or the individual itself; Tang-Martinez, 2001). A generalization is made from the recognition template, so familiarity with the individual to be recognized is not required (Mateo, 2004). Finally, recognition alleles, or so-called green-beard genes (Dawkins, 1976), are genes that simultaneously code for the expression of a (rare) phenotypic trait, the recognition of the trait in others, and the differential treatment of individuals with the trait (Hamilton, 1964). Such genes are suspected to be very rare, if they exist at all (Penn and Frommen, 2010; Tang-Martinez, 2001).

The central problem for all these mechanisms is to optimize the risk for acceptance errors (i.e. false positives) with the risk of rejection errors (i.e. false negatives; Penn and Frommen, 2010). This balance is likely context-dependent: acceptance errors should be avoided especially in the context of more costly or risky behaviour (such as agonistic support), while rejection errors should be avoided if they strongly impact the receiver (which is the case for infanticide for example). It is also important to keep in mind that various types of kin recognition are not mutually exclusive, and in fact most likely co-occur (Mateo, 2004). The mechanism used might also depend on the developmental state of the individual and/or the context. Finally, the classification of kin mechanisms might be somewhat artificial. For example, kin recognition based on cohort-sharing has been classified as both a mechanism based on contextual cues (considering an age cohort as an entity wherein all individuals are likely kin, e.g. litters; Mateo, 2004) and a mechanism based on familiarity (in which members of the same age cohort are thought to be familiarized through growing up together; Altmann, 1979a; Widdig, 2013).

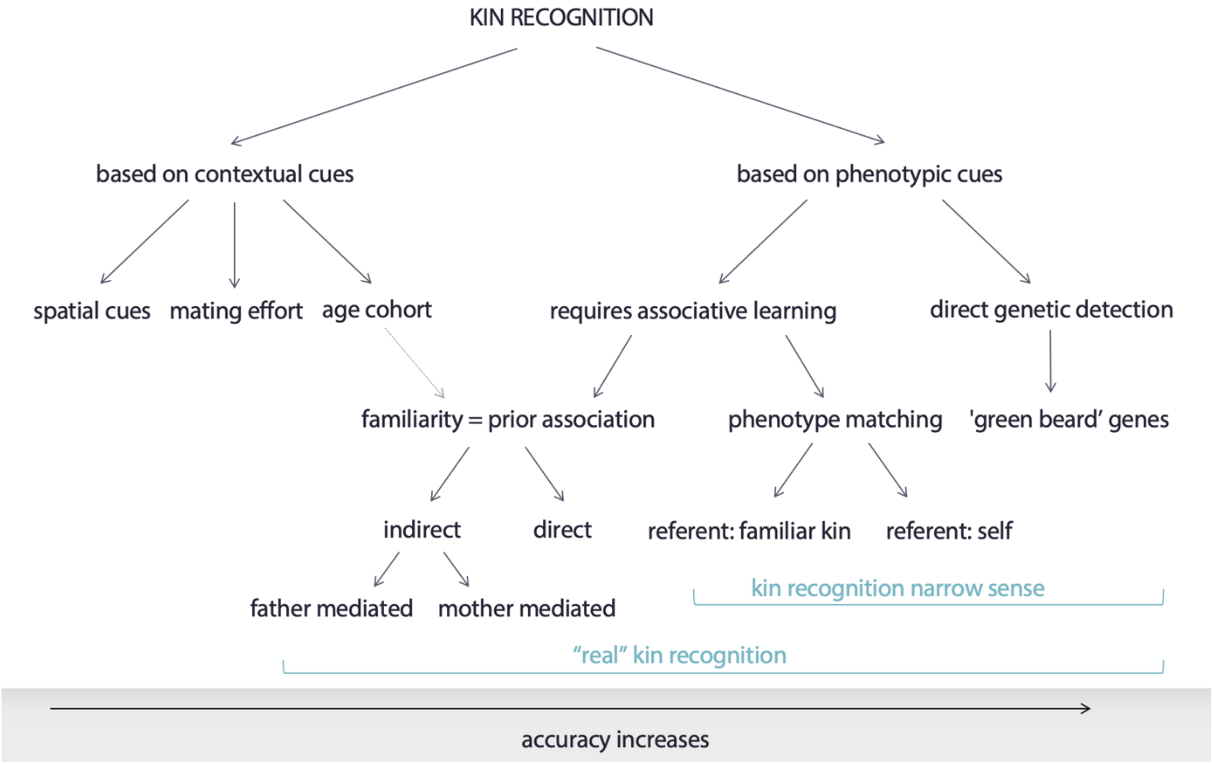

Figure 1

Kin recognition mechanisms. Age cohort membership can be considered both a contextual cue and a familiarity-based mechanism.

Box 1: Definitions used in this thesis

Social bond: a strong, equitable and enduring social relationship (Ostner and Schülke, 2014)

Cooperation: a behaviour which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient (West et al., 2007b)

Kin selection: process by which traits are favoured because of their beneficial effects on the fitness of relatives (West et al., 2007b)

Reciprocity: contingent cooperative investments that are based on the cooperative returns, with enforcement through partner control and/or partner choice (Carter, 2014)

Mutualism: cooperation that generates immediate synergistic benefits shared by cooperators that exceed the costs of providing assistance (Clutton-Brock, 2009)

Genetic relatedness (r): a measure of the genetic similarity of two individuals, estimated by comparing observed genetic similarity to that expected from a random sample of the population (Hoelzer et al., 2004)

Kin: individuals that are genetically related due to common descent (Penn and Frommen, 2010)

Direct fitness: the component of personal fitness due to one's own behaviour (West et al., 2007a)

Indirect fitness: the component of fitness gained from aiding related individuals (West et al., 2007a)

Inclusive fitness: an individual's own reproductive success plus its effects on the reproductive success of its relatives weighed by the coefficient of relatedness (Penn and Frommen, 2010)

Kin bias: the differential treatment of kin versus non-kin (Penn and Frommen, 2010)

Kin recognition: the ability to identify, distinguish and classify kin versus non-kin (Penn and Frommen, 2010)

Kin discrimination: the observable, differential treatment of conspecifics based on cues that correlate with relatedness (Mateo, 2004)

Familiarity: prior association during early development (Mateo, 2004)

Coalition: two (or more) individuals acting together against a third party in an aggressive or competitive context (Bissonnette et al., 2015)

Alliance: a long term relationship characterized by repeated coalitions and high levels of association between the partners (Bissonnette et al., 2015)

1.2.2. Maternal and paternal kin

Many of the studies on the effect of kinship in mammals have used pairwise relatedness among group members rather than pedigree information as the measure of kinship, therefore not allowing for a distinction between maternal and paternal kin (Widdig, 2007). The vast majority of studies that did make such a distinction focused on maternal kin biases, for which ample evidence is present across a wide variety of animal taxa (Smith, 2014; Widdig, 2007). Kin recognition via familiarity is considered the main mechanism through which maternal kin is recognized in mammals (Chapais, 2001; Holmes and Sherman, 1983; Widdig, 2007). Infants are closely associated with their mother through lactation and an extended juvenile period (Broad et al., 2006). Moreover, females are typically the philopatric sex (Greenwood, 1980; Smale et al., 1997), meaning that mothers are embedded into a social network of their own close maternal kin, which in turn familiarizes their offspring with other maternal kin. Particularly in species with multi-generational matrilines, the gradient of familiarity strongly correlates with kinship (so much so that it has been argued that observed kin biases might simply be a by-product of proximity; Chapais, 2001). Familiarity might in fact even be a better mechanism than direct genetic detection, as it allows for discrimination of more categories than based on degrees of relatedness alone (e.g. half-siblings and grandparent-grandoffspring both have r=0.25; Rendall, 2004).

Paternal kin discrimination, on the other hand, is much less understood. Many mammals mate promiscuously (Clutton-Brock, 1989; Jennions and Petrie, 2000), which conceals paternity and, by extension, hampers paternal kin recognition (Widdig, 2007). The inability to recognize paternal kin would, however, expose individuals to fitness costs such as inbreeding (Alberts, 1999; Keller and Waller, 2002) and infanticide (Alberts and Fitzpatrick, 2012; Hrdy, 1979). It would also hamper the development of close bonds with paternal kin, and thus the gain of indirect fitness benefits (Hamilton, 1964; West et al., 2007a). Some evidence for paternal kin biases exist in the form of inbreeding avoidance, offspring protection against infanticide or preferential affiliation (Widdig, 2007), although it is much more limited than the evidence for maternal kin biases – in terms of both the number of species for which it has been reported and the extent of the kin bias (e.g. out of 31 studies with data on agonistic support, only 10 included paternal kin, and no clear pattern emerged from them; Smith, 2014).

Several mechanisms of paternal kin recognition have been proposed (Widdig, 2007). The first mechanism is based on mating effort: a male might estimate his likelihood of being the sire of an infant based on the mating access he had to the mother during her receptive period (Alberts and Fitzpatrick, 2012). Paternal kin recognition might also rely on familiarity, either through age proximity or mediated by the infant's mother or father early on in life. In species with a high male reproductive skew and short alpha male tenure relative to the interbirth interval, infants that are born close in time are likely sired by the alpha male and thus have a high chance of sharing the same father. As close-aged individuals grow up together, age proximity could be a potential mechanism through which paternal kin are familiarized with each other (Altmann, 1979a; Widdig, 2013; alternatively, belonging to the same age cohort can represent a contextual cue, as mentioned above; Mateo, 2004).

Familiarity could also be mediated by the mother. If she has reliable information on paternity, she might exert maternal control over who her offspring is familiarized with during infancy. She might bring her offspring in proximity to its father or spend time with other mothers with offspring sired by the same male, and, in this way, familiarize her offspring with paternal siblings (Berman, 2004; Widdig et al., 2001). Offspring might also be indirectly familiarized with their father if their parents are engaged in an association (such as "friendships" sensu Smuts, 1985) that is maintained post-birth. If several females share the same male as their primary associate, this could familiarize paternal siblings to each other (Seyfarth and Cheney, 2012). Alternatively, fathers might perform paternal care, which would allow offspring to be familiarized with their father and, by extension, to other infants that the father is taking care of. Finally, paternal kin recognition might also be based on phenotypic matching based on cues such as appearance, odour and vocalizations (Holmes and Sherman, 1983).

1.3. Variations in kin biases in sociality

1.3.1. Factors affecting the development of kin biases

Three main factors have a pervasive influence on the opportunities animals have to interact with kin: demography, dispersal patterns and the mating system (Strier, 2004). Demographic variables such as group size, group composition and interbirth interval determine the number and nature of potential social partners. In large groups, in which animals have a lot of related partners to choose from, kin biases are usually more restricted to close kin because of constraints on the available time and energy that animals have to spend on socializing (Chapais, 2001). In stable bisexual groups, sires have the possibility to interact with their offspring (Van Schaik and Paul, 1996; Widdig, 2007). Finally, interbirth intervals determine the likelihood of having similarly aged, maternally related siblings, as well as the extent to which there is overlap in generations, and thus the potential for grandparent-grandoffspring interactions (Hill, 2004).

Dispersal is another major influence on the coexistence of kin in the same group (Hoelzer et al., 2004; Strier, 2004). When dispersal is low (i.e. for the philopatric sex), same-sex group members have a high degree of relatedness, which can facilitate tolerance, affiliation and cooperation (Cords and Nikitopoulos, 2015; Silk, 2009). Moreover, social relationships can last longer (even throughout a lifetime), which in turn can lead to a higher degree of sociality (Hill, 2004; Strier, 2004). However, when dispersal is high, adult individuals are mostly surrounded by unrelated group members, unless they disperse together with kin or join groups already containing kin (Albers and Widdig, 2012; Gerber et al., 2016; Schoof et al., 2009). Dispersal patterns also determine how kinship is structured within the group: in female-philopatric species, kinship accumulates along maternal kin lines, while in male-philopatric species kinship accrues along paternal kin lines (Chapais, 2006).

Finally, the mating system and the extent of reproductive skew, together with male tenure, define the probability of paternal kinship between group members and the age spread among paternal siblings (Altmann, 1979a; Hill, 2004). In species in which fertilizations are strongly monopolized by one (or a few) males for a relatively long time (i.e. in species with one-male groups or with multi-male groups with strong reproductive skew), a large number of individuals will be paternally related (Strier, 2004). However, if monopolization is restricted to a shorter time (one reproductive season), this will lead to age cohorts of (likely) paternal siblings (Altmann, 1979a). Finally, if reproductive skew is limited but male tenure is rather long, several group members will be paternally related, but paternal kin will mostly not be close in age.

1.3.2. Sex differences in sociality

Variation in kin bias patterns between sexes can also be explained, to some extent, in terms of variation in availability of kin, which is determined mostly by sex-biased dispersal. The philopatric sex (usually females) tend to form the strongest and longest lasting social bonds, and these are usually biased towards the close kin they spend their entire life with (Berman, 2004; Strier, 2004). Another reason for differences between males and females is that they face different socioecological pressures, setting the stage for different social and reproductive strategies in males and females (Trivers, 1972).

1.3.2.1. Females

Female kin biases, and female relationships in general, are believed to be closely linked with the pathways to female group living and the extent of competition within and between groups. This has been formalized for the primate order in the socio-ecological model of female relationships (Sterck et al., 1997; Van Schaik, 1989; Wrangham, 1980). According to the model, females aggregate due to predation risk, due to between-group competition over defendable high-quality resources and/or due to benefits from aggregating around males that can protect them against infanticide. Once female groups form, the competitive regime determines social relationships, which have been classified into four types.

If within-group feeding competition is high, linear dominance hierarchies and supportive coalitions are likely to develop, and support should be strongly kin-biased to maximize inclusive fitness benefits ("despotic-nepotistic" relationships). If, additionally, between-group competition is strong, tolerance is expected to be favoured among group members ("despotic-nepotistic-tolerant" relationships). For females living in such despotic-nepotistic societies, dispersal is costly due to the loss of allies and the strong resistance to immigration from resident females of any new group. Under low within-group competition, on the other hand, hierarchies and supportive alliances are no longer expected to develop, which in turn relaxes constraints on female dispersal. Still, strong between-group competition is expected to favour kin-based coalitions to defend resources at the group level ("resident-egalitarian" relationships). If between-group competition is weak, however, females might commonly leave their natal group to minimize scramble competition ("dispersal-egalitarian" relationships); this is the only scenario under which unrelated females are expected to aggregate.

Although the socio-ecological model was formulated for primates, it can likely be applied to other taxa too. In lions (*Panthera leo*), females face potentially high within-group competition (Holekamp and Sawdy, 2019). They live in groups of philopatric kin, but do not form dominance hierarchies, most likely because group mates rely on each other for cooperative hunting and communal cub rearing (Packer et al., 2001). Lions thus seem to fit the "resident-nepotistic-tolerant" category. Spotted hyenas (*Crocuta crocuta*), on the other hand, are a prime example of “resident-nepotistic” societies. They live in large clans that typically contain several matrilines of philopatric females (Holekamp et al., 2012). Maternally related females associate more closely than non-kin, are more affiliative towards each other, hunt together and tolerate each other more often while feeding at kills, despite intense feeding competition (Holekamp and Sawdy, 2019; Smith et al., 2010). Moreover, maternal kin support each other in agonistic encounters, and are crucial allies in conservative and sometimes even revolutionary coalitions, which can even lead to complete female dominance over males (Strauss and Holekamp, 2019; Vullioud et al., 2019).

It is worth pointing out that the socio-ecological model, although powerful, has been criticized for not accounting for phylogenetical constraints, as well as for the lack of evidence linking feeding competition to either dominance or dispersal patterns (Clutton-Brock and Janson, 2012; Koenig et al., 2013; Thierry, 2008). It has been argued that it is the variance of relatedness within a group, rather than feeding competition, that seems to be the driver of supportive alliances and therefore stable linear hierarchies (Broom et al., 2009). In line with this, linear hierarchies tend to develop in large, stable groups containing several matrilines in which kinship varies widely between group members (Clutton-Brock and Janson, 2012). For dispersal patterns too, an alternative driver has been proposed. In species with long alpha male tenure, females are at the risk of not having access to paternally unrelated mating partners, which in turn might force them to disperse from the natal group (Clutton-Brock and Lukas, 2012). Regardless of the underlying mechanisms, female aggregations, associations and coalitions very often follow the original prediction of being kin biased.

1.3.2.2. Males

While females benefit from aggregating, males would do best with no other males around. The high intensity of intrasexual competition over access to fertile females is expected to constrain tolerance, affiliation and cooperation in males (Van Hooff and Van Schaik, 1994; Van Schaik, 1996). Whenever females are solitary or form groups that are small enough to be defended by a single male, males should aim at monopolizing those females through the exclusion of rivals (Clutton-Brock, 1989). If females are numerous and/or female receptivity is temporally concentrated, however, one male alone might not be capable of monopolizing all females in his group or territory (Emlen and Oring, 1977; Ostner et al., 2008b; Reeve et al., 1998). Males then compete for mating access to fertile females in multi-male groups, which manifests itself in the formation of dominance hierarchies, often reflecting variation in fighting ability (Alberts et al., 2003; Ellis, 1995). As a result, mating opportunities and reproduction are skewed, with higher-ranking males having priority of access to fertile females (Altmann, 1962). The extent to which dominance rank predicts reproductive success varies considerably between species, and it strongly depends on the level of contest competition. As the number of male competitors increases, the defendability of females decreases, which subsequently relaxes the selection for male fighting ability (Cowlishaw and Dunbar, 1991; Ellis, 1995; Ostner et al., 2008b; Weir et al., 2011). Rather than investing in attributes like large body size and sharp canines, male competitors might benefit from other forms of mating competition, such as the formation of coalitions (Alberts et al., 2003).

Similar to females, the competitive regime is believed to determine which types of coalitions are formed, thus influencing the nature of male relationships. Likewise, a framework has been formulated for the primate order (Ostner and Schülke, 2014; Van Schaik et al., 2006). Males can increase their access to fertile females by gaining or maintaining high rank, forming rank-changing or conservative coalitions respectively, or by temporarily decreasing the priority of access across ranks through levelling coalitions to break up consorts of dominant males (Bissonnette et al., 2015; Van Schaik et al., 2006; Young et al., 2014b). The degree of within-group competition determines the feasibility of coalitions, with feasibility being lower in species with large differences in contest potential between group members. The degree of within-group competition also determines the level of reproductive skew and therefore the profitability of coalitions, with higher profitability for higher skew (Van Schaik et al., 2006). While rank-changing coalitions are more profitable than levelling coalitions, they are also much riskier and more time-consuming because repeated coalitions are usually necessary for a change in ranks to occur (Ostner and Schülke, 2014).

When within-group competition is absent, cooperation in between-group conflicts might lead to the formation of undifferentiated affiliative relationships between all males in the group (Ostner and Schülke, 2014). On the other extreme, where within-group contest competition is high, rank-changing coalitions would be highly profitable but are not feasible (Van Schaik et al., 2006). Subordinate males can still benefit from cooperation through levelling coalitions, temporarily breaking up consorts of dominant males (Alberts et al., 2003; Bissonnette et al., 2015; Van Schaik et al., 2006). As partner choice for this short-term cooperation is opportunistic, no affiliative relationships are expected. Yellow baboon males, for example, experience high contest potential, with pronounced sexual dimorphism leading to large power differentials between closely ranking males (Alberts et al., 2006). Moreover, their time budget is restrained by the formation of year-round consorts (Alberts et al 1996) and male-female primary associations (i.e. "friendships"; Nguyen et al., 2009). The formation of rank-changing coalitions would thus be costly, in both the risk they represent and the invested time they require. Instead, yellow baboons form levelling coalitions to break up consortships of higher-ranking males, and they seem to choose their partners based on their combined fighting ability relative to the target (Noë, 1994; Noë and Sluijter, 1995; Silk et al., 2003).

On the other hand under medium to low within-group contest competition, feasibility and profitability are ideally balanced, allowing males to form rank-changing coalitions (Ostner and Schülke, 2014; Van Schaik et al., 2006). As such coalitions result in males gaining a higher position in the hierarchy than based on their individual fighting ability, these coalitions are risky affairs. Having a reliable partner is crucial so as not to incur retaliation by the out-ranked stronger male (Ostner and Schülke, 2014). This is why social bonding is thought to have co-evolved with the formation of rank-changing coalitions as a means to mediate partner choice (Chapais, 1995; Ostner and Schülke, 2014). In chimpanzees (*Pan troglodytes*), for example, contest competition is relatively low, with alpha males siring about a third of the offspring (Boesch et al., 2006; Bray et al., 2016; Constable et al., 2001; Newton-Fisher et al., 2010). Males engage in rank-changing coalitions (Gilby et al., 2013) as well as conservative coalitions (Bray et al., 2016), and they have been shown to exchange agonistic support for other commodities, such as grooming, mating access and meat sharing (Bray et al., 2016; Duffy et al., 2007; Samuni et al., 2018). Rank-changing coalitions are formed between closely bonded males, and have been shown to improve reproductive success (Gilby et al., 2013; Mitani, 2009; Muller and Mitani, 2005).

Although this framework has been formulated for primates, it can probably be applied to other taxa living in multi-male groups also. Male bottlenose dolphins (*Tursiops* spp.) have limited sexual size dimorphism (Möller, 2012) and paternity is shared over several males (Krutzen et al., 2004; Wiszniewski et al., 2012b), which suggests moderate levels of contest competition. Males form up to three levels of long-term, stable alliances to consort females as well as to steal them from competing alliances (Connor and Krützen, 2015). The vast majority of offspring is sired by males that engage in alliances (Krutzen et al., 2004), and reproductive success increases as the size of alliances increases (Wiszniewski et al., 2012b). Male coalitions are based on social bonds, as alliance partners associate year-round and show affiliative behaviours such as petting and synchronous displays (Connor et al., 2006; Gerber et al., 2019).

The framework of male cooperation in primates also neatly mirrors the findings of a trait-based approach to the evolution of complex coalitions in male mammals (Olson and Blumstein, 2009). According to this meta-analysis, three key traits define complex coalitionary behaviour in mammals: mutual tolerance, collaboration in within-group or between-group competition, and partner preference in within-group competition. This is equivalent to the idea that male cooperation complexity gradually increases from the formation of multi-male groups without benefits from the presence of other males (~ mutual tolerance), over multi-male groups in which co-resident males form undifferentiated relationships and cooperate in between-group competition or levelling coalitions (~ collaboration), to males forming stable alliances with reliable partners to increase their potential in within-group competition through rank-changing coalitions (~ partner preference).

1.4. This thesis

As stated at the outset of this introduction, the overall aim of this thesis was to investigate how kinship underlies sociality in wild female and male Assamese macaques (*Macaca assamensis*) and, in doing so, contribute to two aspects of kin biases in mammals that are still not well understood: paternal kin discrimination (Chapter 2), and kin biases in male bonding (Chapter 3).

The Assamese macaques of the Phu Khieo Wildlife Sanctuary in Thailand lend themselves ideally to research on kinship and sociality. They have been observed for over ten years in their natural habitat, and many aspects of their social lives, which likely impact kin biases in affiliation, have been previously studied (Figure 2). Assamese macaques live in stable multi-male-multi-female groups with female philopatry and male dispersal and relatively long male tenure (Ostner et al., 2013). Four groups are followed, meaning that many of the males in our population can be observed throughout (a large part) of their dispersal careers. Because Assamese macaques are highly frugivorous (Schülke et al., 2011) they face high levels of feeding contest competition and form linear hierarchies. Reproduction is seasonal, female receptivity is synchronized and ovulation is concealed (Fürtbauer et al., 2011; Fürtbauer et al., 2010). This impedes monopolization of fertilizations by high-ranking males, which is reflected in a relatively low reproductive skew (29% alpha male paternity: Sukmak et al., 2014). Strong social bonds have been reported for both sexes (Kalbitz et al., 2016; Macdonald et al., 2014), and have been linked to feeding tolerance in females and to agonistic support leading to increased paternity success through the acquisition of higher ranks in males (Heesen et al., 2014; Schülke et al., 2010). Stable opposite-sex bonds are formed too, which result in increased mating success for males, and agonistic support and increased feeding tolerance for females (Haunhorst et al., 2017; Haunhorst et al., 2016; Ostner et al., 2013).

To investigate how kinship impacts the social life of Assamese macaques, I genotyped all individuals that were (or had been) adult by 2016 at 16 autosomal microsatellite loci and at the hypervariable region I of the mtDNA D-loop region. DNA was extracted from faecal samples collected non-invasively since the establishment of the field site. Based on those genotypes, I estimated average pairwise relatedness for all dyads, and ran parentage analyses for pedigree reconstruction, in order to be able to distinguish paternal from maternal kin. I then combined this kinship data with the longitudinal behavioural data that have been collected on both males and females since the start of the field site in 2006.

The first chapter of this thesis focuses on maternal and paternal kin biases in the affiliation of females. Female Assamese macaques live in stable groups often containing both paternal and several categories of maternal kin, as well as unrelated individuals. Because of the low reproductive skew, age cohorts of paternal half-siblings are not expected. The aim of this study was therefore to investigate whether paternal kin biases in affiliation can develop in a species in which age proximity is not likely to be a reliable cue of paternal relatedness.

The second chapter investigates the importance of kinship in the social bonding of post-dispersal males. Assamese macaques are one of the few species for which male social bonds have been reported. Because males disperse, they likely have few close kin available in the group, prompting the question whether bonds are restricted to the few related dyads, or whether factors other than kinship underlie bond formation in this species. Because bonded males are reliable partners in cooperation, understanding partner choice in bonding will help us understand male cooperation.

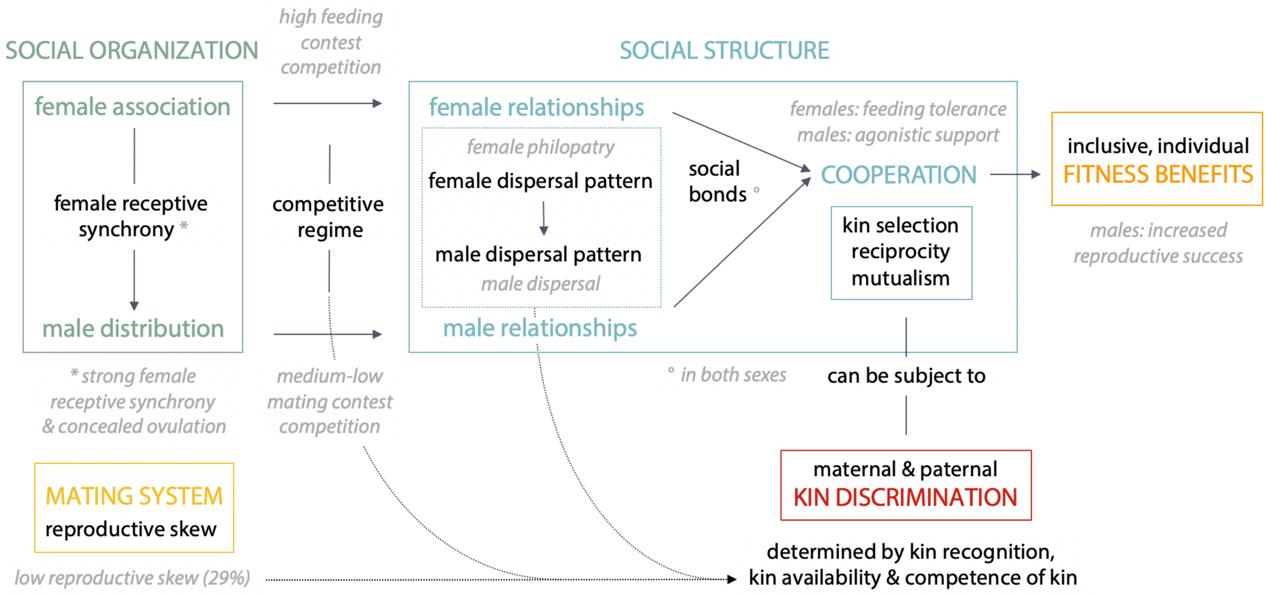

Figure 2

General framework of factors affecting kin discrimination patterns. In grey italics what we know so far for Assamese macaques.

Chapter 2

Female Assamese macaques bias their affiliation to paternal and maternal kin

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Abstract

Forming strong social bonds can lead to higher reproductive success, increased longevity, and/or increased infant survival in several mammal species. Given these adaptive benefits, understanding what determines partner preferences in social bonding is important. Maternal relatedness strongly predicts partner preference across many mammalian taxa. The role of paternal relatedness, however, has received relatively little attention, even though paternal and maternal kin share the same number of genes, and theoretically similar preferences would therefore be expected for paternal kin. Here, we investigate the role of maternal and paternal relatedness in female affiliation in Assamese macaques (*Macaca assamensis*), a species characterized by a relatively low male reproductive skew. We studied a wild population under natural conditions using extensive behavioural data and relatedness analyses based on pedigree reconstruction. We found stronger affiliative relationships and more time spent grooming between maternal kin and paternal half-sisters compared with nonkin, with no preference of maternal over paternal kin. Paternally related and nonrelated dyads did not form stronger relationships when they had less close maternal kin available, but we would need a bigger sample size to confirm this. As expected given the low reproductive skew, affiliative relationships between paternal half-sisters closer in age were not stronger than between paternal half-sisters with larger age differences, suggesting that the kin bias toward paternal kin was not mediated by age similarity. An alternative way through which paternal kin could get familiarized is mother- and/or father-mediated familiarity.

Key words: kin discrimination, kin selection, nepotism, relatedness, social bonds.

Chapter 3

Bonds of bros and brothers: Kinship and social bonding in post-dispersal male macaques

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Abstract

Group-living animals often maintain a few very close affiliative relationships – social bonds -

that can buffer them against many of the inevitable costs of gregariousness. Kinship plays a central role in the development of such social bonds. The bulk of research on kin biases in sociality has focused on philopatric females, who typically live in deeply kin-structured systems, with matrilineal dominance rank inheritance and life-long familiarity between kin. Closely related males, in contrast, are usually not close in rank or familiar, which offers the opportunity to test the importance of kinship per se in the formation of social bonds. So far, however, kin biases in male social bonding have only been tested in philopatric males, where familiarity remains a confounding factor. Here, we studied bonds between male Assamese macaques, a species in which males disperse from their natal groups and in which male bonds are known to affect fitness. Combining extensive behavioural data on 43 adult males over a 10-year period with DNA microsatellite relatedness analyses, we find that postdispersal males form stronger relationships with the few close kin available in the group than with the average nonkin. However, males form the majority of their bonds with nonkin and may choose nonkin over available close kin to bond with. Our results show that kinship facilitates bond formation, but is not a prerequisite for it, which suggests that strong bonds are not restricted to kin in male mammals and that animals cooperate for both direct and indirect fitness benefits.

Key words: coalitions, cooperation, kin selection, nepotism, relatedness, social bonds

General discussion

The objective of this thesis was to advance our understanding of the role of kinship in female and male sociality. Specifically, the purpose was to provide a crucial contribution to the debate on paternal kin discrimination in animals (Chapter 2) and on the importance of kinship for male social bonding (Chapter 3). To this end, I combined extensive behavioural data on a wild population of Assamese macaques with relatedness analyses based on pedigree reconstruction. In my first study, I found that females bias their affiliation towards both close maternal and paternal kin, with no significant difference between both kin classes. Relationship strength between paternal half-sisters was independent of both the number of maternal kin available and age similarity between the partners (Chapter 2). In my second study, I found that post-dispersal males had few close kin available in their new group and formed stronger relationships with those few close kin than with the average non-kin. However, males formed the majority of their bonds with non-kin, and they sometimes even chose non-kin over available close kin to bond with (Chapter 3). In this final chapter, I frame these findings in a larger perspective and discuss their further implications.

First, I discuss maternal and paternal kin discrimination in animals. Based on the limited research done so far, it seems that relationships between paternal kin are usually intermediate in strength between maternal kin and non-kin, and that bonds with paternal kin might be formed to compensate for a lack of close maternal kin. However, I argue that paternal kin might be equally good – or sometimes even better – bonding partners than maternal kin. Second, I focus on paternal kin recognition mechanisms. Age proximity as a proxy for paternal relatedness has received a disproportionate amount of attention compared to other kin recognition mechanisms. Yet based on both theoretical grounds and on the data available, the role of age proximity as a cue for paternal kinship should be re-evaluated. I also highlight some of the issues with the current data on phenotypic matching, and I propose parent-mediated familiarity as an alternative kin recognition mechanism that warrants further research.

Next, I turn towards male sociality and discuss the importance of kinship in the formation of male social bonds. Based on theoretical models, male bonding was long assumed to be rare and restricted to male-philopatric species. Counter to these expectations, evidence that male bonds might develop independently of kinship is accumulating, and I suggest other factors that might be more influential in partner choice. I generally discuss that kin might often be ideal bonding and cooperation partners, even outside the context of kin selection, and I point out three main factors constraining preferences towards kin: kin recognition, kin availability and the suitability or competence of kin in light of the task at hand. Finally, I conclude and provide an outlook on possible directions for future research.

4.1. The ties that bind

Kinship has emerged as one of the most important factors affecting the development of long-term bonds in animals (Seyfarth and Cheney, 2012; Silk, 2009; Smith, 2014). Female social mammals form enduring relationships with their offspring and other close maternal kin and selectively support them during agonistic encounters. This is particularly the case in stable social groups with female philopatry and overlap of generations in which such kin biases lead to the clustering of closely ranked maternal kin into matrilines (Archie et al., 2006; Berman, 2015; Diaz-Aguirre, 2017; Smith et al., 2010). The social life of spotted hyenas (*Crocuta crocuta*), for example, is rooted in kinship, with tolerance and support of close relatives, despite intense feeding competition (Holekamp and Sawdy, 2019).

Similarly, the evidence of maternal kin biases in affiliation and coalitionary support is compelling throughout the primate order (Silk, 2002b, 2009), with maternal kinship even affecting the distribution of females in solitary species, such as Coquerel's dwarf lemurs (*Mirza coquereli*; Kappeler et al., 2002) and Bornean orang-utans (*Pongo pygmaeus*; Arora et al., 2012), as well as female association and affiliation in female-dispersing species, such as chimpanzees (*Pan troglodytes*; Foerster et al., 2015) and Western gorillas (*Gorilla gorilla*; Bradley et al., 2007). Maternal kin also tend to stay together, both during temporal fission in species with fission-fusion dynamics and during permanent group splits (Archie et al., 2011; Van Horn et al., 2007; Widdig et al., 2006a; Wittemyer et al., 2009). In line with the overwhelming evidence for maternal kin biases in female sociality, I found that in Assamese macaques (*Macaca assamensis*), maternal half-sisters and mother–daughter dyads formed stronger affiliative relationships and spent more time grooming than did non-kin. Accordingly, the one group fission observed in this population since the establishment of the field site occurred fully along matrilines.

Evidence for paternal kin discrimination, on the other hand, is much more limited (Smith, 2014; Widdig, 2007). In many mammal species, females mate with multiple males during their fertile period so that paternity is concealed (Jennions and Petrie, 2000). Uncertainty of paternity not only hampers the development of paternal kin discrimination in animals but has also hindered our understanding of paternal kin biases. Before the development of (non-invasive) genotyping techniques based on molecular markers about thirty years ago (Woodruff, 2004), researchers relied on maternal genealogies based on observations to infer kin relationships, often pooling paternal kin together with non-kin, since it was not possible to distinguish them. Moreover, since then, kinship relations are often based on pairwise relatedness without accounting for pedigree information, so distinctions between maternal and paternal kin are not made. Explicitly studying paternal kin discrimination is crucial, however. Paternal kin biases can be expressed in the form of inbreeding avoidance, paternal care, and increased affiliation or cooperation; all of which are expected to have an important impact on an individual's fitness (Widdig, 2007).

Behavioural inbreeding avoidance of paternal kin in wild populations has been reported for African elephants (*Loxodonta Africana*), as well as for a number of primate species (Alberts, 1999; Archie et al., 2007; Charpentier et al., 2005b; Godoy et al., 2016b; Muniz et al., 2006; Vigilant et al., 2015). There is also evidence showing that males are capable of recognizing their offspring with some reliability, as sires seem to avoid killing their own offspring, and to protect them against infanticide or aggression by other males (discussed in more detail later; Busse, 1985; Widdig, 2007).

Paternal kin biases in affiliation and coalitionary support have received relatively little attention so far, and have been reported only for spotted hyenas, mountain gorillas (*Gorilla beringei*), and several species of cercopithecine monkeys under natural conditions (Charpentier et al., 2012; Charpentier et al., 2007; Cords et al., 2018; Lynch et al., 2017; Silk et al., 2006; Smith et al., 2010; Smith et al., 2003; Wahaj et al., 2004; Watts, 1994, 1997; Widdig et al., 2001, 2002; Widdig et al., 2006b). Studies in other primate taxa found evidence only for biases towards maternal kin, and no differences in affiliation between paternal kin and unrelated individuals (Charpentier et al., 2008b; Langergraber et al., 2007; Perry et al., 2008; Sargeant et al., 2016; Wikberg et al., 2014a). This lack of kin biases in species in which paternal kin are present in the group, combined with the notion that the magnitude of paternal kin biases is typically much lower than maternal kin biases, has led researchers to believe that strong bonds between paternal kin might develop only when preferred close maternal kin are lacking (Langergraber, 2012; Silk et al., 2006). Evidence of such a compensatory effect comes from two studies on yellow baboons (*Papio cynocephalus*).

In a first study, during which maternal kin availability was exceptionally low, females were found to bias their affiliation towards paternal half-sisters to the same extent as towards maternal half-sisters (Smith et al., 2003). In a later study, during which females had more maternal kin in the group, affiliative relationships between paternal half-sisters were of intermediate strength between maternal kin and non-kin (Silk et al., 2006).

In the Assamese macaques, however, I found no significant difference in affiliative relationship strength between maternal half-sisters and paternal half-sisters, and the number of close maternal kin available did not impact affiliative relationship strength among paternal half-sisters and non-kin. In fact, no study that explicitly tested for an effect of maternal kin availability on paternal kin relationship strength found such an effect since the study on yellow baboons (Charpentier et al., 2012; Cords et al., 2018; Lynch et al., 2017). The strongest compensatory effect in yellow baboons was observed when both paternal half-sisters had no mother or daughters present in the group (Silk et al., 2006). This might partly explain why the effect was not replicated in my and other more recent studies, in which most or all females had at least one close maternal kin available to bond with (Charpentier et al., 2012; Cords et al., 2018; Lynch et al., 2017). Nevertheless, this suggests that bonds with paternal kin might develop because they are valuable *per se* and not just when preferred close maternal kin are not available.

From the perspective of kin selection, viewing paternal kin as equally good bonding partners makes sense: maternal and paternal half-sisters share the same number of genes ($r = 0.25$), so cooperation with them leads to the same indirect fitness benefits (Hamilton, 1964). This idea is supported by evidence from mandrills (*Mandrillus sphinx*), in which juveniles who have less close paternal kin available tend to form stronger affiliative relationships with more distant maternal kin (with whom they share a smaller number of genes; Charpentier et al., 2012). Moreover, females who received little affiliation as juveniles give birth approximately one year later than females who were well-integrated into the group as juveniles, regardless of whether affiliation was received from paternal or maternal kin. Therefore, it seems that individuals might benefit from expanding their kin networks to include paternal half-sisters (rather than more distant maternal kin).

In some cases, paternal half-sisters might even be better bonding partners than close maternal kin. In species in which females produce a single offspring at birth, maternal half-sisters are born at least one, and usually several years apart, while paternal half-sisters can be born within the same age cohort. Relationships between paternal half-sisters might thus develop early on through playing and growing up together, and paternal half-sisters close in age could share needs and capabilities throughout their lives (Altmann, 1979a; de Waal and Luttrell, 1986; Mitani et al., 2002). Moreover, maternal kin often occupy adjacent ranks in the hierarchy, whereas paternal kin might differ strongly in their dominance status (Cheney, 1977; Holekamp and Smale, 1991). Particularly for females belonging to lower-ranking matrilines, paternal half-sisters might therefore be valuable allies. In Assamese macaques, social bonds enhance feeding tolerance (Heesen et al., 2014), so by forming bonds with higher-ranking paternal half-sister, females might increase their access to food resources.

The accumulating evidence that females form bonds with both maternal and paternal kin can help understand differences in tolerance between species. Interspecific differences in female relationships have typically been considered from the perspective of feeding competition, whereby affiliation among maternally unrelated females is attributed to increased tolerance in light of group members relying on each other's participation in between-group competition (Sterck et al., 1997). Alternatively, it has been suggested that in species with high reproductive skew, most group members are closely related, which then leads to indifferent tolerance towards all group members (Lukas and Clutton-Brock, 2018). It might be, however, that the observed tolerance in fact reflects "hidden paternal relatedness" so that females are not tolerant towards any group member, but selectively towards both maternal and paternal kin. In species with a high male reproductive skew and/or a long alpha male tenure, many paternal links might exist within the group, which can form bridges between matrilines, resulting in increased tolerance at the group level (Schülke and Ostner, 2008).

4.2. O Sister, Where Art Thou?

A key issue in the development of behavioural kin biases is kin recognition (Mateo, 2004; Penn and Frommen, 2010). Mammal infants are continually associated with their mother from birth (Broad et al., 2006), so maternal kin recognition is both easy and accurate, and consequently, mother-offspring bonds are the strongest bonds found in the mammalian kingdom (Seyfarth and Cheney, 2012). Any other kin relationship needs to be assessed more indirectly, which in turn decreases accuracy (Berman, 2015). Whereas social cues of maternal relatedness are usually strong and unambiguous, paternal kin discrimination is based on proxies that are likely more prone to error (Widdig, 2007). Whether animals can assess paternal relatedness from such proxies and how accurate those cues are is currently under debate (Widdig 2007, 2013; Langergraber 2012; Godoy et al. 2016).

One paternal kin recognition mechanism that has received particular attention is familiarity via age proximity (Altmann, 1979a; Godoy et al., 2016a; Langergraber, 2012; Langergraber et al., 2007; Silk et al., 2006; Smith et al., 2003; Widdig, 2007, 2013; Widdig et al., 2001, 2002). In species with a high male reproductive skew and a short alpha male tenure relative to the interbirth interval, infants that are born close in time are likely paternal siblings. Because infants of the same age cohort grow up together, potentially forming early and enduring social bonds, age cohort membership might thus be a mechanism for the familiarization of paternal kin (Altmann, 1979a; Widdig, 2013). The issue is however that although seasonal reproduction should create clear age cohorts of paternal siblings, increased seasonality also decreases monopolization potential, and therefore reproductive skew among males, thereby reducing the chance that age cohort members are paternal kin (Langergraber, 2012). Now that actual paternities are known for natural populations, male reproductive skew at any given time is hardly ever as extreme as was predicted, and males often produce offspring over multiple cohorts of infants (Langergraber et al., 2007). As a result, the majority of closely aged individuals are not paternal siblings, and members of different age cohorts can be as closely (or even more closely) related to each other as individuals born in the same cohort. This means that if paternal kin recognition is based on age cohort membership, unrelated individuals born into the same age cohort would wrongly be considered kin, and more importantly, fathers, offspring and older or younger siblings would not be distinguished from unrelated individuals.

Based on the limited data so far, the importance of age proximity as a proxy for paternal relatedness might not be as important as originally assumed. Although in some species kin biases towards paternal kin tend to be more pronounced between individuals closer in age, they are not limited to age mates, indicating that age similarity alone cannot fully explain the development of paternal kin biases (Alberts, 1999; Lynch et al., 2017; Silk et al., 2006; Smith et al., 2003; Widdig et al., 2001, 2002). Moreover, other species show paternal kin biases in affiliation but no effect of age similarity, even though reproduction is rather strongly skewed towards the dominant or resident male (Charpentier et al., 2007; Cords et al., 2018). I studied Assamese macaques specifically with the intention to test whether biases towards paternal kin might also develop in a species with a relatively low male reproductive skew (29% alpha male paternity; Sukmak et al., 2014) and a relatively long alpha male tenure (Ostner et al., 2013), so that age proximity would not be a reliable cue to paternal relatedness. As expected, I found that age cohort membership and age proximity did not affect paternal kin biases, adding to the idea that age proximity varies in quality as a proxy of paternal relatedness, and is neither necessary nor sufficient to reliably mediate paternal kin biases in affiliation.

A second kin recognition mechanism that has received increased attention in recent years is phenotypic matching. Several studies have reported auditory, visual and olfactory cues that contain information about relatedness (Bower et al., 2012; Charpentier et al., 2008a; Deecke et al., 2010; Huchard et al., 2010; Kazem and Widdig, 2013; Levréro et al., 2015; Mateo, 2002, 2017; Setchell et al., 2011). There is also evidence that animals respond differently to stimuli from related versus unrelated individuals (Charpentier et al., 2010; Charpentier et al., 2017; Gilad et al., 2016; Henkel and Setchell, 2018; Kessler et al., 2012; Leclaire et al., 2013; Levréro et al., 2015; Pfefferle et al., 2014b, 2015). Cues co-varying with relatedness do not always elicit different responses, however, nor are different responses necessarily based on cues reflecting relatedness (Deecke et al., 2010; Huchard et al., 2010; Pfefferle et al., 2016). Different responses are also only evidence for kin recognition (the ability to distinguish kin from non-kin) but not for the second component of kin discrimination, that is, kin bias (the differential treatment of kin). The fact that animals are capable of recognizing kin does not necessary translate into their treating kin differently, as has been shown in meerkats (*Suricata suricatta*) and two species of ground squirrels (*Spermophilus beldingi* and *Spermophilus lateralis*; Leclaire et al., 2013; Mateo, 2002).

A further issue with the current evidence for phenotypic matching is that only some of the studies were able to control for familiarity (Charpentier et al., 2010; Charpentier et al., 2017; Leclaire et al., 2013; Levréro et al., 2015; Pfefferle et al., 2014a; Pfefferle et al., 2014b), a prerequisite for demonstrating true phenotypic matching (Mateo, 2004; Penn and Frommen, 2010; Rendall, 2004). A common misconception is that if kin recognition is based on phenotypic cues, the mechanism behind it is phenotypic matching (Tang-Martinez, 2001). The recognition of familiar individuals also relies on such cues, but the critical difference is that cues specific to the individual are learned and recognized, whereas kin recognition through phenotypic matching operates through the learning of kin-specific cues from familiar kin or the animal itself (Mateo, 2004). That animals use themselves as template for facial traits or vocal characteristics, however, is unlikely, as they hardly ever see their own face and perceive their own calls acoustically differently than those of others (Pfefferle et al., 2014b). This means that at least some kin must be recognized through familiarity for animals to learn the kin-distinctive template.

A final issue with phenotypic matching is that very accurate kin recognition might not always be beneficial. In species with high infanticide risk, for example, paternity might better be concealed so that multiple males who have a high enough probability of paternity would protect an infant and refrain from attacking it (Alberts and Fitzpatrick, 2012; Nunn, 1999). The benefit of concealed paternity to the infant (life versus death) outweighs the cost for the male (potentially wasted resources), which might have hampered the selection for very accurate kin recognition mechanisms (Rendall, 2004).

4.3. It is a wise father who knows his own child

An alternative, yet so far rather understudied, mechanism of paternal kin recognition in primates is mother- and/or father-mediated familiarity (Widdig, 2007). Primates are exceptional among mammals when it comes to male-female associations. In about two-thirds of the genera, males and females are associated throughout the year, whereas in the majority of other mammals, adult males and females only briefly meet during the period of female receptivity (Van Schaik and Kappeler, 1997). Moreover, male-female relationships and paternal care in most mammals are usually limited to pair-living species or species living in small family groups in which males have a high paternity certainty (Lukas and Clutton-Brock, 2013; Trivers, 1972). In contrast, associations between males and females have evolved in a number of primate species living in multi-male-multi-female groups in which females mate with multiple males during their fertile period (Chapais, 1983; Haunhorst et al., 2016; Huchard et al., 2010; Kerhoas et al., 2016; Langergraber et al., 2013; Lemasson et al., 2008; Ménard et al., 2001; Moscovice et al., 2010; Nguyen et al., 2009; Ostner et al., 2013; Palombit et al., 1997; Takahata, 1982). These relationships, sometimes called “friendships” (Smuts, 1985), are characterized by close spatial proximity, grooming, support, and low rates of aggression, and they typically continue for many months, persisting beyond the female’s receptive period (Cheney et al., 2012; Haunhorst et al., 2017; Lemasson et al., 2008; Seyfarth, 1978b). The adaptive function of such associations is addressed by two main hypotheses: the mating effort hypothesis (or “care-then-mate”), and the parental effort hypothesis (or "mate-then-care"; Ménard et al., 2001; Ostner et al., 2013; Van Schaik and Paul, 1996).

According to the mating effort hypothesis, males form relationships with females in order to sire their future offspring, and this with the assumption of effective female choice for males that behaved affiliatively towards them and their dependent offspring (Seyfarth, 1978a; Van Schaik and Paul, 1996). Support for this hypothesis is quite limited. Only three studies so far found that forming a relationship with a female and/or her offspring outside of the mating season led to increased mating access (Langergraber et al., 2013; Ménard et al., 2001; Smuts, 1985), while several studies failed to find such a link (Baniel et al., 2016; Kuběnová et al., 2019; Kulik et al., 2012; Murray et al., 2016; Nguyen et al., 2009; Ostner et al., 2013; Weingrill, 2000). A variant of the classical mating effort hypothesis is the "friends-with-benefits" hypothesis, which relates mating patterns to stable affiliative relationships between males and females that last longer than the period just before the mating season (Ostner et al., 2013). There is some evidence in support of this hypothesis (Kuběnová et al., 2019; Kulik et al., 2012; Langergraber et al., 2013; Ostner et al., 2013). Male-female associations might be an alternative mating strategy for males who are not able to consort a female successfully (Ostner et al., 2013).

Alternatively, the parental effort hypothesis proposes that male-female associations represent a form of paternal care (Trivers, 1972; Van Schaik and Kappeler, 1997). From this point of view, males associate with females with whom they sired offspring, in order to provide protection against infanticide (Engh et al., 2006b; Palombit, 1999; Palombit et al., 1997; Weingrill, 2000) and harassment (Huchard et al., 2013; Lemasson et al., 2008; Moscovice et al., 2009; Nguyen et al., 2009; Smuts, 1985). This hypothesis has received greater support. In several species, most male-female associations are formed between a female and a male who had mated with her during her fertile period (Bercovitch, 1991; Moscovice et al., 2010; Nguyen et al., 2009; Palombit et al., 1997; Smuts, 1985; Weingrill, 2000). Genetic studies confirm that male associates are often sires of the female's infant (Baniel et al., 2016; Huchard et al., 2010; Moscovice et al., 2010; Nguyen et al., 2009; Ostner et al., 2013; Städele et al., 2019).

An important assumption of the parental effort hypothesis is that males are able to (at least somewhat) reliably distinguish their offspring from other infants. Males are expected to associate with infants and their mothers based on their likelihood of paternity, which they might assess based on behavioural proxies such as previous mating success with the mother (Buchan et al., 2003; Busse, 1985; Moscovice et al., 2010; Moscovice et al., 2009; Van Noordwijk and Van Schaik, 1988). In species in which sexual swellings are accurate indicators of ovulation, paternity certainty might be rather high despite promiscuous mating (Alberts and Fitzpatrick, 2012). In yellow and olive baboons (*Papio anubis*), swellings accurately signal conception probability (Gesquiere et al., 2007; Higham et al., 2008), and relationship strength between a male and a fully swollen female reliably predicts paternity (Buchan et al., 2003; Städele et al., 2019). Alternatively, male-female associations might start at conception, rather than at the time of birth of an infant, and the relationship might then be maintained throughout pregnancy and lactation (Baniel et al., 2016). In line with this, male-female associations during pregnancy have been reported in olive baboons, chacma baboons (*Papio ursinus*) and Assamese macaques (Baniel et al., 2016; Ostner et al., 2013; Smuts, 1985; Städele et al., 2019; Weingrill, 2000). Associations between a male and the female that is pregnant with his offspring might reduce the stress the female experiences and in turn increase foetal survival (Weingrill, 2000), as well as provide protection against feticide (Städele et al., 2019; Zipple et al., 2017).

Further evidence for the parental effort hypothesis is that male-female associations often result in male-infant associations that last beyond weaning. There is evidence that these associations are between a father and its offspring in a variety of primate species (Godoy et al., 2016a; Huchard et al., 2013; Langos et al., 2013; Lehmann et al., 2006; Minge et al., 2016; Murray et al., 2016; Onyango et al., 2013; Ostner et al., 2013; but see Kerhoas et al., 2016; Ménard et al., 2001; Sargeant et al., 2016), with preferential associations even still occurring between adolescent chimpanzees and their father (Sandel et al., 2020). Even more convincing is evidence that males provide paternal care selectively to the infants they sired. Males avoid committing infanticide against their own offspring and protect them against other infanticidal males in several primate species (Borries et al., 1999; Soltis et al., 2000; Watts, 1989). Yellow baboon males support their juvenile offspring in agonistic conflicts (Buchan et al., 2003), and immatures whose father is present in the group for a longer time reach maturity at a younger age (Charpentier et al., 2008c). In chacma baboons, fathers tolerate their infants while feeding so that they gain access to high quality food (Huchard et al., 2013).

It seems that the long-held view that paternal care in primates is rare, except for in monogamous species, needs to be reconsidered. Primates have slow life histories and low reproductive rates, and infant mortality is relatively high, meaning that male primates will sire only a few offspring who survive infancy. Offspring survival might therefore be of greater importance to overall fitness than reproductive rates, even in males (Alberts and Fitzpatrick, 2012). Although paternity certainty can never be perfect in promiscuous species, providing paternal care with a certain degree of error might still be selected for as long as the costs of providing care to an offspring (rejection error) outweigh the costs of providing care to an unrelated infant (acceptance error; Clarke et al., 2009; Moscovice et al., 2009; Penn and Frommen, 2010).

Coming back to kin recognition, it seems plausible that males associate with the likely mothers of their offspring, either by associating with them right after conception or by estimating their chances of being the sire based on their previous mating effort. This in turn might facilitate the development of male-infant associations and paternal care. Infants could become familiarized with their father first through the association between their parents and/or later on through paternal care. If females share a common male associate (Haunhorst et al., 2016; Seyfarth and Cheney, 2012), or if males provide care to several of their offspring (Huchard et al., 2010), this might subsequentially allow for paternal half-siblings to be familiarized with each other, much like maternal half-sibling familiarity is mediated by attraction to the common mother. In olive baboons, affiliative relationships between immature paternal half-siblings are stronger if the shared father is present in the group, which suggests that shared association with a common father might be important for the development of kin biases towards paternal half-sisters (Lynch et al., 2017). More studies investigating the impact of father presence and of father-offspring associations on kin biases between paternal half-siblings are necessary to better estimate the role of parent-mediated familiarity in paternal kin recognition. It might be, for example, that the age proximity effects on paternal kin discrimination result from similarly-aged juveniles being associated to their shared father at the same time, rather than from age cohort membership. Two points need to be further established: (1) whether fathers associate more with their genetic offspring than with other juveniles, and (2) whether paternal half-siblings who are both associated to their father early in life form stronger relationships than paternal half-siblings who were not simultaneously associated to their father or whose father was not present in the group during ontogeny.

4.4. Bros and brothers

As is clear by now, kin-biased bonds between females are widespread throughout the mammalian kingdom. Before turning to male sociality, it’s important to keep in mind two major differences between the sexes. First, female lifetime reproductive success is determined by a long life in good condition, which depends mostly on safety and access to food resources (Sterck et al., 1997). By forming strong bonds, females can benefit from feeding tolerance and agonistic support, which increases their access to shareable resources (Ostner and Schülke, 2018). Male bonding, on the other hand, seems to be both rare and fragile in comparison to female bonding. Because males compete over unshareable fertilizations, male relationships were long expected to be strictly competitive in nature. However, male bonds can and do develop but only under specific socio-ecological conditions (Ostner and Schülke, 2014; Whitehead and Connor, 2005). Second, females are usually the philopatric sex (Greenwood, 1980), so they spend their entire life surrounded by familiar relatives, which promotes tolerance, affiliation and bonding among kin (Möller, 2012; Silk, 2006). Males, on the other hand, usually disperse from their natal group and spend the greater part of their life surrounded by unfamiliar, unrelated individuals (Albers and Widdig, 2012; Greenwood, 1980). Social bonding among co-resident males was therefore believed to be confined to the rare male-philopatric species, in which familiar kin can gain inclusive fitness benefits from tolerating and supporting each other (Van Hooff, 2000; Van Hooff and Van Schaik, 1994; Van Schaik et al., 2006).

Since male sociality first came into the spotlight about twenty-five years ago, data on the diverse ways males affiliate and cooperate have accumulated, and a next generation of theoretical modelling has emerged to explain when and why males are expected to develop social bonds (Jack and Riley, 2014; Ostner and Schülke, 2014). It is now believed that when within-group competition is relaxed, bonds can develop as a way to build and test mutual trust between partners. Under these circumstances, rank-changing coalitions are both feasible and profitable (Bissonnette et al., 2014; Ostner and Schülke, 2014; Van Hooff and Van Schaik, 1994), and alliance stability is important to avoid costly retaliation by the outranked male, creating the need for reliable partners (Muller and Mitani, 2005; Ostner and Schülke, 2014; Van Schaik et al., 2006). Empirical data support this, as strong male bonds have been linked to coalitionary support in a number of species (Berghänel et al., 2011; Connor et al., 2006; Gerber et al., 2019; Kulik et al., 2012; Muller and Mitani, 2005; Silk, 1994).

If bonding mediates the formation of coalitions from which both partners gain benefits, then the role of kinship in bonding might be less influential than originally assumed. In line with this, there is increasing evidence of male affiliation and coalitionary support in male-dispersing species (Adiseshan et al., 2011; Berghänel et al., 2011; Berman et al., 2007; East and Hofer, 2001; Freeman et al., 2016; Gabriel et al., 2014; Jack and Riley, 2014; Kulik et al., 2012; Mitchell, 1994; Packer et al., 1991; Riley et al., 2014; Schoof and Jack, 2014; Silk, 1994; Teichroeb et al., 2014; Widdig et al., 2000; Young et al., 2014a). Still, kinship does seem to facilitate male association, affiliation and support, even in dispersing males (Chiyo et al., 2011; Packer et al., 1991; Silk, 1992; Vidya and Sukumar, 2005; Wahaj et al., 2004; Widdig et al., 2000). Post-dispersal males might have close kin available if they disperse together with kin or join groups containing kin (Albers and Widdig, 2012; Gerber et al., 2016; Mitchell, 1994; Packer and Pusey, 1982; Schoof and Jack, 2014; Schoof et al., 2009; Strier, 2004). Whether male bonds can develop in the absence of a strong kin bias remains ambiguous.

So far, the impact of kinship on the formation of strong, stable social bonds has been explicitly studied only in three male-philopatric species, partly because male bonding is so rare. In chimpanzees, males affiliate and cooperate at higher rates with maternal half-brothers and their father and sons, but do not discriminate paternal half-brothers from non-kin, and form most of their social bonds with unrelated individuals (Langergraber et al., 2007; Mitani, 2009; Sandel et al., 2020). In bottlenose dolphins (*Tursiops sp.*), maternal kinship and biparental relatedness underly the formation of stable alliances in some populations (Diaz-Aguirre et al., 2018; Parsons et al., 2003), but not in others (Connor and Krützen, 2015; Gerber et al., 2019; Möller et al., 2001; Wiszniewski et al., 2012a). In Guinea baboons (*Papio papio*), strongly bonded males are on average more related, but unrelated males also form strong bonds, and close kin do not necessarily form strong bonds (F. Dal Pesco, pers. comm.). Taken together, it appears that bonds are not restricted to related individuals, which can possibly be attributed to limited availability of kin as coalition partners. Although all three species are male-philopatric, they are also characterized by long interbirth intervals and relatively low male reproductive skew (at the party level for Guinea baboons, F. Dal Pesco, pers. comm.; Langergraber et al., 2007; Mitani, 2009; Mitani et al., 2002; Möller et al., 2001). Even if bonds can also develop between unrelated males in these species, philopatry might still have been a crucial mechanism driving the evolution of male social bonding. It could be that cooperation initially originated among kin, providing males with the basic behavioural and emotional mechanisms that were subsequently applied to cooperation among non-kin (Van Schaik and Kappeler, 2006; West et al., 2007a). In addition, male group composition is more stable in male-philopatric than in male-dispersing species, better allowing for the development of long-term alliances (Freeman et al., 2016; Ostner and Schülke, 2014).

In contrast to the previous studies, I investigated the role of kinship in the formation of strong social bonds in a male-dispersing species, the Assamese macaque. As expected, I found that post-dispersal males have few close kin available in their group (Table 2). Nevertheless, males formed stronger relationships with those few related group mates than with the average non-kin, and average relatedness among strongly bonded dyads was twice as high as between males forming weak relationships (strong bonds: average r = 0.16; weak ties: average r = 0.08; N = 642). On the other hand, I also found that males form most of their bonds with non-kin, independent of the number of close kin available, and bonds between non-kin could be as strong as bonds between close kin. Since males sometimes even chose non-kin over available close kin to bond with, bonding with unrelated individuals could not be explained by a lack of available kin. It therefore appears that although kinship facilitates bonding, it is not a prerequisite for it. Males might have formed bonds with unrelated males rather than with available kin either because they could not recognize unfamiliar kin or because non-kin might have possessed traits that available kin partners lacked.

Table 2: Average (±SD) number of partners, of close kin partners and of strongly bonded partners, proportion of strong bonds formed with close kin and average (±SE) relatedness for females and males

	Average no. partners	Average no. close kin	Average no. strong bonds	Proportion strong bonds with close kin	Average relatedness
Females	13.05 ± 3.54	3.52 ± 1.75	1.48 ± 1.39	58%	0.15 ± 0.006
Males	7.36 ± 2.46	1.05 ± 1.07	1.27 ± 1.30	29%	0.10 ± 0.004

Values calculated over all groups throughout the study period

Relatedness calculated using the TrioML estimator (Wang, 2007)

Partners: same-sex adult group members; close kin: relatedness > 0.25

Strong bonds: for males Elo-rating > mean Elo-rating + SD; for females CSI > 2 (with CSI > 1: 4.94)

Average relatedness calculated between same-sex adult individuals

As discussed above, there is strong evidence that kin recognition in mammals is mediated by familiarity, particularly early on in life (Tang-Martinez, 2001; Widdig, 2007). When males leave their natal group, they leave the majority of their kin behind and enter a new group of (mostly) unfamiliar individuals, among which some might be kin (Albers and Widdig, 2012). Immigrant males, which lack a period of familiarization with those related individuals early in life, might not be capable of discriminating kin from non-kin in their new group. However, if males disperse from their natal group together with kin they grew up with, they should be able to discriminate those joint dispersal partners as kin (Albers and Widdig, 2012). Based on a still very limited sample size, however, even plausibly familiar kin do not seem to be preferred bonding partners in male Assamese macaques. The few related males in my dataset for whom we know that they left their natal group together formed affiliative relationships of average strength with each other (average Elo-rating over groups and years = 0.495, N = 11, based on 5 unique dyads). Moreover, kin do not always form strong bonds in philopatric males, in which familiarity should not be an issue (unless males disperse as juveniles together with their mother after the crucial period of familiarization; Connor and Krützen, 2015; Gerber et al., 2019; Langergraber et al., 2007; F. Dal Pesco, pers. comm.; Möller et al., 2001; Wiszniewski et al., 2012a). It therefore seems that factors other than kinship might play a larger role in male partner choice for bonding.

Because bonded partners act as allies in risky coalitions, males can maximize their reproductive success by forming bonds with competent, reliable and compatible alliance partners. The tendency to form coalitions with higher-ranking males to optimize the probability of the coalition being successful has been demonstrated repeatedly (Bissonnette et al., 2009; Kajokaite et al., 2019; Noë, 1992; Noë and Sluijter, 1995; Perry et al., 2004; Schino et al., 2006; Silk, 1999; Smith et al., 2007; Young et al., 2014a). Although a preference for high-ranking partners is typically considered in the context of opportunistic, short-term coalitions (Kajokaite et al., 2019; Noë and Sluijter, 1995; Ostner and Schülke, 2014; Young et al., 2014a), there is no reason why dominance rank should play no role in the choice of partners for long-term alliances. Given the long-term nature of social bonds underlying partner choice in such coalitions, males might be constrained to some extent in their flexibility of whom to support (Young et al., 2014b). Still, males would benefit from "bonding up the hierarchy" (Seyfarth, 1977), forming strong bonds with the most dominant partner available, as this would increase their chances of forming successful coalitions (Van Schaik et al., 2006). Moreover, males might also obtain other benefits from their bond partners, such as food sharing (Samuni et al., 2018) and mating concessions (Bray et al., 2016; Duffy et al., 2007), which are best provided by high-ranking individuals.

The effective strength of a coalition might not only depend on the combined dominance rank of both partners, but might also be affected by its level of coordination (Connor et al., 2006; Noë, 1994; Smuts, 1985). Males might therefore bond with group mates similar in traits such as dominance rank, age and personality because they are more compatible partners (principle of homophily; Fu et al., 2012; McPherson et al., 2001). Individuals close in rank have similar needs, access to resources, and are well placed to exchange social benefits (de Waal and Luttrell, 1986; Mitani et al., 2002; Watts, 2000). Likewise, males close in age are at similar life-history stages with similar capabilities and interests (de Waal and Luttrell, 1986; Mitani et al., 2002). Moreover, age mates that grew up together are likely familiar with one another, either because they are philopatric or because they engaged in joint natal dispersal. Males with similar personalities might be able to perform more coordinated coalitions because they are more predictable and might communicate their intentions more effectively (Fu et al., 2012; McPherson et al., 2001; Noë, 1992). Finally, males with a long, (positive) shared demographic history might know each other better, making them more predictable and reliable partners (Noë and Sluijter, 1995; Schoof and Jack, 2014).

There is evidence that relationship quality and/or affiliation rates are affected by similarity in rank, age and personality in several species (Chiyo et al., 2011; de Villiers et al., 2003; de Waal and Luttrell, 1986; Foerster et al., 2015; Gerber et al., 2019; Higham and Maestripieri, 2010; Massen and Koski, 2014; Mitani, 2009; Mitani et al., 2002; Morton et al., 2015; Ramp et al., 2010; Seyfarth, 1977; Seyfarth et al., 2014; Silk et al., 2006; Watts, 2000; Widdig et al., 2001), as well as by the extent of shared demographic history (or "familiarity", not to be confused with familiarity during early life, as used throughout this thesis (Box 1); Elliser and Herzing, 2014; Higham and Maestripieri, 2010; Schoof and Jack, 2014; Wikberg et al., 2014a). Whether similarity in rank between affiliative dyads reflects an attraction to high-ranking partners constrained by competition for those partners or an attraction for partners close in rank is hard to tell. Moreover, rank similarity might be the consequence rather than the cause of bonding if close partners pull each other to similar ranks (Schülke et al., 2010). I found no effect of rank similarity for the Assamese macaques, which is in line with previous findings showing that social bonds predict rank and not vice versa (Schülke et al., 2010). There is evidence for personality homophily however as males more similar in the personality trait “Gregariousness” form stronger social bonds (Ebenau et al., 2019; an effect independent of kinship, as personality similarity and relatedness are not correlated; De Moor, Ostner and Schülke unpublished data). Because most males in my dataset were already adult at the start of data collection, I could not infer any effects of age (hard to estimate) or shared demographic history (largely unknown). The latter would be especially interesting, as this could be particularly important in dispersing males.

Rather than basing their partner choice on only one of the above-mentioned factors, males should consider the balance of direct and indirect fitness benefits of cooperating with a certain partner. To gain the highest indirect fitness benefits, cooperation should be directed at the closest relatives available (Altmann, 1979b; Chapais et al., 1997). Direct fitness benefits on the other hand, depend not on kinship but rather on the adequacy of partners for the task at hand, which in turn depends on traits such as age, dominance rank and specific skills (Chapais, 2006). A non-kin partner should therefore be preferred over a kin partner if $b + r * b < q * b$, with b the benefit of the cooperation, r the relatedness between the potential cooperation partners, and q the ratio of competence between the potential non-kin partner and the potential kin partner (Chapais, 2006). For example, a non-kin partner should be 1.25 times more competent to be chosen over a half-sibling ($r = 0.25$). Particularly for cooperation requiring specific characteristics, such as fighting capability and compatibility in the formation of potentially dangerous coalitions, q can vary strongly between potential partners, and cooperation with competent non-kin might be more profitable than cooperation with less qualified close kin (Chapais, 2006).

Disentangling the importance of different factors operating in concert is particularly challenging. When recruiting coalition partners, animals often have a choice between multiple group members present in the vicinity. Coalitionary behaviour therefore offers the opportunity to investigate which factors play a role in partner choice (Kajokaite et al., 2019; Perry et al., 2004; Schino et al., 2006; Young et al., 2014a). Recent statistical developments allow to pit different decision rules, as well as combinations of rules, against each other, rather than testing the importance of each decision rule independently against a null hypothesis (Kajokaite et al., 2019). Making use of such novel methods will allow testing what criteria go into male partner choice, and what criteria increase the probability of a coalition being successful.

In general, the fact that males form bonds with kin and non-kin alike, irrespective of dispersal mode, suggests that males gain direct fitness benefits from bonding. Indeed, bonding mediates partner choice in cooperation, which can provide males with substantial fitness benefits through increased reproductive success (Feh, 1999; Gilby et al., 2013; Muller and Mitani, 2005; Schülke et al., 2010; Wiszniewski et al., 2012b). Mutualism (or perhaps reciprocity), rather than kin selection, might therefore be the main mechanism that maintains cooperation, and, by extension, bonding in males (Clutton-Brock, 2009; Connor, 2010; Langergraber et al., 2007; Ostner and Schülke, 2014).

4.5. The kin selection bandwagon

On the whole, I found that bonding in both male and female Assamese macaques is biased towards kin, at least to some extent. With this, I add to a substantial and ever-growing body of literature showing that kinship is one of the main factors affecting animal behaviour (Seyfarth and Cheney, 2012; Silk, 2006, 2009; Smith, 2014). This has been considered as crude but convincing evidence for kin selection, as "an implicit equation between kin bias and kin selection was forged in the minds of many researchers" (Chapais and Berman, 2004; p. 5). A high degree of relatedness between cooperating individuals is, however, not sufficient evidence that kin selection is operating. Cooperation between kin might very well have been selected for the direct individual benefits it generates (Chapais, 2006; Clutton-Brock, 2002).

A fundamental distinction between cooperation between related individuals (driven by kin selection, leading to indirect fitness benefits) and between unrelated individuals (driven by reciprocity or mutualism, leading to direct fitness benefits) is typically made (Clutton-Brock, 2009; Van Schaik and Kappeler, 2006). In reality, however, direct and indirect fitness benefits operate in concert to shape social evolution (Carter et al., 2018; Chapais, 2001, 2006; Smith, 2014; Smith et al., 2010). For example, recent evidence shows that reciprocity takes place among kin as well as among non-kin, that kin biases might mask the evidence for reciprocity, and that reciprocity might in certain cases be an even be a better predictor of cooperation than kinship (Carter et al., 2019; Schino and Aureli, 2010; Schweinfurth and Call, 2019; Silk, 2013). Similarly, a shift in perspective has taken place in the framework of male social bonding, where the emphasis is placed on factors beyond kinship that should influence partner choice (as described in detail above).

The influential role of kinship needs to be considered beyond the context of kin selection. Three reasons explain why kin are ideal partners, even in the context of mutually beneficial cooperation. First, it pays more to engage in cooperation with relatives because of the added indirect fitness benefits, which holds true if the primary cause for the cooperative behaviour resides principally in direct benefits (Chapais, 2001). Second, kin are mutually dependent to obtain both direct and indirect fitness benefits, which gives them less incentives to defect, making them more reliable partners (Van Hooff and Van Schaik, 1994; Van Schaik and Kappeler, 2006). Finally, especially in the philopatric sex, relatives often possess traits, such as familiarity and proximity, that make them more predictable (Allen-Arave et al., 2008; Chapais and Bélisle, 2004).

Why then, if kin are the best collaborators and if bonding mediates cooperation, is it that strong bonds between non-kin have been reported for both males and females in a variety of species (Cameron et al., 2009; Candiotti et al., 2015; Gerber et al., 2019; Langergraber et al., 2007; Seyfarth et al., 2014; Silk et al., 2006; Wikberg et al., 2014b)? Three main factors constrain the development of kin biases in bonding: kin recognition, kin availability and kin competence (Chapais, 2006). As is evident throughout this thesis, kin biases in behaviour can develop only if kin can be (at least somewhat reliably) recognized. Familiarity, particularly during ontogeny, seems to play a crucial role in animals' ability to discriminate both maternal and paternal kin from non-kin (Rendall, 2004; Widdig, 2007; see also earlier in this chapter). Animals might not be capable of recognizing kin when they are only encountered after the learning phase, which can be the case for dispersing individuals (Mateo, 2004). A second factor limiting the development of kin biases is the availability of kin, both in the sense of having kin present in the group and having social access to related individuals. As epitomized in the idea of "grooming up the hierarchy" (Seyfarth, 1977), preferred partner choice and realized partner choice are not necessarily the same, and individuals might not be able to direct their affiliation towards their kin if other group members have prioritized access. Finally, even if kin are available and can be recognized, they might not be the most adequate cooperation partner. When engaging in attribute-dependent cooperation, such as the formation of coalitions, it might be more beneficial to choose competent and compatible partners over kin.

These constraints can help understand much of the variation in kin-biased behaviour discussed throughout this thesis. First, they can explain differences between the sexes. Males are usually the dispersing sex and tend to engage in risky coalitions, whereas females usually spend their entire life in close proximity of familiar kin, often of similar rank, in a rather stable hierarchy, in which coalitions mainly occur to reinforce existing dominance positions (Langergraber, 2012; Schülke and Ostner, 2012; Strier, 2004). It is therefore not surprising that kin biases are so pronounced in females in a wide variety of taxa, because kin can be recognized, are available, and are usually competent for the type of cooperation females engage in. For males, however, kinship seems to be only one of several factors underlying male partner choice. Males might not be able to recognize their kin, might not have kin available, or might prefer to bond with competent partners, a crucial factor determining the success of the coalitions they form. Such sex differences are already detectable early in ontogeny, with male juveniles typically less integrated into their maternal family than female juveniles (Cords et al., 2010; Kulik et al., 2015).

Second, these constraints can clarify differences between paternal and maternal kin. Paternal kin recognition relies on proxies that are less accurate than maternal kin recognition (Strier, 2004; Widdig, 2007). Biases in affiliation are still expected to develop despite a higher level of error but costlier behaviours such as agonistic support might be less pronounced towards paternal kin. Rhesus macaques (*Macaca mulatta*), for example, refrain from harming their paternal kin but do not actively support them in potentially costly conflicts (Widdig et al., 2006b). Paternal kin might also be attractive bonding partners for lower-ranking females, who might not have social access to their half-sisters because of social competition for high-ranking partners (Seyfarth, 1977).

A final point is that animals can take several criteria into account when making social decisions, as has been shown repeatedly (Bergman et al., 2003; Kajokaite et al., 2019; Mielke et al., 2017; Perry et al., 2004; Schino et al., 2006; Seyfarth et al., 2014; Young et al., 2014a). Moreover, partner choice does not need to be indefinitely stable. Animals live in dynamic social and ecological landscapes where "the ideal partner" is likely to change throughout their lives and among contexts (Henzi et al., 2009; Smith 2014). Taken together, it becomes apparent that to really understand partner choice in animals, direct and indirect fitness benefits as well as constraints on kin biases need to be integrated. Partner choice is likely to be driven not only by one, but by a complex set of interacting, context-dependent decision rules, based on several factors, such as kinship and partner competence, to maximize inclusive fitness (Carter, 2014; Smith, 2014).

4.6. Conclusion, future challenges and research avenues

"While a great deal of progress has been made in describing kin-related behavior patterns, our understanding about some of the most basic aspects of the concept (including the mechanisms of kin recognition, the precise categories of kin discriminated, and the role of kin selection) has not progressed at the same pace. In this sense, the concept of kinship is still, to a large extent, a black box. At the same time, this situation has begun to change rapidly over the last 10 years or so, and some light is beginning to penetrate parts of the black box."

– Chapais and Berman (2004; p. 3)

It has been sixteen years since this observation was made. Since then, much more light has penetrated the black box but with it, new dark areas have been uncovered too. Although more evidence for paternal kin biases has emerged, we still know little about how paternal kin recognize each other. An even darker spot in the kinship black box is that of the role of kinship in male social bonding. For dispersing males in particular, almost nothing is known about relatedness patterns of bonding partners. In this thesis, I addressed these two crucial gaps by studying a wild population of Assamese macaques. I found that females bias their affiliation and bonding to paternal half-sisters, even though age proximity was not a reliable cue of paternal kinship in this species. I went on to show that age proximity is not a necessary or sufficient cue for paternal relatedness, and I proposed an alternative paternal kin recognition mechanism: father- and/or mother-mediated familiarity. For post-dispersal males, I found that bonds can be formed between kin and non-kin alike, and I suggested that in general, partner competence and compatibility might play a larger role than kinship in male partner choice. Overall, I found that Assamese macaques form strong bonds with paternal kin and unrelated group members that could not be explained by a compensatory effect for preferred (maternal) kin, indicating that additional factors to (maternal) kinship play a role in partner choice. With this, I have shed a bit more light into the kinship black box and I hope to have encouraged other researchers to look beyond maternal kinship when studying partner choice in animals. Still, many dark corners remain, and I will now suggest some interesting future challenges and research avenues.

The genotyping of all individuals in the four study groups of Assamese macaques at the Phu Khieo Wildlife Sanctuary is underway, and individuals that have been observed since birth are starting to become adult. We know (and have sampled) the mothers of all individuals born into our study groups, allowing for better paternity assignment. While there are still substantial gaps in our current knowledge of kinship patterns of the population, the more recent branches of the pedigree will become more and more resolved. All together, this will allow us to tackle questions that so far remained largely unanswered: How many adult and immature kin does each individual really have available in the group? Is there, for example, an effect of how many offspring a female has on her relationship with her mother, or with paternal half-sisters? Are bonds between paternal half-sisters stronger if their father was present while they were growing up? Are the kin biases I observed in males between maternal kin or paternal kin, or both?

Because we follow four groups in our population, we also know (a large part of) the demographic history of many of the males that we have observed since birth. This will permit investigating how association history affects male bonding. Are kin biases in males more pronounced before they leave the natal group? Are males who were closely bonded in a previous group more inclined to bond again when they encounter each other in a new group? Do males who are closely bonded tend to migrate together, or do males who disperse together form strong bonds, or both? Does bond strength between males change as male characterics change, for example, if a bonded partner starts to be a less effective cooperation partner due to old age? On a shorter time scale too, shared association history likely impacts male bonding. Using the affilative Elo-rating method to track the dynamics of social bonding will allow us to answer questions on how positive and negative interactions impact relationship strenght. Do males who managed to gain in rank through coalitions subsequently stay in close proximity of each other as a protection against retaliation by the outranked male? If a male fails to come to help to his bonded partner, does this break down the relationship?

On a broader level, my studies add to two still very limited bodies of research: paternal kin biases in sociality and kinship effects on male social bonding. For a more general understanding of kinship and sociality in animals, more data are needed from species with a wider variety of dispersal patterns and mating systems. Only then can the variation in kin biases be explained in light of the interspecific demographic constraints.

Studies on kinship also tend to focus on the relatedness between cooperation partners, and ignore two other crucial factors: the costs and benefits (both direct and indirect) of cooperation. Animals, however, base their partner choice not just on one decision rule (e.g. "bond with kin"), but need to balance the direct and indirect fitness benefit they would obtain with each potential partner to maximize inclusive fitness. Disentangling the complex set of interacting factors that go into the social decisions that animals make represents a real challenge for future research.

One way to tackle this is to look at context-dependent cooperation in natural contexts (e.g. agonistic support against a juvenile vs. against an adult male, or feeding tolerance for a coveted vs. a widely available food resource). This way, costs and benefits can be compared among situations, and kinship (and other traits) can be compared among cooperation partners. It is also important to take into consideration which partners are available when animals recruit help, and how bystander composition affects partner choice (e.g. not recruiting a strongly bonded male for a coalition against that male's kin). Novel statistical methods allow to pit different (combinations of) factors, against each other, rather than considering their importance independently, which will undoubtedly greatly improve our understanding of the interplay between several possible factors.

Finally, the focus of this thesis has been on social bonds: strong, stable partnerships with a few group mates that individuals can rely on for support. But kinship might also impact other ways in which animals are connected into their group. Even though individuals might not form strong social bonds with all their related group mates, having a large number of relatives in the group might be beneficial. Considering indirect connections and higher level social network structure, females interacting with paternal kin and linking different matrilines might fundamentally change the structure of the social network of the group, which could impact information (or disease) transfer, again with possible fitness implications. Future research is needed to understand which aspects of sociality drive fitness benefits and how kinship affects all the different ways individuals can be well-connected.

Summary

Social bonds are found in social species spanning the entire mammalian kingdom. The formation of such bonds can be adaptive: strong links have been established between social integration and increased survival and/or reproductive success in a diverse range of taxa. A crucial step in understanding how animals benefit from forming social bonds is to understand what drives social partner preferences, and how partner choice can contribute to fitness consequences. One factor that has repeatedly been shown to have a profound influence on the social life of animals is kinship. Social mammals tend to associate, affiliate and cooperate with their relatives more than with unrelated group mates. The bulk of this research, however, has focused on maternal kinship in females. Much less is known about the role of paternal kinship in the development of social bonds and about the importance of kinship in male social bonding.

A key issue for the development of paternal kin biases is that many mammal females mate promiscuously so that paternity is concealed. Nevertheless, there is accumulating evidence showing that individuals can and do discriminate their paternal kin from non-kin. One mechanism proposed for paternal kin recognition is familiarity through age proximity. In species with relatively high reproductive skew and relatively short alpha male tenure, infants born into the same age cohort are likely paternal kin, and they might become familiarized with each other through growing up together. Based on both theoretical grounds and the limited data available, however, is seems that the role of age proximity for paternal kin recognition might have been overestimated.

Additional limitations constrain the development of kin biases in males. First, males face strong competition for access to fertile females, which is expected to hinder the formation of male relationships. Second, males usually disperse from their natal group, leaving most of their kin behind. For these two reasons, male social bonds were originally assumed to be restricted to the rare male-philopatric species in which males would have familiar kin available, and indirect fitness benefits would tip the balance in favour of risky cooperation in the contest for access to females. Counter to this idea, strong male bonds have also been reported in male-dispersing species. The question now is whether those bonds are restricted to the few close kin that post-dispersal males have available in their group, or whether factors other than kinship might underlie male partner choice in bonding.

In this thesis, I investigated how relatedness affects social bonding in wild Assamese macaques (*Macaca assamensis*), combining extensive behavioural data with relatedness analyses based on pedigree reconstruction. Assamese macaques are characterized by male dispersal and a relatively low reproductive skew, which allowed me to address two key questions that have remained largely unanswered so far: "Can paternal kin biases in affiliation develop in a species in which age proximity is not a reliable cue for paternal relatedness?" and "Are strongly bonded post-dispersal males generally closely related?"

My results show that female Assamese macaques biased their affiliation towards their paternal half-sisters, independent of age proximity and maternal kin availability. With this, I show that females did not just form strong bonds with their paternal half-sisters to compensate for a lack of close maternal kin, and that the role of age proximity as a cue for paternal relatedness might be less important than originally assumed. Instead, I propose that in primates, paternal kin might be recognized through the stable male-female associations that mothers typically form with the likely fathers of their offspring (i.e. mother- or father-mediated familiarity).

For male Assamese macaques, the results of the role of relatedness on bonding are more ambiguous. Post-dispersal males formed stronger bonds with the few close kin they had available than with the average non-kin. However, strong bonds were not exclusively formed with kin, and non-kin partners were chosen over available close kin partners in some cases. Relatedness seems to be only one of several factors influencing male bonding. Because bonds mediate partner choice in cooperation, which can provide males with substantial direct fitness benefits through increased reproductive success, competence and compatibility between partners might be more important than kinship.

In conclusion, kinship affects animal sociality beyond maternal kin biases in females. Nonetheless, kinship is only one piece of the puzzle, and individuals likely choose their partners based on a complex set of interacting, context-dependent decision rules. To better understand when and why kin biases develop, more data are needed from species with a wider variety of dispersal patterns and mating systems. Only then can the variation in kin biases be explained in light of the interspecific demographic constraints.

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Teachers open the door, but you must enter by yourself.
– Chinese proverb

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Göttingen, 22nd of January 2020

Delphine De Moor