REVIEW

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Growing into adulthood—a review on sex differences in the development of sociality across macaques

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Abstract

Preferential affiliative relationships, or social bonds, play a crucial role in primate social life, but little is known about their development. Here, we review macaque studies investigating the social development of both sexes. Firstly, we highlight the emergence of sex differences in mother–offspring bonds, as macaque mothers form stronger bonds with daughters, while being more aggressive towards sons, possibly contributing to maintain female philopatry and/or male dispersal. Secondly, despite paternity uncertainty, we discuss studies reporting that fathers of several macaque species preferentially engage with their offspring, but less than mothers and only in periods of high infant mortality. Thirdly, we show that immature females, the philopatric sex in macaques, already form stronger bonds with close maternal kin than immature males, mirroring social patterns during adulthood. However, this bias seems not caused by kin availability, as kin availability is similar for both sexes prior to male dispersal. Moreover, immature males might preferentially affiliate with paternal kin over non-kin, possibly because of lower maternal integration in their maternal family and/or in preparation of dispersal. Fourthly, we discuss how immature females engage in grooming and proximity with female partners as they grow older, while immature males preferentially interact with adult males and peers, playing more than females from early on. Finally, we show that most developmental changes in sociality happen around 2–3 years of age, probably representing a milestone in macaque social development. We conclude that sex differences in sociality emerge early in development and increase through time, with sexes gradually growing into their adult roles.

Keywords Social development · Macaques · Primates · Ontogeny · Sociality · Aggression

Introduction

Sociality plays a crucial role in primate life. Although primates mainly form preferential affiliative relationships (hereafter social bonds, see Silk 2007) with their close relatives (see Silk 2002a, for a review), such bonds can also occur among unrelated individuals (see Silk 2002b, for a review). Recently, several studies have shown that the strength and stability of these affiliative relationships significantly increase primate fitness. For example, the quality of social relationships positively affects females' (Engh et al. 2006a, b; Crockford et al. 2008; Wittig et al. 2008) and males' ability to deal with stressful events (Young et al. 2014) and considerably increases females' longevity (Silk et al. 2010). Social bonds also enhance individual reproductive performance (Schülke et al. 2010; Kulik et al. 2012; Langergraber et al. 2013) and increase infant survival (Silk et al. 2003, 2009). Even in humans, social integration significantly enhances longevity, as well as physical and mental health (e.g. Olsen et al.

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1991; Eriksson et al. 1999; Berkman and Glass 2000; Cacioppo and Hawkley 2003; Berkman et al. 2004; Smith and Christakis 2008; Holt-Lunstad et al. 2010).

While sociality and fitness have recently influenced the focus of many primate studies (see Kappeler et al. 2015), it is time to summarize what we actually know about the development of social bonds during ontogeny. A comprehensive understanding of such topic would come from studies covering the entire period from birth to sexual maturation, describing the development of several social behaviours (e.g. bonding behaviours, like grooming, shared spatial proximity, coalitionary support, play; but also behaviours negatively affecting bonding, like aggression, or behaviour repairing relationships, such as reconciliation) and discussing differences in social development in relation to the most important social partners, such as mothers, fathers, other kin and peers. However, available data from several primate species are often limited in this respect.

Firstly, they often cover only short time frames, failing to include infants, juveniles and adolescents (here respectively defined as nutritionally dependent offspring, weaned offspring who have not yet entered puberty, and offspring in puberty; see Pereira and Altmann 1985; Lonsdorf 2017). Secondly, few behaviours are usually observed in developmental studies. Aggressive behaviour, for instance, serves an important function in social relationships (e.g. Fraser et al. 2008), but they are only rarely studied from a developmental perspective. Thirdly, social relationships can critically vary depending on the identity of the focal sex and the social partners involved. For example, members of the philopatric sex may form closer bonds with their mothers given their permanent association, while members of the dispersing sex may form stronger relationships with same-sex peers likely to migrate around the same time. In general, individuals of the philopatric sex have close kin available as long-term partners; accordingly they are typically more closely related; hence, the philopatric sex is expected to form stronger social bonds than the dispersing sex (Di Fiore 2003; Clutton-Brock and Lukas 2012; see Widdig et al. 2016).

Even more important, however, is perhaps whether primate sociality follows different developmental trajectories in males and females. Given that primates are only weakly sexually differentiated at birth, sex differences in social behaviour mostly develop during the postnatal period (e.g. Lee 1984; Bentley-Condit 2003; Nguyen et al. 2012). If sex-specific social behaviours are an important aspect of adult behavioural competence, and hence linked to higher reproductive success, the proximate mechanisms underlying the development of sex-specific social behaviours become targets of selection (see Meredith 2013). Moreover, sexual selection will favour sex differences in social development, with females developing more caretaking and affiliative behaviour and males showing more competitive and aggressive behaviour (see Lonsdorf and Ross 2012). Depending upon their sex, immatures may therefore benefit from changing their social behaviour through development by increasing their future adult performance (i.e. practicing behavioural patterns typical of adulthood), without reducing their actual chances to survive. While philopatric females, for instance, could be expected to increase their frequency of affiliative behaviours, especially toward long-term social partners such as maternal kin, dispersing males could be expected to increase the frequency of social behaviours toward other males and age peers, with whom they either compete with or will likely migrate (see below).

To gain a comprehensive view of primate social development, we will extensively review literature to discuss how affiliative and aggressive behaviours develop from birth to sexual maturation depending on the social partners, with a special focus on the emergence of sex differences. We will especially draw attention on the results of longitudinal studies on free-ranging populations, including comprehensive genetic and demographic data, as these may provide a more exhaustive and representative picture of primate social development. We will, however, restrict our review to the genus *Macaca* (only referring to other primates when relevant), as with more than 20 species it represents a socio-ecologically highly diverse taxon (reviewed in Thierry 2007). All macaque species live in multi-male male–female groups, with males dispersing from their natal group around puberty (Gouzoules and Gouzoules 1987; Schülke and Ostner 2012) and females remaining in their natal groups (Gouzoules and Gouzoules 1987). Accordingly, macaque groups are characterized by maternally related females organized in matrilines. However, striking variations are apparent, for instance, in male ability to gain or maintain dominance and monopolize fertile females, resulting in different male reproductive skews (compared in Engelhardt et al. 2017). This has important consequences for the kin structure of social groups, as differences in male reproductive performance and ability to maintain high dominance lead to differences in the availability of paternally related peers (Widdig 2013). Moreover, both sexes mate with several partners, but mating relationships vary from regular transition of partners to prolonged mate guarding (Thierry 2007). Several macaque species are strictly seasonal breeders, while others give birth year-round or have several birth peaks (reviewed in Estrada and Estrada 1976; Smith 1984; Marty et al. 2017b). Finally, and perhaps most crucially, macaque species exhibit social relationships varying from intolerant or despotic (e.g. rhesus, *Macaca mulatta*, and Japanese macaques, *M. fuscata*), to more tolerant or egalitarian ones (e.g. crested macaques, *M. nigra*, and Tonkean macaques, *M. tonkeana*), in response to the different qualities of food resources (Thierry 2000). Such a variety of socio-ecological characteristics may have deep effects on the development of social relationships, as we will discuss below.

In the following sections, we will review the impact of mothers, fathers, other kin or other partners on the social relationships of immature macaques. In particular, we will focus on the developmental aspect of social bonding in male and female macaques throughout their first 4 years of life (representing the approximate period of sexual maturation in macaques; see, e.g. Dixson and Nevison 1997; Zehr et al. 2005). Throughout our contribution, we will highlight the variability of macaque sociality if data are available, we will discuss how the frequency of affiliative and aggressive social interactions change until adulthood in males and females, and we will show how different social circumstances may affect the development of offspring sociality.

The role of mothers in offspring social development

As in other primates, macaque mothers provide extensive care to their offspring and may thus strongly affect their development (starting as early as in the prenatal stage: see Schülke et al. in this Topical Collection). Consequently, mothers form the strongest social relationships with their offspring (e.g. Schülke et al. 2013). Their mothering styles vary from highly protective to highly tolerant, depending upon the social structure of the species (Thierry 1985; Maestripieri 1994a, b, c, for review see Maestripieri 2018 in this Topical Collection). For example, maternal protection is high in despotic species such as rhesus macaques (Berman 1980b) and pig-tailed macaques (*Macaca nemestrina*; Maestripieri 1994c), while stumptail macaques (*M. arctoides*) show low maternal protectiveness and low rejectiveness (Maestripieri 1994c).

Even within the same species, mothering style can vary strongly, with important consequences for offspring independence. In Japanese macaques, for example, infants of protective mothers are less interested in interacting with other social partners, while infants experiencing high maternal rejection initiate more social contacts with other juveniles and adults, suggesting that maternal rejection may promote independence, whereas maternal protectiveness may delay it (Schino et al. 2001; Bardi and Huffman 2002). In addition, parity was suggested to influence mother–offspring relationships in the first few months: in despotic species, for instance, multiparous mothers show higher rates of suckling rejection than primiparous mothers (Japanese macaques: Tanaka 1989) and higher maternal protection when no older sisters are present (rhesus macaques: Berman 1992). The lack of older offspring in primiparous females has even been suggested to influence infant personality (Hooley 1983).

If the development of sociality is affected by the social context experienced, and mothers are extensively present for their offspring, the way mothers behave toward their offspring may strongly affect the way their sociality develops (reviewed

in Lonsdorf 2017). Therefore, sex differences in sociality, which have been reported in adults across several macaque species (e.g. Bernstein and Ehardt 1985; Kapsalis and Berman 1996; Cooper and Bernstein 2000; see Ellis et al. 2013), might at least be partially triggered by the differential way in which mothers behave toward sons and daughters. Indeed, a study on Barbary macaques (*Macaca sylvanus*) showed that mothers of female newborns mainly interact with maternally related females, while mothers of male newborns preferentially interact with females of other matrilines, with the consequence that, by the age of 5 months, daughters stay closer to mothers than sons do (Timme 1995). These sex-specific differences may help daughters to integrate into their matrilines and sons into the more general network of the social group (Timme 1995). Other studies also reported that female juveniles associate with their mothers significantly more than male juveniles do (e.g. rhesus macaques: Missakian 1974; Japanese macaques: Itoigawa 1973; Nakamichi 1989; reviewed in Nakamichi and Yamada 2010).

Mothers also treat infants in a different way depending on their sex, moving and breaking contact more frequently with male rather than female offspring (Japanese macaques: Eaton et al. 1986). After their first year of life, both male and female Japanese macaques decrease the variety of social behaviours exchanged with their mothers (Nakamichi 1989), but males decrease the time spent with their mothers more than females do (Eaton et al. 1986; Nakamichi 1989). Moreover, immature male Japanese macaques bond more with male age peers, especially through social play, preceding peripheralization (Nakamichi 1989). In general, long-term studies reported a consistent bias in mother–daughter affiliative bonds (Missakian 1974; Nakamichi 1989), while less consistent patterns emerged from shorter-term studies (Hinde and Spencer-Booth 1967; Eaton et al. 1985; Tanaka 1989; Schino et al. 1995; Brown and Dixson 2000).
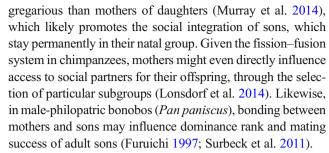
In an attempt to comprehensively investigate the effect of mothers on the development of offspring's sociality, a recent study on rhesus macaques assessed both affiliative and aggressive interactions between mothers and their offspring, from birth to sexual maturation. The results confirmed that mothers develop different bonds depending on the sex of their offspring but revealed in addition that the social context matters (Kulik et al. 2016). Firstly, no differences in mothers' investment are apparent, as suckling rates are the same for both sons and daughters (Kulik et al. 2016). This supports previous studies on rhesus macaques demonstrating that milk energy received is similar for both sexes, because sons receive richer milk but daughters more milk (Sear et al. 2009; but see Bercovitch et al. 2003 for similar sex-biased maternal investment). In addition to suckling, mothers have similar probabilities to share spatial proximity or grooming with sons or daughters in the first half year, but the probability of grooming and proximity decreases significantly more for sons than for

daughters between 6 and 12 months of age (Kulik et al. 2016). In contrast, a different pattern is found with regard to aggression, which is exclusively initiated by mothers. The probability to receive maternal aggression is higher for sons than daughters, within the first year; by that time, affiliative bonding between mothers and sons has already decreased. Similarly, maternal aggression peaks around 2 years of age for daughters, hence considerably later in life. Notably, maternal aggression towards sons largely occur spontaneously (i.e. not as a response to son's precedent behaviour), while daughters receive maternal aggression mainly when trying to handle newborn siblings (Kulik et al. 2016). Furthermore, older maternal sisters and unrelated adult females also direct more aggression toward male than female infants in the first year of life (Kulik et al. 2015b). These results have several potential implications. Firstly, they suggest that maternal aggression toward daughters may promote bonding inversely to the daughters' birth order, so that maternal investment can shift from older to younger offspring to maximize maternal fitness (see Godfray 1995; Crespi and Semeniuk 2004).

Secondly, maternal aggression has a strong negative impact on social bonding (e.g. Hinde and Simpson 1975; Worlein et al. 1988; Nakamichi 2001), so that early maternal aggression toward sons may be the most effective way to inhibit social bonds between sons and maternal family (Kulik et al. 2016). Such rejection may open opportunities that sons (i) search for alternative bonding partners (Kulik et al. 2016), (ii) become independent earlier (Bardi and Huffman 2002) or (iii) even disperse earlier from their natal group. Indeed, there is some indication that male immatures spending less time with their mothers and receiving more maternal aggression disperse earlier from their natal group (Kulik et al. 2016). This observation supports earlier suggestions in Japanese macaques that sons would leave their natal group as a function of their association with their mother (Itoigawa 1975). Similar findings on rhesus macaques, although based on a small sample, suggest that mother–son relationships between 2 and 3 years are predictive of the time of natal dispersal (Colvin 1986). Hence, mothers forming weaker bonds toward sons than daughters may contribute to promote male dispersal (cf. Timme 1995).

Finally, the stronger bonding between mothers and daughters is likely to promote female kin bonding and hence female philopatry (cf. Timme 1995). Previous studies have suggested a sex-bias in maternal behaviour in favour of the non-dispersing sex, resulting in stronger bonds between the mother and offspring of the philopatric sex. Such maternal bias may even allow mothers to positively affect future reproductive success of the philopatric sex (see Clark 1978; Dittus 1979; Bulmer and Taylor 1980). Interestingly, this pattern reverses when females disperse, so that maternal behaviour is generally biased in favour of the non-dispersing sex. In chimpanzees (*Pan troglodytes*), for instance, mothers of sons are more

gregarious than mothers of daughters (Murray et al. 2014), which likely promotes the social integration of sons, which stay permanently in their natal group. Given the fission–fusion system in chimpanzees, mothers might even directly influence access to social partners for their offspring, through the selection of particular subgroups (Lonsdorf et al. 2014). Likewise, in male-philopatric bonobos (*Pan paniscus*), bonding between mothers and sons may influence dominance rank and mating success of adult sons (Furuichi 1997; Surbeck et al. 2011).

In summary, existing studies suggest an important role of mothers in determining early social development in immatures. By selectively directing their affiliative and aggressive behaviours, mothers appear to determine the strength of future bonds with their offspring, facilitate male dispersal and foster daughters' integration in the maternal family.

The role of fathers in offspring social development

As female macaques mate promiscuously, paternity uncertainty is high (e.g. Manson 1992; Engelhardt et al. 2006; Dubuc et al. 2011, 2012; Ostner et al. 2013). Given this uncertainty, it seems unlikely to expect that male–infant bonds reflect paternity, unless males successfully mate-guard females and/or maximize their mating effort when the chance of fertilization is high (van Schaik and Paul 1996). Across macaques, however, female fertility signals vary from highly reliable (crested macaques, *Macaca nigra*: Higham et al. 2012) to being concealed to males (Assamese macaques, *M. assamensis*: Fürtbauer et al. 2011). In several macaque species, cues of fertility seem less precise, so that mate-guarding only partially matches female fertility, suggesting that in these species mate-guarding alone may not efficiently ensure paternity certainty (e.g. rhesus macaques: Dubuc et al. 2012; but see Engelhardt et al. 2004 for an opposite example in long-tailed macaques, *M. fascicularis*).

Given these facts, it seems unlikely that male macaques generally recognize their offspring (e.g. based on their mating success with the mother), thus reducing the chances that fathers significantly contribute to the development of offspring sociality. However, it is possible that fathers recognize their offspring post-birth, for example through specific phenotypic cues (see Widdig et al. 2001; reviewed in Widdig 2007). Recent studies have shown that human raters (Kazem and Widdig 2013) and even untrained rhesus monkeys (Pfefferle et al. 2014a) can reliably use visual cues to detect paternal relatedness in rhesus faces alone, with parent–offspring resemblance increasing with offspring age (Kazem et al. 2018). It is therefore plausible that immatures and fathers may recognize each other, despite paternity being uncertain. Consequently, fathers can be expected to bias their behaviour toward their own offspring and by doing so positively affect

their survival, but potentially also their social development. The evolution of male–infant bonds, at least father's presence and/or protection, should be favoured by selection, particularly in species with high risk of infanticide (van Schaik and Janson 2000). Given that mortality in macaques is considered highest within the first 2 years of their life (Dittus 1979; Blomquist 2013), both fathers and infants would enhance their fitness if male–infant bonds increase the chance of offspring survival (compare Kerhoas et al. 2016).

Primate studies on male–infant interactions have largely focused on baboons, reporting a behavioural bias of males towards their genetic offspring, with fathers providing protection, preferential access to food and spatial proximity (e.g. Buchan et al. 2003; Huchard et al. 2013; Onyango et al. 2013), while studies on macaques (particularly those with genetic paternity analysis) were more restricted and not conclusive. Male Barbary macaques, for instance, were shown to frequently handle infants, but not to preferentially interact with their genetic offspring (Kuester and Paul 1986; Paul et al. 1996). This result was confirmed in wild Barbary macaques, rejecting the mate-then-care (or paternal investment) hypothesis in this species (Ménard et al. 2001). However, the same study found that males providing infant care achieve higher mating success, supporting the care-then-mate hypothesis (Ménard et al. 2001). Similarly, genetic data in captive pigtail macaques suggested no preference in affiliation between fathers and offspring (Gust et al. 1996).

More evidence for paternal investment (although highly variable) was instead reported in captive rhesus macaques, where immatures selectively initiate associations with their fathers (Berenstain et al. 1981), and in free-ranging rhesus macaques, where immatures form persistent associations with specific males over the first 2 years of infancy (although paternity confirmation was lacking; Hill 1986). Finally, some troops of Japanese and stumptail macaques may also perform paternal care (including protection), but paternity in these studies was not confirmed by genetic analyses (Itani 1959; Gouzoules 1975; Smith and Peffer-Smith 1984).

More recent studies on free-ranging rhesus macaques, using genetic paternity analyses and longitudinal behavioural data from birth to sexual maturation, provide strong evidence that fathers are more likely to affiliate with their offspring, as compared to non-sires with unrelated infants (Langos et al. 2013). This bias is independent from the presence of the offspring's mother, suggesting that rhesus fathers preferentially interact with their offspring not simply to be closer to their mothers (Langos et al. 2013). The frequency of male–infant affiliation peaks at 2 years of age (Langos et al. 2013), matching the period when infant mortality is highest (Blomquist 2013). In contrast to previous studies, rhesus fathers preferentially initiate affiliation more than offspring do, especially toward sons (Langos et al. 2013). Possibly, this sex bias develops in response to the looser bonds that immature

rhesus males have with their mothers (cf. Kulik et al. 2016), forcing them to bond with individuals outside of their maternal family. However, rhesus fathers appear to do little more than being affiliative in the first 2 years of infants' lives. For example, despite many opportunities, males fail to provide agonistic support toward their offspring, when they are involved in conflicts with other group members (Kulik et al. 2012), contrasting findings on yellow baboons, *Papio cynocephalus*, who bias their agonistic support towards genetic offspring (Buchan et al. 2003).

In a longitudinal study on wild Assamese macaques, genetic paternity predicted male–infant associations after weaning, although such paternal care might be facilitated by male–female associations before weaning (Ostner et al. 2013). A recent study of the same population confirmed that these associations persist until the juvenile period is reached; however, infants maintain these bonds as they approach males more than vice versa. It was therefore suggested that infants actively seek male protection, and indeed, males provide agonistic support to immatures, which increases with the strength of their relationship (Minge et al. 2016).

While Assamese and rhesus macaques have a less pronounced skew in male reproduction, reproductive skew in male crested macaques is generally much higher (reviewed in Engelhardt et al. 2017). This indicates that high-ranking male crested macaques leave more offspring each, which might favour the formation of strong father–offspring bonds in this species. However, male crested macaques do not appear to form affiliative bonds with their offspring, at least not within the first year of life (Kerhoas et al. 2016). Given the intense male–male competition in this species, resulting in an extremely low mean alpha tenure of 12 months (Marty et al. 2017a), it is possible that males are selected to maximize their mating success rather than investing in bonds towards their genetic offspring. Nevertheless, despite absence of large predators, infant mortality in crested macaques reaches almost 20% in the first year of life (Engelhardt and Perwitasari-Farajallah 2008). A study of infant survival revealed that take-overs in alpha male position are the best predictor of infant mortality in crested macaques (Kerhoas et al. 2014). Particularly, aggressive encounters may be highly risky for infants; hence, fathers might be especially responsive in these circumstances, rather than generally investing in affiliative bonds with offspring. Indeed, infant screams, signalling risk, trigger more responses in fathers than in unrelated males (D. Kerhoas et al. unpublished data).

Apart from affiliation or support, father's presence alone might be beneficial for immatures. A study on yellow baboons suggests that the presence of fathers in the same group at the age of maturation can accelerate infants' physiological maturation (Charpentier et al. 2008), for example because infants benefit from male tolerance at richer food patches (Huchard et al. 2013). If the presence of fathers can impact offspring
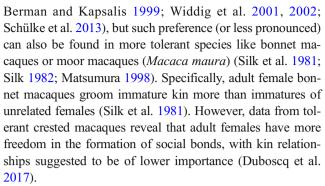
fitness, the same might be true for the strength of father–offspring bonds. However, longitudinal data on rhesus macaques suggest rather weak and sex-specific effects (Langos et al. 2015). For example, immature rank and more affiliation with dominant males tend to increase female (but not male) offspring's body mass (Langos et al. 2015). On the other hand, body mass gain is higher for male (but not female) offspring, when affiliation is more evenly distributed across adult males. Similarly, co-residence with fathers during the first 4 years of life has no positive effect on the offspring's lifetime reproductive success, while the presence of mothers clearly has a significant impact (Langos et al. 2015).

In summary, results from macaques suggest that even in species with low paternity confidence, males bias some behaviours toward their genetic offspring, providing low-cost paternal care. However, fitness benefits of such care for immatures might be limited, suggesting that paternal care provided during offspring development may be marginal when compared to that of mothers, at least across macaques. Possibly, fathers provide fitness benefits through more indirect pathways (e.g. epigenetic inheritance through male germline), accounting for the variation in offspring physiology, metabolism, disease risk and social development (reviewed for mammals in Braun and Champagne 2014).

The development of social interactions with maternal and paternal kin

Given that kin share some proportions of their genes, kin selection theory predicts the evolution of social behaviours increasing the fitness among relatives (Hamilton 1964). As a consequence, kin are expected to preferentially affiliate and cooperate with each other as compared to unrelated group members. Given the matrilineal structure of macaque societies, females (and males up to natal dispersal) have maternal kin of various degrees available in their social group and, depending on the degree of male reproductive skew, the availability of paternal kin might even be higher (e.g. Widdig et al. 2004, 2016).

Indeed, there is broad evidence from different primate species, including macaques, that individuals form stronger affiliative bonds with related than unrelated individuals (e.g. Silk et al. 2006; Langergraber et al. 2007; reviewed in Silk 2002a). This is particular true for the philopatric sex, sharing a higher average relatedness than the dispersing sex (Altmann et al. 1996; de Ruiter and Geffen 1998). Among female philopatric macaques, adult females preferentially interact with close maternal kin (especially mother–daughters and maternal half-sibling dyads). Such preferences for close maternal kin are especially strong in despotic species such as rhesus, Japanese and pigtailed macaques (e.g. Kurland 1977; Massey 1977; Kapsalis and Berman 1996; Chapais et al. 1997;

Berman and Kapsalis 1999; Widdig et al. 2001, 2002; Schülke et al. 2013), but such preference (or less pronounced) can also be found in more tolerant species like bonnet macaques or moor macaques (*Macaca maura*) (Silk et al. 1981; Silk 1982; Matsumura 1998). Specifically, adult female bonnet macaques groom immature kin more than immatures of unrelated females (Silk et al. 1981). However, data from tolerant crested macaques reveal that adult females have more freedom in the formation of social bonds, with kin relationships suggested to be of lower importance (Duboscq et al. 2017).

The preference for close maternal kin as social partners is a shared characteristic among macaques as well as in other primates (e.g. Silk et al. 2006; Langergraber et al. 2007; reviewed in Silk 2002a). However, evidence accumulates that individuals of different primate species also favour paternal siblings as social partners (e.g. Smith et al. 2003; Silk et al. 2006; Charpentier et al. 2007; Lynch et al. 2017; Cords et al. 2018) even though paternal kin share a much lower degree of familiarity requiring other kin recognition mechanisms such as phenotype matching (reviewed in Widdig 2007). Similarly, adult female rhesus macaques preferentially interact in several behavioural contexts with paternal half sisters as compared to unrelated females (Widdig et al. 2001, 2002, 2006; Schülke et al. 2013). Given male reproduction is skewed and male breeding tenure tends to be relatively short across several macaque specis (reviewed in Widdig 2007), paternal siblings might be especially abundant and close in age (see Altmann 1979; Widdig 2013). Male reproductive skew influences the kin structure and hence the potential of the development of social bonds within groups of primates, as paternal relatedness (potentially in interaction with age proximity) can affect social relationships (see references above). Macaques are particularly interesting in this respect, as some evidence suggests that low levels of nepotism and high tolerance might be linked to male reproductive skew, a proxy of the 'hidden' paternal relatedness of a given species (Schülke and Ostner 2008). As such, future studies should test whether high levels of paternal relatedness indeed correspond to the presence of low maternal kin bias and high degree of social tolerance.

In the competitive context, kin selection theory further predicts that kin should direct less aggression to each other than towards unrelated individuals (Hamilton 1964). Depending upon the age difference of siblings, older siblings might influence the development of an infant and/or the mother–offspring relationship (Hooley and Simpson 1983). However, in adult rhesus macaques, for example, maternal half sisters share the highest rates of both affiliation and aggression, following mother–daughter dyads (Widdig et al. 2002). In contrast, paternal half sisters are significantly more affiliative than unrelated females, but they do not differ in rates of dyadic aggression (Widdig et al. 2002). However,

adult female rhesus avoid targeting their paternal sisters when involved in agonistic conflicts (Widdig et al. 2006). Data on aggressive interactions in macaques are rare in the context of kinship, particularly for juvenile individuals, and previous studies on rhesus macaques provide no clear picture: some found a higher frequency of dyadic aggression by maternal kin, particularly directed at younger kin (Bernstein and Ehardt 1986) and infants born to low-ranking mothers (Berman 1980a), while others comparing rhesus and stump-tailed macaques (*M. arctoides*) reported no differences in the frequency of aggression towards maternal kin and non-kin (de Waal and Luttrell 1989). However, aggression among kin seems less pronounced among bonnet macaques who direct severe aggression more towards unrelated than related individuals (Silk et al. 1981).

Only recently could we gain some more insights into the effect of both maternal and paternal relatedness on the development of social relationships in rhesus macaques (Kulik et al. 2015a, b; Widdig et al. 2016). Again, these studies consider the development of affiliative and aggressive behaviours covering the entire period from birth to sexual maturation. Starting with the first years of life, immature male and female rhesus form the strongest bonds with their maternal kin (Kulik et al. 2015a). The development of strong social bonds toward maternal kin by both males and females can be explained in terms of immatures being closely associated with their mothers, despite the sex difference in mother–offspring bonds reported (see Kulik et al. 2016); however, these bonds most likely optimize survival and sexual maturation during ontogeny. In particular, strong social bonds with maternal kin appear to have immediate benefits for daughters, apart from constituting the basis of their future social network as adults. Overall, infants' social network mirrors their mother's one throughout the first months of life, with infants especially engaged in positive social interactions with close kin (rather than distant kin or unrelated individuals) (de Waal 1996), particularly in top-ranking lineages (Berman 1982; see Ilany and Akçay 2016 on the social inheritance of animal social networks).

The development of social bonds toward paternal kin can also be explained by kin selection. Starting at the age of one, immature rhesus males (but not females) preferentially interact with paternal kin as compared to non-kin (Kulik et al. 2015a). These results suggest that at least male rhesus can discriminate paternal kin from an early age. Moreover, these findings indicate that male immatures, being less integrated in their maternal families (cf. Kulik et al. 2016), might have a stronger need to search for alternative social partners from early on. Loose integration of males within the maternal family, likely caused by the enhanced rate of aggression toward male immatures by both mothers (Kulik et al. 2016) and maternal sisters (Kulik et al. 2015b), might foster male immatures to look for alternative partners, like paternal kin or fathers,

from earlier on (Langos et al. 2013). Interactions with paternally related age mates may be especially beneficial to male immatures, not only in the immediate term (being valuable social partners sharing the same genes within their natal group), but also in the longer term, as males leave their natal groups most likely with age mates, who are often paternal kin (Widdig et al. 2002). Forming social bonds with paternal kin might actually reduce dispersal costs of males, for example, by migrating with or into groups containing paternally related brothers (rhesus macaques: Albers and Widdig 2013; long-tailed macaques: Gerber et al. 2016). Female immatures, in contrast, probably have to rely less on their paternal kin at this stage. Indeed, females remaining in their natal group usually have several maternal kin available and bonding with maternal kin might more likely enhance their fitness than bonding with paternal kin. Some evidence for this hypothesis comes from baboons. When both kin classes are available, females preferentially form bonds with maternal kin; however, once close maternal kin are not available anymore, adult females increase their bonds with paternal kin (Smith et al. 2003; Silk et al. 2006). A recent study on olive baboons (*Papio hamadryas anubis*) reports that immatures form stronger bonds with their paternal siblings when fathers are present in the group, suggesting that the development of such bonds is facilitated by the presence of the shared father (Lynch et al. 2017). These studies together with other studies in mandrills (Charpentier et al. 2007) suggest that immatures can discriminate paternal kin, which calls for more studies investigating the importance of paternal kin across macaques.

As mentioned earlier, stronger social bonds in primates have been reported among adult individuals of the philopatric sex compared to the dispersing sex (e.g. Strier et al. 2002; Slater et al. 2009; Cords et al. 2010). This was expected, given that individuals remaining in their natal group typically have a higher number of kin around, and kin are more likely to form stronger social bonds than unrelated individuals (reviewed in Silk 2002a). Interestingly, this bias in social bonds towards to philopatric sex holds true when kin availability does not yet differ. Analysis of kin patterns at the time of sexual maturation in macaques (approximately fourth year of life, i.e. before first maternity and natal dispersal) revealed that kin availability is still similar for both sexes. Consequently, at the time of sexual maturation, maternal kin are still the closest social partners for both sexes, but even more for philopatric females (Widdig et al. 2016). These findings suggest that sex differences in the development of sociality do not simply reflect kin availability but partially follow different developmental trajectories in the two sexes, which largely reflect adult patterns of social interactions.

As only female macaques remain in their natal group, they are more likely than males to compete with relatives (Silk et al. 1981). In addition, mothers are primarily responsible for offspring socialization (Bernstein and Ehardt 1986). Therefore, it
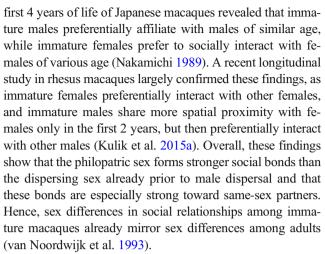
was expected and found, at least in captive rhesus macaques, that females show a higher frequency of aggression toward maternal kin than males, particularly to younger once (Bernstein and Ehardt 1986). However, results from longitudinal data on the development of aggression in the same species revealed that the probability of initiating aggression is similar for both sexes, with both male and female immatures more frequently initiating aggressive interactions with maternal kin (as compared to paternal kin and non-kin) throughout development (Kulik et al. 2015b). Both males and females also have a higher probability to receive aggression from maternal kin until one and a half years of age, although males have a higher probability to receive aggression from paternal kin than non-kin, as compared to females. In contrast to affiliative behaviour, therefore, aggressive behaviour may only partially differ between sexes through development (Kulik et al. 2015b). This suggests that being aggressive might largely serve a similar function for both sexes during the first years of development, and aggressive behaviour does not necessarily anticipate adult patterns in the same way as affiliative behaviours do. While affiliative behaviour allows individuals to construct relationships over long-time frames, aggressive behaviour may serve a more immediate function, largely reflecting contingent needs (e.g. competition over resources; see Camilla and Fawcett 2018).

Overall, some patterns of social relationships of immature macaques already reflect adult patterns of social interactions. This is especially true for affiliative behaviours, which likely serves a longer-term function in building up relationships. Social interactions with maternal and paternal kin partially differ for males and females, and these differences increase through development as both sexes gradually grow into their social roles as adults, with males preparing for migration and females integrating more in their social network where they will spend the rest of their lives together with their offspring. In contrast, aggressive behaviour may have more direct consequences and likely serves a more immediate function, with minimal differences between male and female immatures.

The effect of partner's sex and age on the development of sociality

Depending on the partner's sex and age, immature male and female macaques may have dissimilar social preferences, enhancing sex-specific differences in the development of sociality. Previous studies have shown that immature female macaques are generally more engaged in social interactions than immature males, throughout development, while individuals of both sexes prefer to interact with same-sex partners (Japanese macaques: Eaton et al. 1985; Nakamichi 1989; long-tailed macaques: van Noordwijk et al. 1993; rhesus macaques: Kulik et al. 2015a). Longitudinal data covering the

first 4 years of life of Japanese macaques revealed that immature males preferentially affiliate with males of similar age, while immature females prefer to socially interact with females of various age (Nakamichi 1989). A recent longitudinal study in rhesus macaques largely confirmed these findings, as immature females preferentially interact with other females, and immature males share more spatial proximity with females only in the first 2 years, but then preferentially interact with other males (Kulik et al. 2015a). Overall, these findings show that the philopatric sex forms stronger social bonds than the dispersing sex already prior to male dispersal and that these bonds are especially strong toward same-sex partners. Hence, sex differences in social relationships among immature macaques already mirror sex differences among adults (van Noordwijk et al. 1993).

In contrast, previous studies suggested that aggressive behaviour fails to anticipate adult behavioural patterns as much as affiliative behaviours do. For example, juveniles show no sex differences in aggressive behaviour (Japanese macaques: Eaton et al. 1986), although males around sexual maturation receive higher rates of aggression (rhesus macaques: Altmann 1962; Wilson and Boelkins 1970), becoming more aggressive than females when entering adulthood (Japanese macaques: Eaton et al. 1986). In contrast to females, who are largely aggressive toward kin throughout development, males receive less aggression by kin they live together when getting older (rhesus macaques: Bernstein and Ehardt 1986). Also, mothers' rank affects the rate of aggression received through development, with infants of high-ranking mothers being threatened less and receiving more protection than infants of low-ranking mothers (Berman 1980a). In rhesus macaques, infants receive aggression as early as a few months after their birth (Kulik et al. 2015b), when they start socializing with others (Kulik et al. 2015a). Interestingly, aggressive behaviour seems to be especially directed from older females toward male immatures, once again suggesting a lower level of male immatures' integration in their natal group (Kulik et al. 2015b).

Through development, immature macaques of both sexes seem to also preferentially affiliate with age peers (Nakamichi 1989; Kulik et al. 2015a). This is not surprising, as age proximity promotes social bonding in young macaques (e.g. Berman 1982; Janus 1989; Nakamichi 1989; Suomi 2005) and in adult macaques (e.g. Widdig et al. 2001). However, this may only be true for seasonal breeding species, as no preference for peers was detected among adult female crested macaques, which breed year round (Duboscq et al. 2017). Interestingly, preference for age peers is higher in males than in females, especially before male dispersal (Kulik et al. 2015a). In species with high male reproductive skew, age peers have a higher probability to share the same father, as male breeding tenure is generally short across species (Altmann 1979). Therefore, stronger bonds with age peers

before dispersal might enhance the probability for males to migrate together with paternal kin (Widdig et al. 2004; Albers and Widdig 2013). Being loosely integrated in the maternal family and preferentially interacting with male peers who will likely migrate around the same time, male immatures might benefit from leaving their natal group together with closely bonded male peers (see Nakamichi 1989; Kulik et al. 2015a). In contrast, preferential interactions with peers, who might be paternal kin, do not seem to be as important for female immatures, at least not at this time of their life, given the strong maternal kin network available (Kulik et al. 2015a). As reproductive skew and male breeding tenure differ across primate species, future studies may reveal inter-specific differences in kin structure, kin preferences and mechanisms of kin recognition. In crested macaques with a high skew in paternity (Engelhardt et al. 2017) and short breeding tenure (Marty et al. 2017a), for instance, paternal kin might most likely be peers, potentially resulting in a kin preferences via age proximity only. In contrast, in species with a lower skew and more relaxed breeding tenure, such as rhesus macaques, paternal siblings are not only restricted to peers (Widdig et al. 2002), and other kin recognition mechanisms, such as phenotype matching, might have evolved (e.g. Pfefferle et al. 2014a, b).

Specific attention should be directed to social play, which is more frequent in primate males than females, across different life stages (e.g. rhesus macaques Brown and Dixson 2000; Japanese macaques Koyama 1985; Eaton et al. 1986; Nakamichi 1989; Assamese macaques Berghänel et al. 2015; reviewed in Fagen 1993; Roney and Maestripieri 2005). Indeed, social play is the only behaviour differing between sexes from the very first months of life, in rhesus macaques, being more frequent in males than females throughout development (Kulik et al. 2015a). It is especially interesting that these differences emerge so early in development. Given that play is a social arena in which individuals practice social behaviour and future adult skills (see e.g. Burghardt 2005; Kuczaj and Horback 2013; see Palagi 2018 in this Topical Collection), early sex differences in social play might trigger further sex differences in social behaviour. These differences in social play, in particular, might elicit different responses in group members, provide male and female infants with different experiences and thus also partially lead them to develop in different ways within the same social group (Kulik et al. 2015a; Palagi 2018 in this Topical Collection).

Importantly, longitudinal studies on Japanese and rhesus macaques found that immatures largely change their way to interact with other group members between 2 and 3 years of age (Nakamichi 1989; Kulik et al. 2015a, b). In rhesus macaques, these major developmental changes encompass all affiliative and aggressive behaviours but social play (Kulik et al. 2015a, b). Around 2 years of age, for instance, male immatures shift their social preferences toward male partners, while female immatures extend their social network to members other than peers (Kulik et al. 2015a). Moreover, major developmental changes in most social behaviours (i.e. grooming, proximity, aggression) appear around 2 years of age, when individuals drastically change their social partners or social behaviours reach a climax and then decrease again in intensity. Other studies have also found a similar peak in social interactions around this age, particularly in macaque species with similar life histories (e.g. *Macaca fuscata*: Eaton et al. 1986; Nakamichi 1989; Gunst et al. 2013; *M. mulatta*: Suomi 2005). This age period might therefore be a key milestone in the development of sociality in macaques. Around this age, immature macaques, like human adolescents (e.g. Liben et al. 2002; Blakemore et al. 2009; Negriff and Susman 2011; Beltz and Berenbaum 2013), might have acquired the behavioural patterns typical of adulthood, but might use them with different intensity. Through time, immatures would further refine their behaviours, with males and females following different developmental trajectories that best match their social roles as adults, adapting to the specific social structure they live in.

Overall, our review presents a dynamic picture of macaques' social development, which varies through age depending on the characteristics of the interaction partners. In particular, sex differences in social behaviour emerge early during development, and gradually increase through time, with a peak between 2 and 3 years of age. These differences increasingly reflect males' and females' social roles as adults (cf. Nakamichi and Yamada 2010), with males migrating into new groups, and thus preferentially interacting with male age peers, and females remaining in their natal group, and thus preferentially interacting with other females and especially with close maternal kin.

Future directions

Despite the existing study bias in favour of despotic macaque species (and particularly rhesus macaques), this review has allowed us to gain a closer view of the development of sociality across macaque species. To achieve a more complete picture on the social development of macaques, more longitudinal studies covering the years up to sexual maturation across a wider range of macaque species will be needed to better understand their socio-ecological diversity. Moreover, future studies should address other current limitations. First of all, it will be beneficial to better understand the complex interplay of aggressive and affiliative behaviours in the development of primate social bonding. For instance, the extent to which aggression negatively affects positive social interactions, in particular during development, is generally not clear in primates, as we do not understand whether aggression is generally directed toward social partners competing over the same resources, forming the strongest affiliative bonds, and/or simply being closer in space. Secondly, it is still not clear which factors cause some individuals to socialize more frequently than

others, given that this is likely linked to higher fitness benefits in adulthood. Thirdly, although social bonding increases adults' fitness (Silk et al. 2003, 2009, 2010; Silk 2007; Schülke et al. 2010; Kulik et al. 2012; Langergraber et al. 2013; but see also Thompson and Cords 2018), little is known on the immediate effects of social bonds on infants' survival. Although social bonds likely have positive effects throughout primates' lives, the effects may vary across particular life history stages, with different social behaviours having a differential impact depending on the immatures' age. Fourthly, future studies should combine behavioural observations with a more experimental approach, to investigate psychological, emotional and physiological changes occurring in macaques between 2 and 3 years of age, and better understand whether these changes are comparable to those happening around puberty in humans. For instance, it would be interesting to understand whether more frequent social interactions provide specific benefits to immatures at this age, and if so, which ones. Moreover, future studies should better disentangle the potential effect of different bonding patterns (e.g. highly versus less social individuals) on dispersal and reproductive success, by analysing the long-term effects on social development in both female and male philopatric species. Finally, more comparative studies on the social development in other (Old world) primates are needed to determine the generality of these patterns or whether they are a unique characteristic of macaque societies.

Compliance with ethical standards

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