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INFANT HANDLING IN MALE BARBARY MACAQUES

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PhD. Thesis

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Annotation

Non-maternal manipulation of infants also called infant handling in male Barbary macaques attracts scientific attention due to its intensity in combination with promiscuity of the species that should select against paternal care. This PhD thesis consists of four studies that investigate male infant handling in wild group of Barbary macaques in Morocco. The studies are based on original data and the results provide new information about the behaviour and thus significantly contribute to its explanation. First, we offer new insights into the relationship between distribution of mating and infant handling and ask whether it can be better explained by paternal effort or future mating success with infants' mothers. Second, we broaden the range of explanations beyond the original hypothesis of relationship management for male-infant-male interactions. Third, we focus on the question whether males use knowledge of third party relationship when distributing infant handling interactions. Fourth, we demonstrate how care of infants can surprisingly contribute to the reintroduction of an infant who is native in the different group.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Barbora Kuběnová

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List of papers and author's contribution

The thesis is based on the following papers:

I. Kubenova B, Schülke O, Majolo B, Ostner J, Smilauer P, Tkaczynski PJ, Waterman JO, Konecna M. Use of male and female perspective in explaining link between male care and mating in Barbary macaques
In preparation

Barbora Kuběnová collected the majority of the behavioural data, evaluated the data, conducted a significant part of the statistical analyses and wrote manuscript with the help of co-authors.

II. Kubenova B, Schülke O, Majolo B, Ostner J, Smilauer P, Konecna M. The effect of dominance rank on the distribution of different types of male-infant-male interactions in Barbary macaques.
In preparation

Barbora Kuběnová collected all behavioural data the study is based on, evaluated the data, conducted a significant part of the statistical analyses and wrote manuscript with the help of co-authors.

III. Kubenova B, Konecna M, Majolo B, Ostner J, Smilauer P, Schülke O (in press). Triadic awareness predicts partner choice in male–infant–male interactions in Barbary macaques. Animal Cognition 1–12, IF = 2,161

Barbora Kuběnová collected all behavioural data the study is based on, evaluated the data, conducted a significant part of the statistical analyses and wrote manuscript with the help of co-authors.

IV. Waters S., El Harrad A, Amhaouch Z, Kubenova B (2016). Releasing confiscated Barbary macaques to improve national awareness of the illegal pet trade in Morocco. In Global-reintroduction Perspectives: 2016, Case-studies from around the globe. IUCN, pp 216-220.

Barbora Kuběnová collected the majority of the behavioural data and made a significant contribution to the manuscript.

Co-authors agreement:

Mgr. Barbora Kuběnová, the author of this PhD thesis, is the first and corresponding author of three papers (manuscripts) and last author of the fourth paper.

For the three papers, she collected the major part of the behavioural data, evaluated the data, conducted a significant part of the statistical analyses and wrote manuscripts with the help of co-authors.

For the fourth paper, she collected the majority of the behavioural data and made a significant contribution to the manuscript.

Dr Sian Waters, the first and corresponding author of the fourth paper agrees with the publication of the paper in the PhD thesis of Barbora Kuběnová and with her significant contribution to the paper and confirms this with her signature.

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Content


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INTRODUCTION

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Infant handling in mammals

Definition

Postnatal maternal investment in the form of lactation is ubiquitous in mammals and typically extends to other forms of caregiving (Trivers 1972; Clutton-Brock and Parker 1992). In the majority of mammalian species, females take care of the infant alone (Woodroffe and Vincent 1994). However, in some species care may be shared by different individuals – juveniles, subadults as well as adult females and males (see e.g. Jennions and Macdonald 1994; König 1997; Solomon and French 1997). Non-maternal care is spread across various taxa, including species of rodents (Jarvis 1981; Carter and Roberts 1997), chiropterans (Kerth et al. 2002), carnivores (Macdonald and Moehlman 1982; Creel et al. 1997), primates (see Hrdy 1976), cetaceans (Gero et al. 2009) and proboscideans (Schulte 2000). The heterogeneity of interactions non-maternal care covers is immense. Individuals may contribute to provisioning (including nursing), carrying, protection, thermoregulation comfort or other maintenance behaviour, or just occasionally share proximity with an infant (Isler and van Schaik 2012).

The behaviour is often explained on the basis of cost and benefits it might bring to the involved individuals, an infant, its mother and caretaker. Interactions may be sorted based on the characteristics of the caretaker, e.g. age, sex, kinship relationship with the infant. Variability is reflected in the vast number of different terms describing the behaviour, e.g. cooperative breeding, cooperative care, allocare, non-maternal care, allomothering, caregiving, helping, babysitting, handling, infant manipulation, exploration, aunting, fathering (e.g. Hrdy 1976). Unfortunately, the use of those terms is often inconsistent and may lead to confusion. The term cooperative breeding for example sometimes describes any system where individuals contribute to the care of infants who are not their offspring (Cockburn 1998), other times describes the care of any individual apart from the infant's mother (Hrdy 1976), or in the strict sense refers specifically to systems when non-breeding caretaker raises young produced by dominant breeders (Clutton-Brock 2002). The term helping is often unfortunate as it implicitly suggests an active altruistic behaviour: a cost to caretaker and benefit to infant (Jennions and Macdonald 1994; Gilchrist 2007).

In this study we further use the term infant handling which covers any interactions between an infant and non-maternal individual (caretaker) regardless from whether the behaviour is likely to bring the benefits to the infant, its mother and/or caretaker.

Infant handling and indirect fitness

Whereas it is relatively easy to explain why mammalian mothers should be selected to care for their infants, selection for infant handling by other individuals is less easily understood (Ross and MacLarnon 2000). Individual selection theory predicts that it is unlikely that the behaviour evolved unless it brings some benefits to caretakers. According to kin-selection theory (Hamilton 1964), infant handling may benefit fitness of a caretaker. Caretaker may increase his/her fitness when taking care of his/her relatives or helping own relative to reproduce (indirect fitness), because they also share the genes with him/her. According to Hamilton's rule individuals' willingness to be involved in the care of an infant depends on the degree of the relativeness with this infant. There is a number of studies that show this to be true for males, females, or juvenile individuals of several mammalian species. For example in male brown hyenas (Owens and Owens 1984) and meerkats (Clutton-Brock et al. 2004) males provide most of the food to closely related immatures. Male golden lion tamarins prefer to carry more related offspring (Tardif 1997). Female African lions prefer to feed an offspring of closely related mothers over more distantly related ones (Pusey and Packer 1994). In Belding's ground squirrels (Sherman 1977) and black-tailed prairie dogs (Hoogland 1983) females who have closely related kin present are more likely to utter costly alarm calls than those without kin present. Sometimes, pattern of infant handling by siblings may be influenced by ecological conditions. Although more known for birds, phenomenon described as delayed dispersal refers to the situation when immatures rather stay with the native group as caretakers than leave the group and rise own offspring. In some species (such as white-footed mice, European badgers, dwarf mongooses; Jennions and Macdonald 1994), the decision may be based on actual environmental conditions, i.e. availability of suitable territories. In primates, infant handling by juveniles and adult females usually appears in the species with female philopatry (e.g. in vervet monkeys, capuchins, squirrel monkeys) where females are likely to be related to each other and each others' infants (Ross and MacLarnon 2000). Juvenile caretakers are usually known to be older maternal siblings of the infant (e.g. Fairbanks 1990) or full siblings in uni-male groups (such as in many colobines; see Hrdy 1980).

Direct benefits of infant handling

Not all infant handling interactions can be however explained by Hamilton's kin-selection theory and indirect fitness. In many cases, caretakers are not relatives of the infants who they care for. In some species, such as in evening bats, ground squirrels, house mice or squirrel monkeys, infant handling is apparently exhibited by non-relatives (König 1997). What are other benefits caretakers (infants' relatives or nonrelatives) may follow besides gene investment? First of all, caretaker does not necessarily have to follow any profit when handling infants. In some species individuals may provide care to "alien" offspring by mistake: In some mammals living in very big social groups (such as in some pinnipeds) for example infant handling may be a type of parasitism – a female may nurse someone else's offspring without actually noticing (Packer et al. 1992). In cooperative breeders in a strict sense (e.g. Clutton-Brock 2002), individuals contribute to the care of offspring of dominant individuals who restrict reproduction of others either via hormonal suppression (as observed in callitrichids; Snowdon et al. 1993) or behaviourally, for example when killing offspring of subordinate individuals (as observed for example in Ethiopian wolves; Sillero-Zubiri et al. 1996). Thus actually individuals' motivation to become a caretaker may be related to the benefits of the group living (e.g. Rubenstein 1978). In some species (such as in wild dogs, dwarf mongoose and tamarins), this system seems to result from high energetic costs of breeding, which does not allow a pair alone to reproduce successfully without the help. By care of offspring of others (typically of the dominant individuals) caretaker actually contributes to the maintenance of the group and thus also to his/her own survival as a group member.

Mainly in species living in stable complex social systems, infant handling may provide a caretaker with various direct social benefits. In African elephants for example non-mothers suckle calves of other females. It has been suggested that communal nursing is a by-product of female sociality, that the behaviour is important for the maintenance of matriarchal societies and brings caretakers benefits related with social bonding and status (Lee 1987). Also in the number of primate species infant handling may be explained by caretaker's motivation to follow various social benefits, whereas positive impact of the handling on the survival of an infant or reproductive success of its mother is not obvious. In general, over 17 non-exclusive hypotheses have been suggested to explain infant handling (Maestripieri 1994). Here we present only selected most popular examples that were used to explain infant handling in primates.

Hypotheses of infant handling in primates

The "learning to mother hypothesis" (Lancaster 1971) predicts that via infant handling females gain skills for rearing their own infants. Thus infant handling improves future reproductive success of the female caretaker as a mother. This idea was supported 1) by the higher frequency of allomothering behaviour in nulliparous females compared to parous females in some species (e.g. Lancaster 1971 for vervet monkeys; Hrdy 1980 for langurs; Kurland 1976 for Japanese monkeys; Nishida 1983 for chimpanzees) and 2) by the finding that females who have had previous contact with infants raise their own infants more successfully than females who have not (e.g. Fairbanks 1990 for vervet monkeys). The „reciprocity hypothesis" predicts that non-mother female helps to rear an unrelated offspring with expectations that this help will be reciprocated once she needs it. The hypothesis became a part of the research focused on evolution of reciprocity (Trivers 1972). It was even suggested that female infant handling allows the formation of cooperative alliances between parous females who will handle each others' infants (e.g. Stanford 1992 for capped langurs). In contrast the „reproductive competition hypothesis" assumes that females use infant handling not to help but to harm offspring of other females in order to obtain better conditions for their own offspring. The support for this hypothesis has been found in bonnet macaques (Silk 1980) and yellow baboons (Wasser and Barash 1981) where infant handling by females involves cases of “kidnapping”, infant abuse and harassment, which may lead into infant’s injury or dead.

Several hypotheses emphasized that infant handling may help maintenance of social relationships that may bring various benefits to female, male and/or juvenile caretakers. The "coalition formation hypothesis” (Paul et al. 1996) suggests that caretakers may follow profit of support in coalition from the infants’ mother, therefore individuals are especially interested in handling the infants of high-ranking mothers who represent the most powerful allies in coalitions (as observed in wedge-capped capuchin monkeys; O’Brien and Robinson 1991). Young females may use infant handling to become better integrated into the adult female hierarchy (e.g. Cheney 1978 for baboons). In tamarins and marmosets, infant handling might be “traded” for a position in a breeding group and may allow inheritance of a breeding position (Tardif 1997). In some species, adult males may handle infants in order to achieve mating access to the mothers (Seyfarth 1978 for savannah baboons; Tardif 1997 for cotton-top tamarins) or to establish bonds with other males. The following chapter focuses in more detail on the hypotheses explaining male infant handling in primates.

Male infant handling in primates

As other caretakers, male primates may follow different motivations when engaging in infant handling. If infant handling is motivated by investment into own genes one might expect father to be one of the most active caretakers of an infant as he shares as much genes with the infant as mother does. However, this is rarely the case. Usually imbalance in the degree of maternal and paternal investment is explained by paternal confusion. Whereas maternity is unquestionable, male always deals with some degree of risk that the infant is not his own offspring. An investment into the infant is thus potentially accompanied by uncertainty whether the male invest in his genes or someone else’s (Trivers 1972; Brock-Clutton and Vincent 1991; Clutton-Brock and Parker 1992). Moreover, the motivation between maternal and paternal care may also differ given their costs. Whereas mother is limited in number of offspring by her investment into gestation and lactation, male care has a cost in terms of the lost opportunities for siring more offspring.

Interspecies variability

Whereas adult males have been observed to provide infant care in only 10 % of mammalian species (Woodroffe and Vincent 1994), in the primate genera, the interest in infants is reported in over 40-50% of species (Hrdy 1976; Kleiman and Malcolm 1981; Clutton-Brock and Isvaran 2006). It may be intuitively assumed that this relatively high percentage (compared to other mammals) is at least to some extent given by high primate sociality, intelligence, and in particular long infant dependency that requires various types of services. The character and intensity of male infant handling across different primate taxa is enormously variable, ranging from occasional proximity with an infant to intensive and apparently time and energy consuming behaviour, that in exceptional cases may time-wise overweight maternal postnatal investment (see e.g. Ross and MacLarnon 2000). Such vast variability within one order is not fully understood, but several factors have been suggested to influence male infant handling in primate species. First type of factors may be related with the importance of the care for the infant and its mother. As often observed in birds (Cockburn 1998), high level of male investment should be characteristic for species where contribution to care by other individual(s) than mother is essential for the infant survival and with low mother-infant body weight ratio. Males are involved in infant handling which includes different types of body contact, grooming, carrying and even assistance with nutrition (Feistner and Price 1991). For example in common marmoset, infants (typically twins) may be carried by male (typically sexual partner of the mother) up to 60% of time (Schradin and Anzenberger 2001; Hrdy 2007). In cotton-top tamarins the assistance seems important to that extent, that mother may rather abandon her newborns than take care by herself (Bardi et al. 2001). Male infant handling in those species profits infants' condition and survival and seems necessary for successful and rapid reproduction of the infant's mother (Bales et al. 2000). This demonstrates, how male care may refect species biology. However, the species revealing such a clear connection are rather exceptional. Another set of factors that are believed to affect the degree and character of male infant handling is related with social system of the species. For example in solitary species (such as bushbabies and orang-utans) limited social interactions with other species members decrease the chances for infant handling, thus the connection between social organization and low or no occurrence of infant handling is clear. However, the amount and character of infant handling significantly varies in pair-living and group living primates too (Ross and MacLarnon 2000).

If infant handling represents a type of paternal investment, two predictors should be fulfiled: The behaviour needs to increase infant survival and the male needs to be sure that he invests into his own offspring. According to this, the big proportion of variability in intensity of male infant handling should be based on variability in paternity certainty across different species (Smuts and Gubernick 1997). Intensive male care is thus expected in monogamous species with low paternity uncertainty and unexpected in promiscuous species with high paternity confusion (Lewis and Pusey 1997; Griffin and West 2003 but see also Lukas and Clutton-Brock 2012). The support for the link between paternity certainty and intensity of male infant handling is mixed. Occurrence of intensive male care in monogamous owl monkeys, titi monkeys, siamangs and howler monkeys supports the expectation (Smuts and Gubernick 1997). In fact, paired males usually show infant care (see exceptions below) and they provide more extensive care than males in other primate species – including instant carrying (Van Schaik and Paul 1996). However, other examples make the link between mating system and infant handling less straightforward (Smuts and Gubernick 1997). High certainty about paternity does not guarantee male involvement in raising infants as for example illustrated by cases of monogamous species such as indri and all gibbons (except the siamang), whose males get rarely involved in interactions with infants. Vice versa, several previously believed monogamous pair-living species (such as top-cotton tamarin, saddleback tamarin, common marmoset; reviewed in Sussman and Garber 1987) are often also polyandrous and live in groups, where both care and mating may be shared by various males. In contrast to prediction of paternal investment hypothesis, males of polyandrous species often participate in infant handling, although they cannot be sure about own paternity and even when the chance of their paternity is especially low or any – even non-breeding males may participate in care. Another example questioning the link between paternity certainty and intensity of male infant handling is variable intensity of infant handling in different *Cercopithecinae* species.

Male infant handling in *Cercopithecinae*

Interactions

In spite of shared multimale-multifemale organisation, intensity and character of male interest in infants ranges across different macaque, baboon and mangabey species. In some of cercopithecine primates, such as rhesus macaques or vervet monkeys, males rarely interact with infants, which would appear to conform to the paternity hypothesis given paternal confusion. In savannah baboons and several macaques species however, males can be observed associating with infants (e.g. Huchard et al. 2012), providing them with the support in conflicts (Buchan et al. 2003) and protection against harassment and infanticide (Palombit et al. 1997; Paul et al. 2000) and even grooming and carrying them (Estrada and Sandoval 1977; Deag 1980; Thierry et al. 2000).

Sometimes, males exhibit specific type of polyadic infant handling during which two or more individuals simultaneously manipulate one infant together. Such interactions were reported in several papionin primates: Barbary (Deag and Crook 1971), Tibetan (Ogawa 1995), stump-tailed (Estrada and Sandoval 1977), long-tailed (de Waal et al. 1976), Assamese (Bernstein and Cooper 1998) and bonnet macaques (Silk and Samuels 1984) and in yellow (Collins 1986), olive (Smuts 1985) and chacma baboons (Busse and Hamilton 1981) as well as in sooty (Busse and Gordon 1984) and gray-cheeked mangabeys (Chalmers 1968) and geladas (Dunbar 1984). Although the behaviour has been variously called male-infant-male interactions (Zhao 1996), bridging (Ogawa 1995), triadic male-infant interactions (Taub 1980a), agonistic buffering (Deag and Crook 1971), or exploitation (Packer 1980), it has relatively similar description across species. The behaviour takes several seconds (exceptionally minutes) during which two individuals simultaneously manipulate one infant, exhibiting teeth chattering and other types of ritualistic behaviour such as lifting the infant above the males' heads, nuzzling, inspection of the infant's genitals, pulling infants from upper and lower part of the body (in a way reminding of bridge; Ogawa 1995). The beginning of male-infant-male interactions may be variable. The infant may be picked by one of the later involved males and brought to the other or the male without the infant may approach the male with the infant, or both males may also arrive to the infant at the same time. In species with extended dyadic male-infant interactions such as Barbary macaques, male-infant-male interactions may be preceeded by dyadic interaction (typically carrying or cradling) of one of males (initiator or receiver of following male-infant-male interaction) of various lengths. However, short male-infant-male interaction itself does not have any apparent importance for the infant. The infant stays more or less passive during the interaction or even shows some degree of reluctance. Exceptionally, the interaction may lead into the infant's injury.

Infant handling as paternal investment

Infant handling occurs even in highly promiscuous species and is often performed by numerous males. The finding that males seem to prefer some infants over others leads to the question whether males are actually able to recognize own progeny and distribute infant handling accordingly. This would support the hypothesis that infant handling is paternal investment (Hamilton 1964). Some indications about this ability have been found in several species of baboons and macaques. Specifically, DNA analyses revealed that some savannah baboons preferentially shared proximity with own offspring (Onyango et al. 2013 for yellow baboons) and also support them in the encounters with other juveniles (Buchan et al. 2003). In chacma baboons (Huchard et al. 2012) and rhesus macaques, male-offspring associated more often than other male-infant (Langos et al. 2013) or male-juveniles dyads (Berenstain et al. 1981). Associations between males and immatures were affected by paternity in Assamese macaques (Ostner et al. 2013). However, the majority of studies on macaques did not confirm straightforward link between paternity (based on DNA analysis) and male infant handling (see e.g. Berenstain et al. 1981; Paul et al. 1996; Ménard et al. 2001). Nevertheless, this does not necessarily lead to refusal of paternal investment hypothesis in sense of male effort to increase his own exclusive fitness.

Several studies found the link between sexual behaviour and consequent care. This link (also called *mate-then-care pattern;* Ménard et al. 2001) suggests that males might estimate their paternity chances on the basis of previous mating and distribute the subsequent care accordingly. In such case male care may be seen as an effort for the paternal investment (although their estimates are not necessarily correct). In yellow and olive baboons males were more likely to take care of infants, if they consorted the mother around the time of conception or mated with the infant's mother than when they did not (Smuts 1985; (Stein 1984; Altmann 2001 but see also Packer 1980). In chacma baboons associations between males and infants and infant carrying were predicted by consortship activities and/or friendship between males and females (Busse and Hamilton 1981; Buchan et al. 2003; Moscovice et al. 2010) that also predicted paternity (Buchan et al. 2003). In crested macaques, likelihood of male-infant affiliation was significantly higher if the male was present in the group at the time around the infant's conception than if he was not (Kerhoas et al. 2016). Finally, in Assamese (Ostner et al. 2013) and rhesus macaques (Langos et al. 2013) distribution of copulations predicted the distribution of infant handling among males.

Infant handling as mating effort

In contrast to paternal investment hypothesis, some authors suggest that males may increase their own fitness even by caring of unrelated infant. Mating effort hypothesis (Seyfarth 1978; Smuts 1985) suggests that males associate with infants in order to increase their future mating success with the infants' mothers. To support this hypothesis, the distribution of male care should predict consequent mating success of involved males, thus so called *care-then-mate pattern* (Ménard et al. 2001) should be followed. It has been suggested that hypothesis may explain male infant handling for example in geladas and some baboons who preferentially carry the infants of their female friends (Dunbar 1984; Stein 1984; Smuts 1985) and seem to use the behaviour to establish and maintain social relationship with the infants' mothers. Those relationships may help males to increase their mating opportunities (Cheney et al. 1986; Kuester and Paul 1992), or may be a part of male tactics how to secure support from the infants' mothers in later conflicts (e.g. Dunbar 1984 for geladas; Smith and Whitten 1988 for yellow baboons; Smuts 1985 for olive baboons).

Mating effort hypothesis was also supported by several studies on macaques. In Tibetan macaques the involvement in the care seemed to predict the number of females who consorted with the male (Zhao 1996). In Barbary macaques, males who spent the most of the time with the certain infant also achieved the highest mating frequencies compared to other males during the following mating season (Ménard et al. 2001; but see also Paul et al. 1996). As another argument for the hypothesis, it has been found that in crested macaques, males increased involvement in male affiliations towards an infant in presence of its mother and also the care seemed to increase an affiliation between the male and female (Kerhoas et al. 2016). However, in rhesus macaques presence of the mother did not seem to pronounce affiliation between males and unrelated immature (Langos et al. 2013). Finally, some authors suggest (e.g. Smuts and Gubernick 1992 in contrast to Paul et al. 1996) that mating effort hypothesis may also explain why males in some species prefer to take care of offspring of high ranking mothers (Gouzoules 1975; Hector et al. 1989; Paul et al. 1996). Increased mating opportunities with high ranking females are considered profitable, as for example offspring of high ranking females have better chances for the fetal and postnatal survival (Paul and Thommen 1984; Silk et al. 2009; Kerhoas et al. 2014) and are in better condition (Altmann and Alberts 2005).

Infant handling as agonistic buffering and relationship management

Another explanation for male infant handling is mainly based on the finding that male interest in infants may elevate once the intergroup tension is high. Males in several species carry infants mainly during or after agonistic encounters in order to initiate male-infant-male interactions with other males. It has been suggested that males carry infants in order to reduce aggression from other males – so the infant plays a role of an "agonistic buffer". The agonistic buffering hypothesis (Deag and Crook 1971) suggests that infant handling mainly helps males to avoid aggression from higher ranking males. Holding infants, males are unlikely to be attacked, thus can approach even higher ranking males, interact with them (via triadic infant handling interactions), establish profitable bonds and renew bonds after conflicts via reducing stress. All predictions have been listed by Taub (1980a). According to his interpretation, the hypothesis predicts that: 1/ frequency of dyadic and triadic interactions increases when group tension is high, 2/ males more often initiate triadic interaction with higher ranking males than with lower ranking, 3/ triadic interactions occur mostly between handlers with small rank distances and 4/ identity of the infant does not play particular role, any infant may serve well as a “buffer” (Taub 1980a). The support for at least some of those predictions has been found in some baboons and also geladas where males carry infants primarily in aggressive encounters with higher-ranking resident and immigrant males (Packer 1980; Stein 1984) possibly in order to reduce the intensity of aggression they receive from them. The evidence related to the rank of males involved in male-infant-male interactions has been also found in macaques (Silk and Samuels 1984; Ogawa 1995a; Paul et al. 1996), however high occurrence of interactions in agonistic context remained controversial (compare Taub 1980a versus Silk and Samuels 1984; Kümmerli and Martin 2008) and in contrast to the predictions, males seem to prefer particular infants over others (Ogawa 1995a; Paul et al. 1996; Kümmerli and Martin 2008). In order to consolidate the first objection – that male-infant-male interactions often occur outside from agonistic context – it has been pointed out that male bonding is profitable even long-term for example in context of coalition formation (Paul et al. 1996 for Barbary macaques, see also Ogawa 1995 for Tibetan macaques) and male-infant-male interactions may respond to different types of stress not only immediately after conflict. Thus the function of bonding and tension reduction assumed by the hypothesis is not necessarily constrained to the agonistic context. To emphasize this, the hypothesis adopted broader term “relationship management hypothesis” (Paul et al. 1996; Kümmerli and Martin 2008), which we further use in our study.

Infant handling: A case of Barbary macaques

Interspecies variability in explanations for infant handling may reflect systematic differences (for example in relation to male reproductive skew and/or with the risk of infanticide, see bellow). However, even studies on a single species sometimes differ in their results and interpretations of occurrence of infant handling in the particular species. Possibly one of the best examples of such species is Barbary macaque. Barbary macaques are both geographically and phylogenetically separated from the other macaque species (Li et al. 2009; Liedigk et al. 2014). Unlike other members of the macaque genus – with the exception of Japanese macaques – they are found outside the tropics, with their present range being restricted to the mountainous regions of Morocco and Algeria (see e.g. Fooden 2007; Majolo et al. 2013). Like other macaques, Barbary macaques live in multimale-multifemale groups characterized by female philopatry and male transfer (Kuester and

Paul 1999; Fooden 2007). The rank of female is matrilineary inherited (Paul and Kuester 1987), whereas immigrating males achieve their position in the hierarchy gradually during life span, thus male rank is not the outcome of takeovers but partly depends on age (Widdig et al. 2000). Reproduction in Barbary macaques is highly seasonal concentrating mainly into 3 months with high degree of female ovarian cycle synchrony (Taub 1980b; Küster and Paul 1984; Brauch et al. 2008) and high level of promiscuity (Small 1990). Male reproductive skew is rather low. Males of Barbary macaques have small interest in mate-guarding and consortship compared to other macaque species (Kümmerli and Martin 2005; Brauch et al. 2008; Bissonnette et al. 2011). The majority of male-female associations seem to disappear shortly after the end of breeding season (Small 1990). Although females may selectively support some males in conflicts (Kubenova personal observation), stable intersexual relationships exceeding mating season have not been described (Small 1990).

Although infants attract attention of individuals of different sex and age classes (usually with the exception of females who have own infants), males are often the most active caretakers besides the mother (Kümmerli and Martin 2008). The intensity of male infant handling in Barbary macaques does not fit into any pattern explaining variability in intensity of infant handling across different primate species. Extreme level of female promiscuity (Small 1990a) does not make the species fit into the model about paternal investment, because it puts males into high risk of taking care of unrelated infant. The harsh winters the species has to deal with opens the question, whether intensive male interest evolved as an adaptation to difficult ecological conditions. However, Japanese macaques live in quite similar conditions (Takasaki 1981) and males do not exhibit any infant handling. Moreover, there is no evidence so far, whether intensive male handling indeed brings substantial benefits either to infants or to their mothers (Kuester and Paul 1986; Paul and Kuester 1996). Specifically, frequent infant handling did not allow mothers to reproduce at a faster rate (Paul and Kuester 1996) as observed elsewhere (see e .g. Fairbanks 1990 for vervet monkeys, Anderson 1992 for chacma baboons). High weight ratio between females and infants (Fooden 2007) also does not indicate why male infant handling should be in particular important for this species compared to others (Wright 1990). Finally, in contrast to some other macaques or baboons, infanticide – that according to some authors might also represent a pressure for more intensive infant handling – has not been described in Barbary macaques (Paul 2000).

Male infant handling in Barbary macaques includes different types of holding, carrying and grooming and resembles of maternal care (Deag 1980; Taub 1980b, but see also Paul 1999). During their first three months of life, infants may spend on nearly 40% of the daytime in close physical contact (being hold, groomed, and carried) with males. Besides dyadic infant handling interactions consisting mainly of different types of body contact, interactions also involve triadic male-infant-male interactions, during which two males shortly manipulate one infant as has been described earlier. The rate of those interactions is also high, although more comparable with other species (e.g. Tibetan macaques) than dyadic infant handling (Smith and Peffer-Smith 1982; Ogawa 1995). Dyadic and male-infant-male interactions often alternate. A male may initiate and/or receive a number of male-infant-male interactions during the single tenure of one infant. Neither dyadic handling nor male-infant-male interactions are randomly distributed among dyads or triads in Barbary macaques. First, several studies confirm that whereas some infants attract almost constant attention from several males, others may be completely ignored (e.g. Small 1990b; Ménard et al. 2001). To some extent, differences in infants' popularity seem to be influenced by infant sex (with the stronger preference for male infants; Small 1990b), age (with stronger preference for young age; Paul et al. 1996) and also maternal rank (with preference for offspring of high-ranking mothers; Deag and Crook 1971; Kuester and Paul 1986; Small 1990b). Second, males differ in duration of time they spend by infant handling and also the way how they distribute infant handling among infants (whether they focus almost exclusively on one or two infants or spread interactions among several infants) differs. Either averall interest in infant handling or the number of handled infants were not explained by male rank (Paul et al. 1996). However, male rank seems to influence the distribution of triadic male-infant-male interactions (Paul and Kuester 1996; Kümmerli and Martin 2008). Distribution of infant handling among different dyads and triads seems important for explanation of the behaviour. Different studies interpret male infant handling in Barbary macaques as paternal investment, mating effort, relationship management (agonistic buffering) or their combination.

Male preferences for particular infants led some authors to the conclusion that male infant handling in Barbary macaques may be paternal investment (Taub 1980) in spite of the promiscuity. However, when using DNA analyses no study confirmed that males would preferably take care of their own offspring (Ménard et al. 1992; Paul et al. 1992; Paul et al. 1996; Ménard et al. 2001) or that the care would reflect previous mating patterns (*mate-then-care* pattern, Ménard et al. 2001). Instead, the connection between care and mating during following season (*care-then-mate* pattern) has been found in one study providing support for the mating effort hypothesis (Ménard et al. 2001). Deag (1980) proposed that male Barbary macaques choose infants for triadic interactions based on the existence of a friendship with the infant's mother, but later study did not confirm that adult male-female friendships would extend to the females' infants (Paul et al. 1996). Instead, several studies found that males preferably initiated triadic male-infant-male interactions with higher ranking males and/or with males who were relatively close to their own rank (Deag and Crook 1971; Paul et al. 1996; Kümmerli and Martin 2008) as suggested by agonistic buffering (Deag and Crook 1971) and relationship management (Paul et al. 1996) hypotheses (Kümmerli and Martin 2008; Henkel et al. 2010). Recently, hormonal analyses were used to test whether infant handling including male-infant-male interaction reduces group tension. The results of these analyses remained controversial (see e.g. Henkel et al. 2010; Young et al. 2014).

Research rationale

In spite of the cumulative knowledge about male infant handling in Barbary macaques – that is based on behavioural, DNA and hormonal analyses – the conclusions about male motivation to handle infants remain inconclusive. The disagreements may be based on several aspects:

First, we can assume that the variability in findings may actually reflect flexibility of the behaviour. Infant handling – either as a paternal investment or as a strategy how to achieve mating success or improve social relationships with other individuals – may highly depend on characteristics of social situation influenced by level of different types of stress given by environmental factors. Obviously, the level of infant handling is influenced by female-male ratio as well as the number of available infants and their sex. Moreover, especially referring to assumed social importance of infant handling, it may also reflect social structure and stability of relationships and patterns of mating. These parts of social system are expected to be affected by food availability, risk of predation and other environmental conditions. Infant handling in Barbary macaques has been studied in several different habitats (Deag and Crook 1971; Burton 1972; Taub 1980a; Smith and Peffer-Smith 1982; Small 1990b; Paul et al. 1996; Ménard et al. 2001), but the most extensive data are available from a long-term study on a semifree-ranging population living in a large outdoor enclosure in Germany (Küster and Paul 1984; Kuester and Paul 1986; Paul et al. 1996). Although the work done in Affenberg Salem by Paul and his colleagues mainly in 80s and 90s is impressive and the number of studies based on this research gave us very complex picture of male infant handling in given population, authors admitted that some behaviours of the Barbary macaques at Affenberg Salem might not be typical for the species in general (Paul 1999). "Although the Salem macaques live in a semi-natural setting where food (including provisioned food items) is widely dispersed, they also live in a predator-free environment where the available space is restricted, and the constant food supply allows for early sexual maturation, high female fertility, and low rates of mortality" (Paul 1999). Also other authors pointed out that the environment may greatly affect male infant handling (Smith and Peffer-Smith 1982; see also Anderson 1992 for chacma baboons). The importance of infant handling for infant survival may be for example very different for captive, semi-free ranking and completely wild populations (Kümmerli and Martin 2008). This suggests that studies of different – and especially wild – populations are needed to disentangle some of the contradictions of the knowledge of infant handling.

Besides actual differences in patterns in infant handling among populations or groups, differences in conclusions may result from use of different methods: This involves the data collection, the definition of the recorded data and also statistics. The differences may especially arise when analyses are based on data sorted into arbitrary categories (see Deag 1980). Previous research also demonstrated that some patterns were rather driven by behaviour of one or two individuals rather than described general behavioural pattern (Zhao 1996; Bauer et al. 2014 for Tibetan macaques), thus the results may be different if identity of individuals is controlled for. Another factor that may lead into disunited explanations for infant handling is the disagreement about the relationship between dyadic and triadic male-infant-male interactions. Although the relationship management hypothesis for example received strong support of several studies, it needs to be pointed out that this hypothesis does not satisfactory explain why male Barbary macaques invest into long dyadic interactions much more than males in other species where male-infant-male interactions also occur and why this care is non-equally distributed among different male-infant dyads. Thus the question remains, whether the support for relationship management hypothesis concerns both types of interaction – dyadic infant handling as well as male-infant-male interactions, or different explanations should be searched.

Our study aimed at providing new information about male infant handling in Barbary macaques, which contribute to the explanation of the behaviour and the inconclusiveness of previous research. In order to provide complex picture of male infant handling, we investigated separately different types of interactions and questioned their relationships. We focused on some details of male-infant interactions that were previously neglected and revised some earlier suggestions using different methods, including modern statistical methods that were not previously available. This study was a part of long-term project The Barbary macaque Project and was based on the observation of one group of wild un-provisioned Barbary macaques inhabiting the cedar and oak forest of the Ifrane National Park in the Middle Atlas Mountains of Morocco (33-240°N, 005-120°W). Data were collected between April 2013 and September 2014 and the followed group consisted of 13 adult and 2 subadult individuals, who were perfectly habituated to the human observer before the study started. Together with great visibility at the field site, this allowed us to focus on infants as our focal individuals (Altmann 1974), which is in contrast to the majority of studies that are based on following of males. Observation of 12 infants yielded into ca 1,400 hours of focal observation that included records of ca 10,500 dyadic interactions between infants and males and almost 2,000 of triadic male-infant-male interactions. This is quite a solid dataset to address several questions related with infant handling.

Results

In our first study, we addressed the question whether infant handling may be seen as a paternal effort and/or mating effort. We investigated relationship between distribution of copulations, male-infant dyadic interactions during previous (*care-then-mate*) and following (*mate-then-care*) birth seasons. We used two different perspectives for evaluation of mating activities (male and female perspective) and two different perspectives for assessing infant-male relationship (male and infant perspective) to find out the importance of the used method. We found that the nature of the link between distribution of copulations and distribution of male care depends on the used perspective (male or female/infant). From the male perspective we found support for both patterns; males cared more for the infants of mothers with whom they had previously mated most frequently, and also they mated more frequently with the mothers of infants that they had previously cared for the most. However, when examining the female perspective for mating and the infant perspective for care support for neither pattern has been found. We suggest that missing pattern from the female/infant perspective is contradictory to mating effort, which assumes that female chooses mating partners who take care of her offspring. However, the male perspective lends a support for paternal effort, given the promiscuity and relatively low cost of the care characteristic for the species contrasting to various benefits infant handling may bring to males – including use of infants in triadic male-infant-male interactions. We also found that males tend to prefer infants of same mothers across seasons and suggested that distribution of care may be influenced by long-term relationships between males and females. Inter-sexual bonds may increase male personal mating success, profit paternal effort and bring additional advantages.

In our second study, we focused on distribution of triadic male-infant-male interactions. We tested the assumptions of the relationship management hypothesis that male initiating the interaction is more likely to choose a partner for the interaction (male receiver) with whom the relationships are the most profitable, and these are either higher ranking males or also males who are relatively close to their own rank. We used GLMM method and tested the effect of rank of the receiver and also importantly the type of the interaction – based on whether the interaction was initiated by male holding the infant or male approaching the infant holder. We found that males were more likely to initiate interactions with males who were higher ranking than themselves. However, the effect of rank differed for two types of studied interactions. Males choose a receiver of the interaction based on his rank only when they (initiators) were holding the infant. Number of interactions initiated by non-holder was not predicted by whether the receiver was higher or lower ranking. This result is in accord with relationship management hypothesis, but also indicates that various male-infant-male interactions may need different explanations.

In our third study, we linked triadic and dyadic interactions with social cognition in Barbary macaques. The capacity to monitor, memorise, and act upon the social relationships of others has already been documented, but previous studies usually focused on different types of relationships and different contexts of use. We investigated whether males initiating triadic male-infant-male interactions use knowledge of the relationship between infant and the receiving male. We confirmed that (i) the number of male-infant-male interactions among initiator-infant-receiver triads was positively affected by the strength of the infant-receiver relationship and (ii) when two males were available as bridging partners, a male was more likely to be chosen as the receiver the stronger his social relationship with the infant relative to the other available male. These results indicate that Barbary macaque males recognise the affiliative relationships between infants and other males and make use of this triadic awareness. We provided evidence for the use of triadic awareness that is not related to aggression and is based on temporary and dynamic affiliative infant-male relationships.

Our fourth study was based on the special event, during which non-native female infant, who had been confiscated from the illegal trade, was introduced into the observed group. The case study described pre-release, release and post-release phase and was conceived mainly to help the conservation of the species that suffers by illegal trade with the infants. A year lasting post-release monitoring brought interesting findings for the reintroduction and mainly showed the importance of male-infant interactions. It confirmed that males may be interested in infant handling of an infant who is not native in the group. The infant started being handled by males immediately after the release but the level of interest in her differed among males. The infant spent the most of time in the proximity and "care" of the single male, who seemed to play a crucial role in the infant's survival, as he carried her when the group was travelling, protected her against potential danger and aggression and also stayed with her overnight

Conclusion

Our study provided new information about male infant handling in Barbary macaques. We investigated separately different types of infant handling interactions and concluded that infant handling is highly heterogeneous phenomenon and different types of infant handling interactions may be driven by various motivations of males and/or profits infant handling brings to females or infants. We concluded, that occurrence of male infant handling in Barbary macaques can be at least partly driven by paternal effort. At the same time, males may use infants as a social strategy how to increase their mating success with females or how to establish social bonds with other males. To use infant handling as a strategic social tool, males are able to use complex social knowledge including awareness about relationship between other individuals. What remains unclear is why infant handling in this extent did not evolve in other species that share similar socioecology, environment and phylogeny. Future studies should focus on detailed comparison of male infant handling in different species to solve this issue.

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MANUSCRIPT I

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Use of male and female perspective in explaining link between male care and mating in Barbary macaques

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ABSTRACT

Paternity confusion selects against male investment in infant care; it is therefore unexpected in polygynandrous species. However, males of several primate species still engage infrequent affiliative interactions with particular infants, despite female promiscuity. Two non-exclusive hypotheses link male infant care to male mating strategies. The first hypothesis views infant care as a male strategy to maximise the survival of sired infants; and thus males should take care of infants whose mothers they have mated with in the previous mating season. The second hypothesis states that males attempt to increase mating success through infant care; and thus females should preferentially mate with males that took care of their infants in the months preceding the current mating season.

We tested both hypotheses in wild Barbary macaques, a seasonally-breeding species with extensive male infant care. Relative mating success was calculated either from the male or from the female perspective, and the amount of care provided was calculated either from the male or the infant perspective. From the male perspective we found support for both patterns; males cared more for the infants of mothers with whom they had previously mated most frequently, and also they mated more frequently with the mothers of infants that they had previously cared for the most. However, when examining the female perspective for mating and the infant perspective for care support for neither pattern was found. We suggest that missing pattern from the female/infant perspective is contradictory to mating effort, which assumes that female chooses mating partners who take care of her offspring. However, the male perspective lends a support for paternal effort, given the promiscuity and relatively low cost of the care characteristic for the species. The consistency in male preference for the offspring of the same mothers across seasons suggests that the distribution of care may be influenced by long-term relationships between males and females, or may even promote such relationships. Inter-sexual bonds may increase male personal mating success, profit paternal effort and bring additional advantages.

Keywords:

Infant handling – male care – paternal effort – mating effort – Barbary macaques

INTRODUCTION

Postnatal maternal investment in the form of lactation is ubiquitous in mammals and typically extends to other forms of caregiving (Trivers 1972; Clutton-Brock and Parker 1992), whereas the investment of the male parent is highly variable. In the majority of mammal species mothers are the only caretakers, but in some species (e.g. of carnivors, rodents and primates; Woodroffe and Vincent 1994) males actively take care of infants. Sexual selection theory predicts that different patterns of investment in infant care are related to the different reproductive investment costs experienced by the sexes, and to the phenomenon of paternity uncertainty. Unlike females, who are limited in the number of offspring they can produce (because of time and energetic costs of gestation and lactation), males lose opportunities to mate when taking care of infants and moreover risk that they invest in others' offspring (Trivers 1972; Clutton-Brock and Parker 1992; Paul et al. 2000). As the motivation to bear this cost should be related to the degree of paternity certainty, the male involvement in care is unexpected in polygynandrous species. In spite of this, males in a number of multimale-multifemale primate species with high paternity confusion can be observed to associate with infants (Huchard et al. 2012); grooming and carrying them (Estrada and Sandoval 1977; Deag 1980; Thierry et al. 2000), providing them with support in conflicts (Buchan et al. 2003) and protection against harassment and infanticide (Palombit et al. 1997; Paul et al. 2000). It has been proposed that males may gain fitness benefits by taking care of infants (Smuts and Gubernick 1992): First, males may invest in the survival of their own genes – by contributing to the survival of own offspring as proposed by the paternal effort (or so called paternal investment) hypothesis (Taub 1980; Charpentier et al. 2008; Moscovice et al. 2010). Second, infant care may increase the chances of a male mating with the infant's mother when she resume estrous, and thus infant care can be interpreted as a mating strategy (Seyfarth 1978; Smuts 1985; Ménard et al. 2001).

The paternal effort hypothesis predicts a positive relationship between the extent of care directed towards a particular infant and the likelihood that a male sired that infant. Support for this hypothesis comes from both genetic and behavioural research. Several DNA analyses confirmed that associations and interactions between males and their offspring were more common than between males and unrelated immatures (Buchan et al. 2003; Huchard et al. 2012; Langos et al. 2013; Ostner et al. 2013), however the majority of studies have not found such a relationship (Berenstain et al. 1981; Ménard et al. 1992; Paul et al. 1992; Ménard et al. 2001a; Kerhoas et al. 2016). In yellow baboons *Papio cynocephalus* (Altmann 1980) and olive baboons *Papio anubis* (Smuts 1985) males were more likely to take care of infants if they consorted the mother around the time of conception, or mated with the infant's mother, than if they did neither (see also Smuts and Gubernick 1992). In chacma baboons *Papio ursinus*, associations between males and infants were predicted by consortship activities (see Manson 1997 for the definition) and/or friendship between males and females (Buchan et al. 2003; Moscovice et al. 2010), that predicted paternity (Buchan et al. 2003). In crested macaques *Macaca nigra*, the likelihood of male-infant affiliation was significantly higher if the male was present at the infant's conception (Kerhoas et al. 2016). In Assamese *M. assamensis* (Ostner et al. 2013) and rhesus macaques *M. mulatta* (Langos et al. 2013) the distribution of copulations predicted the distribution of care. This link – also called the *mate-then-care* pattern (Ménard et al. 2001a) – suggests that males estimate their paternity chances when distributing care. Notably, the control over the distribution of care lies with the male and may either be based on how he spread his matings in the past mating season, or how the mother spread hers.

According to the mating effort hypothesis, males associate with infants in order to increase their future mating success with the infants' mothers. If so, males may gain mating opportunities through infant care regardless of whether they have sired those infants. To support this hypothesis the link between care and mating behaviour needs to follow the *care-then-mate* pattern: the distribution of individual male care should predict that male's mating success in following mating seasons and/or that male's success in siring future offspring. Here the male endears himself to the female, the amount of care is assessed from the infant's perspective, and the mother provides the male with mating privileges, i.e. the distribution of copulations is affected by female choice (see e.g. Hector et al. 1989; Small 1989) which is based on the distribution of care, thus the male mating success should increase from her perspective. Whereas the studies in baboons found rather weak evidence of this pattern (e.g. Nguyen et al. 2009; but see Smuts 1985), some finding of the studies in macaques supported the hypothesis. For example, in Tibetan macaques *M. thibetana*, the amount of infant care that a male provided predicted the number of females who later consorted with that male (Zhao 1996). In Barbary macaques *M. sylvanus*, males who spent the most time with certain infants also achieved the highest mating frequencies with their mothers compared to other males during the following mating season (Ménard et al. 2001; but see also (Paul et al. 1996). Moreover, in crested macaques males increased infant care in the presence of the infant's mother, and male infant care increased affiliation between males and females (Kerhoas et al. 2016). However in rhesus macaques the mothers presence did not seem to increase affiliation between males and unrelated immatures (Langos et al. 2013). Finally, the mating effort hypothesis may also explain, why males sometimes preferentially care for the offspring of high ranking mothers (Gouzoules 1975; Hector et al. 1989; Paul et al. 1996) (see Smuts and Gubernick 1992 in contrast to Paul et al. 1996). Increased mating opportunities with high ranking females are considered profitable, as for example, the offspring of high ranking females have higher rates of foetal and postnatal survival (Paul and Thommen 1984; Silk et al. 2009; Kerhoas et al. 2014), and are generally in better condition (Altmann and Alberts 2005).

In summary, different studies provide mixed support for the paternal effort and mating effort hypotheses. In different species variability may reflect systematic variation especially in relation to male reproductive skew (Berenstain and Wade 1983; Smuts and Gubernick 1992) and/or with the risk of infanticide. (Reproductive skew is expected to positively correlate with the amount of male care because it decreases paternity confusion; Berenstain and Wade 1983; Smuts and Gubernick 1992, whereas risk of infanticide should enhance the care as a form of protection against infanticidal males; Paul et al. 2000.) For example the effect of paternity has been observed in promiscuous Assamese macaques (Ostner et al. 2013) and rhesus macaques (Langos et al. 2013), but was missing in crested macaques, where paternal skew and danger of infanticide is high (Kerhoas et al. 2016). In highly promiscuous Barbary macaques, one study did (and another did not) find support for the mating effort hypothesis (Paul et al. 1996; Ménard et al. 2001); illustrating that conclusions may differ even when focusing on the same species.

Such inconsistencies within species may reflect differences in the methods used: For instance, conclusions may depend on which measure was used as a proxy for paternity chances and estimation (e.g. presence vs. absence in the group during the preceding mating season, relative number of consortship days, or number of copulations) Moreover, some results are open to various interpretations. Although the *mate-then-care* pattern is usually interpreted as a support for the paternal effort hypothesis, and the *care-then-mate* pattern for the mating effort hypothesis, distinguishing these two motivations may be complicated, especially when both patterns occur at the same time, which is often the case. The coexistence of both patterns may suggest that care is driven by the benefits afforded by bothIt has been also suggested that one pattern might actually be an extension of the other, for example, apparent paternal investment can be a by-product of mating effort, if this extends over several seasons (Smuts and Gubernick 1992). Alternatively, both patterns may be mediated by the quality of male-female relationships that may result into mating privileges and paternal care ("friends with benefits hypothesis"; Ostner et al. 2013). Similarly, observing the connection between female rank and the provision of infant care by males is not a sufficient criteria for discriminating between the mating effort and paternal effort hypotheses, i.e. unless we can distinguish whether the male first adjusts care according to female rank (mating effort) or first mates with the highest ranking females and provides increased care after the fact (paternal effort). Thus conclusions may also differ depending on whether only one pattern or both (*mate-then-care* and *care-then-mate)* are studied together and which variables are controlled.

In this study we investigated *care-then-mate* and *mate-then-care* patterns in Barbary macaques in order to analyse the relative importance of the paternal effort and mating effort hypotheses. Interactions between males and infants (further referred to as male infant handling) in Barbary macaques have long been a target of scientific interest because of its extraordinary intensity (compared to other multimale-multifemale *cercopithecinae* (Deag 1980; Whitten 1987; Maestripieri 1998)) in combination with the high promiscuity of females (Small 1990a). Male infant handling involves both long dyadic interactions (further referred to as male care), during which males carry, cradle and groom infants in a similar way to the mother, and triadic male-infant-male interactions, during which two males shortly manipulate one infant together. Interactions of both types are non-equally distributed among dyads or triads (Deag 1980; Taub 1984). The extent of the involvement in infant handling differs for different infants as well as males. Whereas some infants may attract much attention from several males, others may be completely ignored (Ménard et al. 2001a). To some degree the differences in infant popularity can be explained by infant sex − with the stronger preference for male infants (Paul et al. 1996), age − with stronger preference for younger infants (Small 1990b; Paul et al. 1996), and also maternal rank − with preference for the offspring of high-ranking mothers (Deag and

Crook 1971; Kuester and Paul 1986; Paul et al. 1996). Male rank may also affect male involvement in triadic interactions (Deag and Crook 1971), but does not seem to predict the extent of male involvement in dyadic care or the way in which males distribute care among infants (Taub 1980; Paul et al. 1996). Males seem to prefer to initiate triadic male-infant-male interactions with males who are higher ranking than themselves, and/or with males who are similarly ranked (as opposed to those whose rank differs more substantially)(Deag and Crook 1971; Paul et al. 1996; Kümmerli and Martin 2008). Males differ in their preferences for particular infants (Taub 1980a; Paul et al. 1996).

The variable distribution of dyadic care and triadic male-infant-male interactions offers several potential explanations for infant handling: Whereas triadic male-infant-male interactions are mainly believed to serve a social function among males (relationship management hypothesis according to Paul et al. 1996 or agonistic buffering hypothesis according to Deag and Crook 1971), the explanations for long dyadic interactions remain inconclusive. The fact that males differ in their preferences for particular infants suggests that male investment into long periods of dyadic infant handling may be driven by paternal effort (Taub 1980). However, no study has confirmed that males preferably take care of their own offspring (Ménard et al. 1992; Paul et al. 1992; Paul et al. 1996; Ménard et al. 2001), or that the care would reflect previous mating patterns (Paul et al. 1996; *mate-then-care* pattern according to Ménard et al. 2001). Instead, the connection between care and mating during the following season (*care-then-mate* pattern) has been found, providing support for the mating effort hypothesis (Ménard et al. 2001 but see also Paul et al. 1996).

Barbary macaques live in multimale-multifemale groups characterized by female philopatry and male transfer (Kuester and Paul 1999; Fooden 2007). Female rank is inherited through the matriline (Paul and Kuester 1987), whereas immigrating males achieve their position in the hierarchy over the course of their life span; thus male rank is not the outcome of takeovers but partly depends on age (Widdig et al. 2000). Reproduction in Barbary macaques is highly seasonal, concentrating into a 3 month period with a high degree of female ovarian cycle synchrony (Taub 1980b; Küster and Paul 1984; Brauch et al. 2008), and a high level of promiscuity (Small 1990). Male reproductive skew is rather low: males rarely display mate-guarding and consortship compared to other macaques species (Kümmerli and Martin 2005; Brauch et al. 2008; Bissonnette et al. 2011), and the majority of male-female associations seem to disappear shortly after the end of the breeding season (Small 1990).

We investigated the relationship between the distribution of copulations, male care during previous (*care-then-mate*) and following (*mate-then-care*) birth seasons, and female and male rank in Barbary macaques. We used continuous variables to evaluate male-infant care and the distribution of copulations. We used two different perspectives for the evaluation of mating activities (male and female perspective), and two different perspectives for assessing infant-male relationships (male and infant perspective) to assess the importance of each approach. We tested 4 non-exclusive predictions: (1) The distribution of the mating activities of a male (among all females of the group) predicts the distribution of his care among all infants of the group during the following birth season, and/or (2) during the previous birth season (=male perspective); (3) The distribution of the mating activities of a female (among all males of the group) predicts the distribution of the care of her infant among all males during the following birth season and/or (4) during the previous birth season (=female perspective). We also assessed the effect of male and female rank on the distribution of copulations and the distribution of male care in order to investigate whether the change in female rank affects male care. We interpret our results in light of the mating effort, paternal effort, and friends with benefits hypotheses.

METHODS

Data collection

We conducted this study in the Ifrane National Park in the Middle Atlas Mountains of Morocco (33-240°N, 005-120°W) with the Research Permission of the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco. We followed one group (Green Group) of individually recognizable macaques, who were well habituated to the presence of human observers. Focal continuous observations (Altmann 1974) of infants were conducted by BK during two field seasons corresponding with two following birth seasons (April–August 2013, April–September 2014). In both seasons the group consisted of 7 adult (older than 5 years old) males, 1 subadult (5 years old) male, and 6 adult females (older than 5 years). There were 19 juveniles in 2013 and 20 in 2014. All adult females gave birth in both seasons, resulting in 6 infants in each season (5 female, 1 male in 2013; 3 female, 3 male in 2014). *Ad libitum* data (Altmann 1974) on adult subjects were recorded by several researchers throughout the whole study period (April 2013 to September 2014). We used handheld HP iPAQ 114 series pocket PCs loaded with Pendragon Forms Version 5.1 (©Pendragon Software Cooperation, U.S.A.) to record the data.

Infants were followed during 2-hour observation sessions, during which all social interactions between the focal infant and other group members were recorded. We pseudorandomized the order in which we observed the infants to ensure that all infants were observed equally often at the different times of the day. In both seasons we started collecting data once 4 infants were born. We observed all infants until the end of the field season, except one male infant (born in 2014), who disappeared approximately 10 weeks after birth. We thus divided the dataset into three subsets: period 1 (corresponding with the birth season 2013), period 2a (birth season 2014 before the infant was lost) and period 2b (birth season 2014 after the infant was lost). To assess what affected the distribution of male care (our main question) we focused only on period 1 and period 2a, however period 2b was used when assessing the effect of rank change between periods.

The data collection on the 12 infants yielded a total of 1,430 hours of observation: 582 hours in period 1 (hours of focal data per infant mean ± sd = 97 ± 11), 321 hours in period 2a (hours of focal data per infant mean ± sd = 54 ± 6), and 527 hours in period 2b (hours of focal data per infant mean ± sd = 105 ± 9). We recorded interactions between the focal infant and adult male(s): start and termination of proximity (less than 1.5m distance), start and termination of body contact (including also triadic male-infant-male interactions). The start of proximity was recorded when the male approached the infant into 1.5m distance, infant approached a male or was brought by another individual to another male. The end of proximity was recorded when the infant went away from the male or vice versa or infant was carried away by another individual. Body contact included cradling, dorsal carrying, ventral carrying, grooming, resting in body contact and "contact crawling" (see Thierry et al. 2000; Deag 1980; Kubenova et al. 2017 for a description of the behaviours) and polyadic interactions involving no more than one adult male. Polyadic interactions involving more males were excluded as they may be driven by a different motivation than dyadic interactions, i.e. male relationship management (Deag 1980; Paul et al. 1996). We recorded the ID of all involved individual(s) and also indicated who initiated the interaction.

Dyadic dominance-submission interactions (between same sex individuals) and copulations were recorded *ad libitum*.

Data analysis

Composite sociality index

We used a composite sociality index (CSI; Silk et al. 2006) to assess the strength of dyadic affiliative relationships between infants and males. The index expresses the relative strength of the relationships between the dyad compared to other dyads by combining several categories of defined behaviours. We used 5 categories of behaviour: 1) frequency of the "active" body contact between the infant and the male (dorsal carrying, ventral carrying, grooming and polyadic interactions (involving 1 adult male)), 2) duration of this body contact, 3) duration of the "passive" body contact (resting in proximity and crawling body contact) , 4) frequency of proximity (defined above) initiated by the male, 5) duration of proximity (substracting duration of body contact between the infant and the male and duration of triadic male-infant- male interactions). We assessed the CSI score separately for each of three periods (period 1, period 2a, period 2b) and also separately for two perspectives, male and infant. To score the CSI from the male perspective (CSIm) we divided the value for each behaviour (between the male and the infant) by the average across all dyads this male formed (with all infants) - thus the index expressed the relative strength of the relationship of the male-infant dyad compared to the relationship this male had with all infants - and averaged the results. To score the CSI from the infant perspective (CSIi) we divided the value for each behaviour between the male and the infant by the average across the dyads this infant formed (with all males) - thus the index expressed the relative strength of the relationship of the infant-male dyad compared to the relationship this infant had with all males - and averaged the results.

Copulations

To evaluate the distribution of copulations, we used copulations recorded *ad libitum* between August 2013 and February 2014. We calculated what proportion of a males total copulations (with all females) took place with each given female to assess the distribution from the male perspective (MateM) and what proportion of a females total copulations (with all males) took place with each given male to assess the distribution from female perspective (MateF). The values could range between 0 and 1 (0 = no copulation with given partner, 1 = all copulations with given partner only).

Social rank

To assess the dominance hierarchy we used dominance-submission interactions. We entered data into a winner-loser dominance matrix and built a hierarchy based on the standardized normalized David's score (Schmid and De Vries 2013). The hierarchy was assessed separately for males and females, and for each period (1, 2a, 2b). The change of female rank (DSfChange) across periods was counted as a difference of female David's score between the periods (DSf2a-DSf1 and DSf2b-DSf2a).

Statistical analysis

To test the predictions of our hypotheses we used six LMM models using the lme4 package (Bates et al. 2015) in R 3.1.1 (R Core Team 2014): Models I.F and II.F refer to the use of the female perspective (more precisely distribution of copulations counted from female perspective – MateF, and distribution of care counted from infant perspective − CSIi) and models I.M and II.M refer to the use of the male perspective for distribution of copulations – MateM as same as the care − CSIm. Models III.A and III.B both use male perspective, the letter refers to two periods of interests.

We used a forward stepwise selection procedure and determined the importance of each predictor variable on the basis of a log-likelihood ratio test (LRT). We used the *add1* function to examine independent (marginal) effects of considered predictors and to compare the fit of the models with and without the addition of each significant predictor one by one. To evaluate the effects of the predictors we computed the 95% confidence intervals (using the *confint* function in lme4). Male and female ID was entered as a random effect in all models.

In the model I.F we wanted to find out what affected the distribution of copulations from the female perspective (MateF). Our predictors of interest were: sociality index during the birth season before the mating season from infant perspective (CSIi1), sociality index during the first part of the birth season following the mating season from the infant perspective (CSIi2a), and male rank during the first birth season (DSm1).

In the model I.M we followed the same procedure but using male instead of female perspective for proportion of copulations (MateM), sociality index from the perspective of male instead of the infant (CSIm1, CSIm2a) and rank of the female (DSf1) instead of the male as fixed effects.

In the model II.F we assessed the possible predictors of the distribution of male care among infants during and after the birth season (expressed as sociality index counted from infant perspective, CSIi2a). We examined the proportion of copulations the female experienced with the given male (compared to all males) during the previous mating season (MateF), the composite sociality index of the previous birth season (counted from infant perspective (CSIi1)), and male rank during previous (DSm1) and contemporary (DSm2a) season.

The model II.M was similar but used the male instead of female perspective for ratio of copulations (MateM), the sociality index from the perspective of the male instead of the infant (CSIm1, CSIm2a), and female rank (DSf1 and DSf2a) instead of male rank as fixed effects.

In the model III.A, we evaluated whether differences between the sociality index score during period 1 and period 2a (CSImDifA counted as CSIm2a-CSIm1) were predicted by changes in female rank between periods 1 and 2a (DSfDifA counted as DSf2a-DSf1).

Model III.B was built in the same way, but concerning the change in the female rank and the change in male care between periods 2a and 2b (CSImDifB counted as CSIm2b-CSIm2a; DSfDifB counted as DSf2b-DSf2a).

RESULTS

Data description

All males were observed in proximity of some infant(s) and in body contact with some infant(s). All twelve infants were observed in proximity with some male(s) and only one infant (born during period 1) was never observed in body contact with any male. Infants spent between 0 and 27 % of observational time in body contact with a male (mean ± sd = 10 ± 11 %). Sociality indices CSI between males and infants were counted based on 5,829 interactions (including proximity and both types of body contact - according to definition) in period 1 (21 - 2,206 per infant, mean ± sd = 972 ± 937), 4,529 interactions in period 2a (404 - 1525 per infant, mean ± sd = 755 ± 421) and 3,073 (362 - 455 per infant, mean ± sd = 410 ± 41) in period 2b. CSIs ranged between 0.027 and 4.150 for infant perspective, CSIi (median = 0.605) and between 0.004 and 4.602 for male perspective, CSIm (median = 0.641). The change in CSIm between periods 1 and 2a (CSIm2a-CSIm1) ranged between -2.054 and 2.365 (median = 0.026). The average change in CSIm for each of the 6 infants ranged between -0.813 and 0.565 (median = 0.213). The change in CSIm for each of the 6 infants between periods 2a and 2b (CSIm2b-CSIm2a) ranged from -2.887 to 0.927 (median = 0.252) and from -0.959 to 0.425 (median = -0.086) for 5 infants (excluding the lost infant) between 2014a and 2014b.

We recorded 152 copulations: between 6 and 49 copulations for each female (mean ± sd = 25.33 ± 16.27) and between 14 and 50 copulations for each male (mean ± sd = 25.33 ± 15.04). All females and males had 5 or 6 mating partners (from 6 possible). The values of proportions of females' copulations with different males (36 female-male dyads, MateF) ranged between 0 and 0.500 (median = 0.140). The values of proportions of males' copulations with different females (36 male-female dyad, MateM) ranged between 0 and 0.58 (median = 0.103).

Female rank was based on 213 interactions in period 1 (0% zero dyads, 0% two-way dyads), 179 in period 2a (0% zero dyads, 47% two-way dyads) and 70 in period 2b (0% zero dyads, 20% two-way dyads). Female David's score ranged between -13.74 and 13.71 (median = -0.21). Male rank was based on 45 interactions in period 1 (20% zero dyads, 7% two-way dyads) and 71 interactions in period 2a (13% zero dyads, 33% two-way dyads). Male David's score ranged between -10.10 and 6.85 (median = 0.65). The change in female David's score between period 1 and 2a (DSf2a-DSf1) ranged from -13.265 to 10.46 (median = 0.08) and between period 2a and 2b (DSf2b-DSf2a) from -8.95 to 8.42 (median = 2.32). Change in male David's score (DSm2a-DSm1) ranged from -3.69 to 2.90 (median = 0.45). Based on pairwise Pearson correlations we found no correlation between total number of copulations and rank before (r = 0.58; p = 0.523) or after the mating season (r = 0.29; p =

0.570) in males, and no correlation between total number of copulations and rank either before (r = 0.73, p = 0.100) or after the mating season (r = 0.54, p = 0.270) in females.

Model I.F

The proportion of copulations between a given female and male (from all her copulations), MateF, was predicted by male rank DSm1 (χ^2_1 = 3.98, p=0.046). With 95% probability, the increase of the male David's score (DSm1) by 1.0 increased the proportion of the female's copulations with that male by 0.00 – 2.09%. The relative amount of care that the infant received from different males prior (CSIi1) or after (CSI2a) a mating season was not considered a significant predictor of the female's distribution of copulations. The addition of those variables did not change the null model (Tab 1) or the model with the significant predictor DSm1 (based on LRT).

Tab 1: Result of log-likelihood ratio test (LRT) for the model selection with the distribution of copulations of the female as a response variable (model I.F), showing marginal effects of considered predictors and confidence intervals for coefficients of their fixed effects

	χ^2_1	p	estimate	SE	CI 95%
Care distribution 1 (CSIi1)	0.747	0.388	0.015	0.017	-0.019, 0.047
Care distribution 2 (CSIi2a)	0.170	0.681	0.006	0.014	-0.022, 0.240
Male rank 1 (DSm1)	**3.975**	**0.046**	**0.011**	**0.005**	**0.000, 0.021**

(CSIi1 = distribution of care from infant perspective before mating season, CSIi2a = distribution of care from infant perspective after mating season, DSm1 = male rank before mating season)

Model I.M

To find out what affects the proportions of copulations from the male perspective (model I.M) we fitted a model with the distribution of male care among infants during the season prior mating (CSIm1) and model with the distribution of male care after mating season (CSIm2a), that were selected as potential predictors based on LRT. When considered separately, both variables had a significant effect on the pattern of copulations, thus in a given male, higher infant care prior and after the mating season led to an increase in the proportion of copulations with its mother. With 95% probability, an increase of the sociality index between the male and the infant (CSIm1) by 1.0 increased the proportion of the male's copulations with the infant's mother by 1.013-1.081; an increase of the CSIm2a by 1.0 increased the proportion of the male's copulations with the infant's mother by 1.036-1.086 (see tab 2). LRT results indicated a strong dependency of the variables (the model with both variables was not significantly different from the model with only one (χ^2_1 = 1.12, p= 0.290 for addition of CSIm1 to the model with CSIm2a; χ^2_1 = 2.28, p = 0.131 for addition of CSIm2a to the model with CSIm1). In model with both predictors, none of them had significant effect (95% CI = -0.021, 0.066 for CSIm1; 95% CI = -0.010, 0.077 for CSIm2a).

Tab 2: Result of log-likelihood ratio test (LRT) for the model I. M, with the distribution of copulations of the male (MateM) as a response variable showing marginal effects of considered predictors and confidence intervals for coefficients of their fixed effects

	χ^2_1	**p**	**estimate**	**SE**	**CI 95%**
Care distribution 1 (CSIm1)	**7.172**	**0.007**	**0.045**	**0.016**	**1.013, 1.081**
Care distribution 2 (CSIm2a)	**8.332**	**0.004**	**0.048**	**0.016**	**1.036, 1.086**
Female rank 1 (DSf1)	3.688	0.055	0.006	0.003	-0.000,

(CSIm1 = distribution of care from male perspective before mating season, CSIm2a = distribution of care from male perspective after mating season, DSf1 = female rank before mating season)

Model II.F

When evaluating the possible predictors of how care of the infant was distributed among different males during the second birth season (CSIi2a; model II.F), only the distribution of care during the previous season (CSIi1) was considered as a possible predictor because adding male rank (DSm1, DSm2a) or the distribution of the female's copulations among males (MateF) did not change he null model,or the model with previous care (CSIi1) (based on the LRT) (see tab 3). An increase of CSIi1 by 1.0 increased CSIi2a by 0.292-0.995 with 95% probability. Thus, male infant care was not predicted by the pattern of female copulations in the previous season, but it was predicted by male infant care from previous season.

Tab 3: Result of log-likelihood ratio test (LRT) for the model II. F with the distribution of male care from infant perspective during the second birth season (CSIi2a) as a response variable, showing marginal effects of considered predictors and confidence intervals for coefficients of their fixed effects.

	χ^2_1	**p**	**estimate**	**SE**	**CI 95%**
Care distribution 1 (CSIi1)	**11.517**	**< 0.001**	**0.463**	**0.219**	**0.292, 0.995**
Copulations (MateF)	0.051	0.820	-0.370	0.336	-3.657,
Maler rank 1 (DSm1)	0.023	0.878	0.005	0.035	-0.064,
Male rank 2 (DSm2a)	0.172	0.678	0.017	0.041	-0.064,

(CSIi1 = distribution of care from infant perspective before mating season, MateF = distribution of copulations from female perspective, DSm1 = male rank before mating season, DSm2a = male rank after mating season)

Model II.M

For the same model using male perspective (evaluating the effect on the male distribution of care among infants during the second season), we excluded only female rank during the same season (DSf2a) as a potential predictor based on LRT. Addition of female rank during the previous birth season (DSf1), distribution of the male's copulations among females during the previous birth season (MateM), and also distribution of male care among infants during the previous birth season (CSIm1) changed the null model, so we fitted 3 models with the addition of 1 of those variables each in the first step. In those models, a 1.0 unit increase in the sociality index during the previous birth season (CSIm1) increased the relative amount of care during the following birth season (CSIm1) by 0.422-0.850. Anincrease in the proportion of the male's copulations (MateM) by 1.0 (100%) increased it by 1.837-6.859, and an increase in female David's score (DSf1) of 1.0 by 0.007-0.085 with 95% probability (see tab 4).

Combining predictors chosen in the second and third step of stepwise selection (based on LRT), we found following: Although female rank (DSf1) as a single predictor affected care during following season (CSIm2a), the effect disappeared when controlling for both the distribution of male care during the preceeding season CSIm1 (χ^2_1 = 0.23, p= 0.630, CI 95% = -0.046, 0.028), and the distribution of male copulations MateM (χ^2_1 = 1.38, p = 0.239, CI 95% = -0.016, 0.063). This distribution of copulations (MateM) affected care during the following birth season (CSIi2a), even when controlling for female rank DSf1 (χ^2_1 = 6.65, p = 0.010, CI95% = 0.932-6.385), but did not when controlling for the care of the first season CSIm1 (χ^2_1 = 2.54, p =0.111, CI95%=-0.440, 4.092). The distribution of the care during the previous birth season affected care in the following season CSIm2a, even when controlling for female rank DSf1a (χ^2_1=19.87, p < 0.001, CI = 0.409, 0.935, and for the distribution of male copulations MateM (χ^2_1 = 16.91, p < 0.001, CI = 0.308, 0.779). In summary, higher female rank, higher male copulation ratio, and higher male infant care during the previous season led to increased male infant care during the following season. However, these effects were nonexclusive.

Tab 4: Result of log-likelihood ratio test (LRT) for the model II. F CSIm2a as a response variable, showing marginal effects of considered predictors and confidence intervals for coefficients of their fixed effects

	χ^2_1	p	estimate	SE	CI 95%
Care distribution 1 (CSIm1)	**24.839**	**< 0.001**	**0.635**	**0.109**	**0.422, 0.850**
Copulations (MateM)	**10.471**	**0.001**	**4.348**	**1.283**	**1.837, 6.859**
Female rank 1 (DSf1)	**5.205**	**0.023**	**0.046**	**0.020**	**0.007, 0.085**
Female rank 2 (DSf2a)	3.290	0.070	0.048	0.026	-0.003, 0.099

(CSIm1 = distribution of care from male perspective before mating season, MateM = distribution of copulations from female perspective, DSf1 = female rank before mating season, DS2a = female rank after mating season)

Model III.A, III.B

The result of LRT indicated that the changes in female rank (DSfChange) between periods 1 and 2a did not predict the changes in distribution of male care among the female's offspring (χ^2_1 = 1.65, p = 0.200, CI 95% = -0.019, 0.074). However, the change in female rank between periods 2a and 2b did predict the changes in male-infant care between these two periods (χ^2_1= 7.64, p = 0.006, estimate = 0.048, SE = 0.016). The change in female David's score by 1.0 (DSfChangeB) increased the expected change in sociality index between the male and her infant (CSImChangeB) by 0.017- 0.079 (CI=95%).

DISCUSSION

Results overview

In order to find out whether male care in Barbary macaques may be seen as paternal effort and/or mating effort, we investigated the relationship between the distribution of mating and the distribution of care during the preceding season (care-then-mate pattern) and following the birth season (mate-then-care pattern). We also examined the effect of male and female rank on the distribution of care and mating. We used two different perspectives (male, and female/infant) to evaluate the distribution of male care and mating. We confirmed that support for the two patterns depends on the perspective used. The way in which males distributed copulations among females predicted how they distributed care among infants during the following season. However, the proportions of copulations the female experienced with different males did not predict the relative amount of care her infant received from different males. The proportion of care that males invested into different infants predicted their relative mating success with the infant's mothers (compared to with other females during following season) but the distribution of care an infant received from different males did not predict how often its mother would copulate with these males (compared to others). The distribution of care in the second season was predicted by care during the previous season, suggesting tendency for "consistency" of care across the seasons, and by female rank. We also found out that a change in female rank may affect the distribution of male care under some circumstances. Male rank predicted how females distributed copulations, but did not predict how the care was distributed among infants. We suggest that the difference in results (depending on which perspective is used) is important when interpreting the results in light of the paternal effort and mating effort hypotheses (discussed bellow).

Paternal effort

If male care is a consequence of paternal effort, males should ideally take care of their own offspring. This appears to be the case in several baboon species (e.g. Buchan et al. 2003), however, studies using DNA analyses found limited support for this hypothesis in macaques (e.g. Paul et al. 1996; Kerhoas et al. 2016, but see Langos et al. 2013; Ostner et al. 2013). However, the number of behavioural studies in macaques supported the view that males may distribute care depending on mating history, which may indicate that males try to increase the chance that they provide the care to their own offspring. Thus the infant care observed in these species may be interpreted as paternal effort (e.g. Berenstain et al. 1981 for rhesus macaques, Ostner et al. 2013 for Assamese macaques). However, similar support for the paternal effort hypothesis in Barbary macaques is missing. It has been shown that male Barbary macaques did not become the main caretakers of the 'relevant' infants even when they were the main sexual partner of their mothers. Previous studies however used only a binomial categorisation of caretakers – main caretaker vs. others, and mating partners – main mating partner vs. others (Paul et al. 1996; Ménard et al. 2001). The question remains whether such a binomial measure is sufficient to test the hypothesis, especially given the difference in time and energy investment into mating and infant care; i.e. although it is possible that a male can be the primary mating partner of several females, it may not be possible to act as the primary caretaker of any more than one infant at a time. In this study we thus tried to evaluate the pattern on a finer scale, using continuous, rather than binomial variables (proportion of the female's copulations and CSI index for the infant-male). We confirmed the result of the above mentioned study by Ménard et al. 2001. The proportions of the mother's copulations did not predict the distribution of male care of their offspring. In other words, infants did not receive more care from males who had a higher chance of being their fathers (based on the relative proportion of copulations).

Although this result contradicts the presumptions of the paternal effort hypothesis, some questions need to be addressed before fully refusing it. First, males might use some other information (besides frequencies of copulations) that was not included in this and other studies. It has been suggested that paternity depends on the timing of copulations, and males may get information about the female ovulatory stage based on the female swelling, or even behaviour, e.g. copulation calls (Semple and McComb 2000; Brauch et al. 2007). However, our study cannot answer this question because we do not have information about the ovulatory stage of females. Second, in this study we found that males cared more often for the infants of mothers with whom they had experienced the most mating success. The observation of this *mate-then-care* pattern (from the "male perspective") can both support and refute the paternal effort hypothesis: Either the pattern is not driven by paternal effort (for example as a result of extended mating effort discussed later) or males track their own mating history in order to decrease the chance of misplacing paternal investment although this strategy is much less effective for progeny estimation. The second option may be supported by two arguments: First, given that Barbary macaques are characterised by high female promiscuity and ovarian synchrony, thelow chances of female monopolisation may lead to low consortship activity and reproductive skew (Taub 1980b; Küster and Paul 1984; Brauch et al. 2008; Bissonnette et al. 2011), all of which means that it may be simply impossible to track others' copulations. Therefore, tracking “at least” one’s own copulations may still provide an evolutionary advantage. The second argument why males might invest incare (even using relatively unreliable information about paternity) may be linked to the relatively small costs of this type of infant care. Where the seasonality of reproduction increases the costs of consortship, it may actually decrease the costs of infant care. Because care is concentrated in the birth season perhaps it does not represent a large cost in terms of lost mating opportunities. The high body weight ratio between males and infants (see Fooden 2007) also suggests a low cost in terms of energy investment (Wright 1990; Woodroffe and Vincent 1994). Such low costs can be easily outweighed by the benefits, e.g. increased infant survival and thus increased group size, but more importantly access to infants for triadic interactions that may regulate male-male relationships (Paul et al. 1996; discussed below).

Mating effort and female choice

The mating effort hypothesis predicts that males may benefit from infant handling by increasing their subsequent mating success with the infants’ mothers (Smuts 1985; Smuts and Gubernick 1992). In accord with this, a previous Barbary macaque study showed that the care may predict the distribution of sexual behaviour in the following mating season (Ménard et al. 2001; but see also Paul et al. 1996). This was not the case in our study however. This result contradicts the findings of the previous study (Ménard et al. 2001a) and the original mating effort hypothesis: this assumes that females distribute copulations among males depending on previous levels of infant care, and thus mating effort should be the most likely in species where females have a chance to choose specific mating partners (Seyfarth 1976; Smuts 1985). Previously, female Barbary macaques have been described as very active in sexual interactions; from being extreme in the degree to which they “assert themselves” (Small 1990)*, to* being responsible for the initiation and termination of consortship (Taub 1980, p.292), and to using copulations calls to achieve mating success and manipulate paternity (Semple 1998; Pfefferle et al. 2008). As such we might expect that sexual behaviour in Barbary macaques would be affected by active female mate choice. Although its role was supported by our finding that the distribution of copulations from the female perspective was positively influenced by male rank, we did not confirm that females would also adjust distribution of copulations according to the amount of care the males provided to their offspring (compared to other males). We may only speculate whether females also consider other male traits, whether they compromise to some extent between the profits derived from male care and promiscuity, or whether they may reward males for care by increasing their paternity chances (e.g. via timing of copulations).

In contrast to the female perspective, the results of the male perspective revealed that infant care predicted future mating successf. Males were more likely to copulate with those females whose infants they cared for more in the previous season. The possible explanation for this pattern is that both *mate-then-care* and *care-then-mate patterns* (as observed from the male perspective) are mediated by male-female relationships, as suggested by the "friends with benefits" hypothesis (Ostner et al. 2013; see also Massen et al. 2012). Those relationships may also explain why males seem to remain consistent in their preferences for the infants of particular mother(s) across seasons.

Consistency in male preferences for the offspring of particular mother(s)

The friends with benefits hypothesis emphasises that males may form relationships with females that allow them to stay in their proximity, provide them with mating privileges during mating season, and further provide them with access to infants in the birth season. This may result in a stable pattern across seasons, as confirmed by our finding that care during the first season was the best predictor of care during the second season (when controlling for mating). This pattern may be male driven, thus the hypothesis differs from the “extended mating effort” hypothesis which assumes that stabilizing pattern of the care is a product of female choice for mating partners (Smuts and Gubernick 1992).

The role of male-female relationships in the distribution of male care is broadly accepted in some baboon species, where the male is believed to stay in proximity to the lactating female in order to protect the dependent infant against infanticide as a part of his paternal effort (Palombit et al. 1997; Weingrill 2000; Moscovice et al. 2010; Goffe et al. 2016 but see also Nguyen et al. 2009; Baniel et al. 2016). However, male macaques rarely remain in proximity tofemales outsideof the mating season, and infants tend to stay apart from their mothers for extended periods during their first year of life (e.g. Taub 1984 for Barbary macaques; Ogawa 1995; Minge et al. 2016 for Assamese macaques). Thereby, unlike in baboons, associations between males and females do not seem to be related to the presence of the infant, and are traditionally believed to be a reflection of mate-guarding activity (Small 1990a) rather than of actual bonding, or “friendship” as is described in baboons. Nevertheless, recent studies have shown that macaques mayform stable heterosexual associations that can persist over several years (e. g. Hill 1990; Massen et al. 2012 for rhesus macaques; Ostner et al. 2013; Haunhorst et al. 2016 for Assamese macaques). The associationsmay be beneficial for individuals of both sexes, increasing mating and reproductive success, and the amount of grooming received (and consequently reducing stress) (Massen et al. 2012; Kulik et al. 2015 for rhesus macaques; Ostner et al. 2013 for Assamese macaques; Aureli and Yates 2010; Kerhoas et al. 2016 for crested macaques). Although male-female relationships extending beyond the mating period have not been systematically described in Barbary macaques, our results indicate their existence and the possible link between the relationships and male care of infants.

In this context, we should mention again the different results for male and female/infant perspective. Whereas male relationships with females may mediate a link between the care of infants and mating, female relationships with males do not seem to play this role – as the link between care and mating when using the female perspective is missing. This first shows that the relationship between care and mating is not only a by-product of the proximity between males and females with their offspring (because such a confound would result in the relationships working from both perspectives, see also Berenstain et al. 1981 refuting this confound). It also suggests that the assumed relationships between sexes may play different roles in the distribution of care for males and females. Whereas male care may influence and/or be influenced by relationships with females, female relationships are not based on care and/or do not affect it. On the other hand, the finding that male rank influenced the way in which females distributed mating indicates that females may use mating to establish the bonds that are likely to bring advantages to them and/or their offspring (e.g. warrant protection against aggression and support in conflicts; e.g. Hill 1990 and Manson 1994 for rhesus macaques). The finding that female rank predicted how males distributed care during the following season is in accord with the prediction that (in order to bond with influential females) males bias their affiliative interactions toward the infants of high-ranking females (Chapais 1983; De Waal 1990; Smuts and Gubernick 1992).

At the same time it seems that males may compromise between the profits derived from bonding with high ranking females and the stable relationships that may profit paternal care. Assessing the effect of female rank on the distribution of male care revealed that a change in female rank between two birth seasons did not lead to a significant change in male care. This suggests that the underlying role of stable male-female relationships may benefit paternal effort as males may keep taking care of the offspring of a female who was a preferred mating partner (maybe even based on her high ranking by the time of mating). In contrast, the finding that changes in male care correlated with changes in female rank during the single birth season contradicts the argument in support of paternal effort. However, we think that this effect was driven mainly by the dramatic rank change of the dominant female who may be expected to have a special role in a group in Barbary macaques (Hemelrijk et al. 2008). Following a dramatic change in female rank this individual became the lowest ranked member and experienced a temporary, but extensive reduction in social interaction with the majority of the other group members.

The consistent preferences of Barbary macaque males for the offspring of particular mothers across seasons may be also driven by other benefits, i.e. stable interaction patterns may contribute to the predictability of behaviour of the other group members, something that benefits group stability and cohesion (de Waal 1986; Sterck et al. 1997; Lehmann et al. 2007). Specifically for Barbary macaques, this consistency may be driven by the benefits related to intensive infant handling of individuals of different age and sex classes, and also the high frequency of male-infant-male interactions, during which the infant is used to maintain and establish bonds among males (Deag and Crook 1971; Paul et al. 1996). First, a consistent pattern in care may help males to reduce competition over infants (Paul 1999). Second, interest in infants of different age and sex classes (and the formation of lasting bonds between males and juveniles) can also intensify the consistency: Juvenile individuals can for example occasionally bring their infant siblings to their male friend, or the infant may be more likely to approach a male who is in interaction with their older, juvenile sibling (Kubenova in prep.). Third, the consistency may allow for more efficient relationship management via male-infant-male interactions, and those interactions may (e.g. by means of a positive behavioural feedback loop) contribute to the high level of consistency (Paul et al. 1996; Kubenova et al. in press) .

CONCLUSION

Our results supports the view that the distribution of copulations, the distribution of male care, and rank are linked in Barbary macaques; but the nature of the link depends on whether the female or male perspective is used to evaluate the distribution of copulations and care. We found that the distribution of care predicts the distribution of mating in the following season (*care-then-mate*), and also that the distribution of mating predicts the distribution of care in the following season (*mate-then-care*), but only when using the male perspective. When using the female perspective no pattern was found. We suggest that missing pattern from the female perspective contradicts the presumptions of the mating effort hypothesis − although support for this hypothesis has been previously reported in the species, but that it may be in accord with the paternal effort hypothesis. Mating effort hypothesis assumes the role of female choice in the distribution of copulations, thus may be only supported based on the female perspective. However, we suggest, that male perspective may lend a support for paternal effort.

The support for the paternal effort hypothesis is rather unexpected given the high level of paternal confusion and the low risk of infanticide, and has not been yet reported in Barbary macaques (as studies usually focus on the female perspective). We suggest that it is possible that males may not take care of infants to whom they are more likely fathers (because they are in fact unable to make this estimation), but that they may still take care of the infants who are more likely to be their own because this may still give them an advantage over other males. This may be specific to Barbary macaques (due to high levels of paternal confusion, and low costs of care, in comparison to various benefits). These benefits may include increased mating opportunities via the establishment of relationships with females; this in turn may allow for/drive the co-existence of *mate-then-care* and *care-then-mate* patterns, and the consistency of care.

Our results indicate that in order to reveal the motivation of males to take care of infants, it is important to study both the *mate-then-care* and *care-then-mate* patterns together, and also to consider different perspectives of the relationship between care and mating. Future research would benefit from including more details about female sexual behaviour during the mating season (e.g. initiation and refusal of copulations), and from incorporating information about the swelling phase of females. Future studies may also pay attention to male-female relationships, the role of infants themselves, and role of other group members in patterns of male care.

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MANUSCRIPT II

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The effect of dominance rank on the distribution of different types of male-infant-male interactions in Barbary macaques

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ABSTRACT

In several cercopithecine species males exhibit a specific type of male-infant-male interactions during which two males briefly manipulate an infant. These interactions occur either after a male carrying an infant (infant holder) approaches another male, or a male with an infant is approached by a (non-infant holder) male. The relationship management hypothesis explains these interactions as a tool for the establishment and maintenance of social bonds among males. It predicts that males preferentially use the opportunity to bond with males dominant to themselves and/or males that are close to them in rank. To test this prediction we collected data on 1,562 male-infant-male interactions during 1,430 hours of focal observation of 12 infants in one group of wild Barbary macaques in Morocco. Using generalized linear mixed models we found that males preferably initiated interactions with males who were dominant to them. However, this effect was observed only during the interactions initiated by the infant holder. In non-holder initiated interactions, the receiver`s relative rank did not predict the frequency of interactions. Our results corroborate the relationship management hypothesis, but also indicate that the different types of male-infant-male interactions may require different explanations. Our

study warrants further investigation of the context and behavior surrounding male-infant-male interactions.

Keywords

Infant handling – *Macaca sylvanus* – relationship management – agonistic buffering – male-infant-male interactions

INTRODUCTION

In more than 90% of mammalian taxa females are the sole providers of parental care (Woodroffe and Vincent 1994). Within the primate order however, in about 40% of species males also attend to infants in various ways (Hrdy 1976; Kleiman and Malcolm 1981; Clutton-Brock and Isvaran 2006). Variation in the type and degree of male care for infants is pronounced. Different terms indicate that the interactions may have positive, neutral, or negative effects on infant well-being (e.g. non-maternal care, caregiving, babysitting, infant manipulation, exploration, kidnapping, abuse, or infant handling; Hrdy 1976) and the evolutionary explanation of their functions is not always clear (Maestripieri 1994; Paul 1999).

In some species, males exhibit a specific type of polyadic infant handling during which two or more individuals simultaneously manipulate an infant. These interactions have been called bridging interactions (Ogawa 1995), triadic male-infant interactions (Taub 1984), agonistic buffering (Deag and Crook 1971), exploitation (Packer 1980), or male-infant-male interactions (Zhao 1996) – the latter being the term used in our study. Male-infant-male interactions have been reported in several species of macaques (Deag and Crook 1971; de Waal et al. 1976; Estrada and Sandoval 1977; Silk and Samuels 1984; Ogawa 1995; Bernstein and Cooper 1998), baboons (Busse and Hamilton 1981; Smuts 1985; Collins 1986), mangabeys (Chalmers 1968; Busse and Gordon 1984) and in geladas (Dunbar 1984). The behavioural description is relatively consistent across species: A male-infant-male interaction usually lasts several seconds (or minutes) during which two (rarely more) individuals simultaneously manipulate an infant, exhibiting teeth chattering and other types of ritualistic behaviour including lifting the infant above their heads, nuzzling, inspection of the infant’s genitals, holding the infant between them (hence the term “bridging”; Deag 1980; Ogawa 1995). Usually the interaction is initiated by one of the two subsequently involved males (thereafter referred to as the initiator of the male-infant-male interactions) approaching another male (thereafter referred to as the receiver of the interaction). The nature of the initiation may be variable: a) an infant may be picked up by one male (holder) and brought to the other, b) a male without an infant (non-holder) may approach a male with an infant, or c) both males may approach an infant at the same time. In species with extended dyadic male-infant interactions (such as Barbary macaques), male-infant-male interactions may be preceded by dyadic male-infant interaction (body contact between the infant and male including carrying, cradling, grooming) between the infant and one of the later involved males. The role of the infant in the interaction may vary from remaining passive, showing some degree of reluctance, or actively seeking the male's presence (Minge et al. 2016; Kalbitz personal communication). Some males and infants engage in male-infant-male interactions more often than others. This individual variation among infants may be related to age (Small 1990a), sex (Paul et al. 1996), and/or mother's rank (Kuester and Paul 1986). Among males, the factors underlying this variation are less clear. Moreover, the composition of the individuals involved in male-infant-male interactions is also non-random. Individual males may be more likely to participate in interactions with specific infants, and with specific male partners (Taub 1980; Silk and Samuels 1984; Stein 1984).

The non-random choice of male receivers for male-infant-male interactions in Barbary macaques led to the formulation of the agonistic buffering hypothesis (Deag and Crook 1971). This hypothesis suggests that given infants are more protected from adult aggression males carrying infants are using this protection and are less likely to be attacked. This "extended" protection enables a male to approach other males, interact with them via male-infant-male, and renew bonds after conflicts. Males might prefer to initiate triadic interactions especially with high ranking males, who under other circumstances may be more likely to act aggressively towards subordinates and with whom bonding may be most profitable (Deag and Crook 1971), because they represent the most dangerous opponents in conflicts but also the most powerful allies in coalitions.

The patterns in accord with this prediction were observed in olive (Packer 1980) and yellow baboons (Stein 1981), bonnet *Macaca radiata* (Silk and Samuels 1984), Tibetan (Ogawa 1995; Zhao 1996), and Barbary macaques (Deag and Crook 1971). However, specifically for Barbary macaques, the relevance of the hypothesis has been questioned. It has been argued that (unlike in baboons) male-infant-male interactions in Barbary macaques are rarely a response to real or potential aggression (Taub 1980; Smith and Peffer-Smith 1982; but see also Kümmerli and Martin 2008), and that because males prefer particular infants for those interactions, they are not being used only as anonymous "tools". Taub (1980, page 53) suggested that male-infant-male interactions in Barbary macaques are "specialized ritualized subsets of a comprehensive system of male–infant caretaking", which represents true caregiving and is formed by male effort to invest into his own offspring or other maternal relatives. However, the main prediction of his hypothesis – that the interacting males share kinship ties with the infant – has never been confirmed (e.g. Paul et al. 1996; Ménard et al. 2001). Instead, several studies have advocated for the agonistic buffering hypothesis (e.g. Paul et al. 1996; Kümmerli and Martin 2008; Henkel et al. 2010). In order to consolidate the objection that (unlike in baboons) male-infant-male interactions in Barbary macaques often occur outside aggressive contexts (see e.g. Smith, 1982, Taub 1980) it has been pointed out that such interactions may be profitable not only in terms of avoiding immidiate aggression, but also in other longer-term ways, for example for coalition formation (Paul et al. 1996; see also Ogawa 1995 for Tibetan macaques) and may respond to different types of stress. To emphasize this view, the hypothesis adopted a broader name, the "relationship management hypothesis" (Paul et al. 1996); and this is the term used throughout this study. Similarly to the agonistic buffering hypothesis, the relationship management hypothesis predcits that males prefer to initiate interactions with higher ranking males. Additionally, the hypothesis suggests that interactions occur more often between males of small rank distance, because these are either the most likely competitors or the most beneficial allies, and thus it may be profitable to establish friendly relationships with them, even if they are actually subordinate (Paul et al. 1996).

Barbary macaques are a suitable species to test the relationship management hypothesis as they show frequent male-infant-male interactions (see Whitten 1987; Paul et al. 1996; Zhao 1996; Paul 1999), and form pronounced male-male affiliationsthat are predictive of coalition formation (Berghänel et al. 2010; Young et al. 2013) associated with better stress attenuation (Young et al. 2014) and higher reproductive success in macaques (Schülke et al. 2010). As such it may be expected that specific behavioral strategies evolved in this species to establish and maintain these bonds. Barbary macaques live in multimale-multifemale groups, with females being the philopatric sex and males emigrating from their natal group after reaching sexual maturity (Kuester and Paul 1999; Fooden 2007). Reproduction is seasonal (Fooden 2007) and characterised by high level of promiscuity (Small 1990b). In spite of the resulting paternity confusion that selects against paternal care (Hamilton 1964), infants may spend a large proportion of the day being groomed, carried, and cradled by different males (see Paul 1999 for the details). Male-infant interactions are mostly positive, mostly initiated by males, and occur most frequently within the first three months after birth (e.g. Paul 1999; see also Deag 1974; Deag 1980; Taub 1984; Paul 1999 for detailed characteristics of male infant handling in Barbary macaques). Dyadic interactions are often alternated with triadic interactions: Males may hold an infant for up to an hour, during which he may initiate or receive triadic interactions. Consequently, males often use the same infants for dyadic and triadic interactions (Paul et al. 1996). Infants are chosen non-randomly, however the pattern of infant choice is currently unclear (Taub 1980; Small 1990a; Paul et al. 1996; Ménard et al. 2001).

Aim of the study

Although the role of rank in the choice of the receiver of a male-infant-male interaction has been supported by several studies, they have several limitations. Different studies have indicated that the trend is driven by one or two individuals, rather than being a more general pattern, e.g. the dominant male may receive many more interactions than other males, and the lowest male may initiate many more interactions than the other males in the group (see e.g. Zhao 1996; Bauer et al. 2014 for Tibetan macaques). Other studies found that the observed preference for higher ranking receivers depended on a) how individuals were categorised (e.g. Deag 1980 only found an effect of rank when merging individuals of different age classes, e.g. adults and subadults) and b) on the definition of observed behaviour (e.g. Paul et al. 1996 found that the effect of rank was driven specifically by interactions initiated by the infant holder). These findings do not invalidate the relationship management hypothesis, but rather suggest that any results should be interpreted with caution. It may be beneficial to use statistical methods that allow the user to control for the IDs of involved individuals (and other potentially influential variables) and different types of interactions.

In this study we used generalized linear mixed-effect models (GLMM) to investigate the effect of rank in male-infant-male interactions in Barbary macaques. Our dataset consists of male-infant-male interactions initiated by either holders or non-holders. In accordance with the predictions of the relationship management hypothesis we expected that the number of interactions among initiator-infant-receiver triads will be affected by the rank of the receiver (in relation to the initiator). Specifically, that males would initiate more interactions with males that are dominant to them, and that interactions were more likely to occur between initiators and receivers of smaller rank distance.

METHODS

Focal observation

The study was conducted in Ifrane National Park in the Middle Atlas Mountains of Morocco (33-240°N, 005-120°W) with the Research Permission of the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco during two consecutive birth seasons (season 1: April–August 2013, season 2: April–September 2014). We followed one wild non-provisioned group (Green Group) of individually recognized and habituated Barbary macaques that consisted of 7 adult (older than 5 years old) males, 1 subadult (5 years old) male, 6 adult females (older than 5 years) and 19-20 juvenile individuals. All adult females gave birth in both seasons, resulting in 6 infants in each season; the 12 infants were followed as focal individuals (more details in Kubenova et al. 2017).

During 2-hour observation sessions all interactions between infants and males were recorded using the focal animal sampling method (Altmann 1974). For each interaction we recorded Ithe Ds of involved individuals and the time at the start and end of interactions (using Handheld PCs with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, U.S.A.). The recorded interactions included dyadic grooming, carrying, cradling, passive body contact between infants and males, and male-infant-male interactions (see Kubenova et al. 2017) for more detailed descriptions of the interactions). The start of a male-infant-male interaction was recorded when both males started teeth chattering while touching the infant at the same time (see definition in Deag 1980 and the introduction of this article). The end of the interaction was recorded when at least one of the involved males stopped teeth chattering or paying attention to the infant; a new, independent interaction was recorded after a >5s break in the interaction. The male was assigned as an initiator if he started the interaction either by approach another male or by starting body contact and teeth chattering (typically staring into the other male's face). The second male was then assigned as the receiver of an interaction. If it was not clear who started the behaviour (e.g. males approached each other simultaneously), the initiator and receiver were labelled as unknown. We also defined an infant holder as a male who was in body contact (including carrying, cradling and grooming) with the infant right before the male-infant-male interaction started, and an infant non-holder as a male without an nfant before the interaction began. In rare cases an infant was not held by either of males later involved in the interaction, and the holder/non/holder categories were recorded as unknown. Based on that information we sorted male-infant-male interactions into three categories (see e.g. Ogawa 1995): Type 1 involved the interactions that were initiated by the infant holder; type 2 involved the interactions that were initiated by the non-holder,; and type 3 included all other cases, e.g. interactions with unknown initiator and receiver roles, and/or interactions that were not preceded by body contact between the infant and either initiator or receiver. Only interactions of type 1 and type 2 were included in the analyses.

Rank

As *ad libitum* (Altmann 1974) we recorded any agonistic behaviour between two males (which did not involve third parties), which suggested a clear role of winner and loser, e.g. where one male displayed aggressive behaviour (open month, lunge, chase, bite, slap grab, charge, stare, displacement) and the second male displayed submissive behaviour (present submission *fl*ee, retreat, see e.g. Deag 1974; Wiper and Semple 2007; McFarland and Majolo 2011). For each season separately we entered the recorded data into a winner-loser dominance matrix and counted the normalized David's score (de Vries et al. 2006). The rank order of 7 adult males was based on 124 and 114 interactions in seasons 1 and 2 respectively. In season 1 the David's score ranged from -14.5 to 11.8 (median = 0.8) with 3 (14.3%) dyads with unknown and 1 (4.8%) with a two-way relationship). In season 2 the David's score showed the same range as in the previous season (median = 0.7) with 2 (9.5%) dyads with unknown and 4 (19%) dyads with two-way relationship. The change of David's score between seasons (in absolute values) ranged between 0 and 9.4 (median = 5.4) for each male. To assess the role of the relative rank of the receiver we used the following rank-based variables: a) David's score of the receiver (DSr), b) rank distance (counted as the difference between the David's score of the initiator and receiver; DSdif = DSi – DSr) and c) absolute value of the rank distance (DSdis = |DSdif|).

Statistical analysis

To test the prediction,that male rank affects the distribution of male-infant- male interactions, we use generalized linear mixed-effect models (GLMM) using the lme4 package (Bates et al. 2014) in R 3.1.1 (R Core Team 2014) with assumed Poisson distribution, and the number of interactions of each initiator-infant-receiver triad as the response variable (N = 1,562). As random effects we included the identity (ID) of the initiator, infant, and receiver. The total observation time of each infant was entered as an offset term to standardize the number of male-infant-male interactions for durations of focal observation. We controlled for the duration of body contact between infant and holder (BCh), and infant and non-holder (BCn) becuase by being in body contact with the infant the male increased his chances of a) being approached as a receiver of male-infant-male interaction, and/or b) using the infant to approach another male as an initiator.

We used the add1 function in R to test the independent marginal effects of rank related predictors: the David's score of a receiver (DSr), the difference between the David's score of an initiator and receiver in actual (DSdif) and absolute (DSdis) value, and also a binary variable (Dir) expressing whether the interaction was initiated up the hierarchy (DSr>DSi), or down the hierarchy (DSi>DSr). We fitted the final model with all significant predictors based on likelihood ratio tests (LRTs) and computed confidence intervals to evaluate their effects using the confint function in lme4.

RESULTS

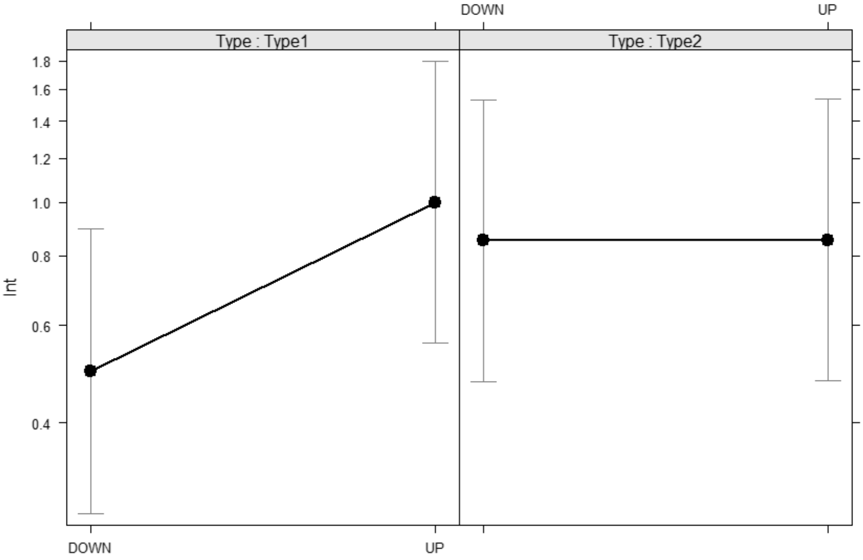
We collected 1,430 hours of focal observation of 12 infants that included 1,562 triadic interactions. These interactions involved only 10 of the followed infants, 2 infants were never observed as participants in male-infant-male interactions. Of these, 732 (47%) were initiated by the holder (type1), and 830 (53%) were initiated by the non-holder (type2). All males were observed participating in both types of interactions. Males initiated between 48 and 197 interactions of type 1 (median = 69), and between 43 and 172 interactions of type 2 (median = 133).Theyreceived between 54 and 192 interactions of type 1 (median = 88), and between 64 and 177 interactions of type 2 (median = 126). All males initiated between 3 and 117 interactions with each of six possible receivers (median = 29).

From 732 male-infant-male interactions of type 1, 492 (~67%) were initiated by a lower ranking male (up the hierarchy); of 830 type 2 interactions it was 421 (~51%). From 913 interactions going up the hierarchy, 492 (~54%) were of type 1, and from 649 interactions going down the hierarchy they were 240 (~37%). Based on LRT, only the independent addition of direction Dir (up vs. down hierarchy) and type of interaction (type 1 versus type 2) changed the model (for Dir $\chi^2_1 = 12.808$, $p < 0.001$; for Type $\chi^2_1 = 6.521$, $p = 0.011$), whereas other variables expressing the initiator's absolute or relative rank did not (for DSr $\chi^2_1 = 0.064$, $p = 0.800$; for DSdif $\chi^2_1 = 0.858$, $p = 0.354$; for DSdist $\chi^2_1 = 0.354$, $p = 0.551$). We thus fitted the final model with these two predictors and their interaction (Tab. 1). In the resulting model the direction, type and their interaction had a significant effect on the number of interactions, as did the duration of body contact between holder and infant, and non-holder and infant, the model controlled for (see table 1). The main effect of the variable direction suggests that the frequency of interactions was lower by 39-60% when the direction was down the hierarchy. However, the interaction term between direction and interactiontype indicates that this concerned only interactions initiated by the holder, and that the effect of rank differed for the two types of male-infant-male interactions. That is, when the initiator holds the infant he is more likely to choose a receiver that is higher ranking than himself. On the contrary however, when a male initiates the interaction without an infant (i.e. by approaching an infant holder) he does not choose the receiver based on their relative rank (see also figure 1).

Tab 1. Results of the final GLMM showing the effect of direction and type of male-infant-male interaction on the number of interactions among initiator-infant-receiver triads.

	Estimate	**SE**	**z**	**Pr(>IzI)**	**CI**
Intercept	-2.766	0.395	-6.994	< 0.001	-3.610, -1.961
Season	0.366	0.415	0.880	0.379	-0.524, 1.299
BC infant-holder	31.696	1.078	29.414	< 0.001	29.592, 33.830
BC infant-nonholder	26.719	1.064	25.091	< 0.001	24.634, 28.821
Type2	-0.157	0.066	-2.370	**0.018**	**-0.287, -0.027**
DirectionDOWN	-0.703	0.108	-6.534	**< 0.001**	**-0.916, -0.492**
Type2:DirectionDOWN	0.700	0.105	6.687	**< 0.001**	**0.495, 0.907**

Fig 1. Effect of the interaction term between direction (Dir) and type (Type) of male-infant-male interaction on the number of interactions among each initiator-infant-receiver triad in the final model



DISCUSSION

<u>Absolute and relative rank of the receiver</u>

The relationship management hypothesis suggests that the receiver of a male-infant-male interaction is chosen based on his rank. Specifically, that males should choose a partner that a) represents the greatest potential threat to the initiator if he were to approach the receiver without an infant, and that b) may be more valuable as a future partner, e.g. as an ally in coalition. The hypothesis predicts that males should therefore 1) prefer high ranking males over low ranking, and 2) males that are relatively closer to their own rank compared to those whose rank is very different (Paul et al. 1996). Our results support the first prediction of the relationship management hypothesis (Deag and Crook 1971; Paul et al. 1996). We found that an initiator holding an infant was more likely to choose a receiver of higher rank than himself. This result confirms the importance of relative rank in the distribution of male-infant-male interactions; something that has been previously reported in Barbary (Deag 1980; Taub 1980; Paul et al. 1996) and other macaque species (Silk and Samuels 1984; Ogawa 1995). However, our results do not support the prediction of a general preference for high or top ranking males, because the actual dominance score of the receiver did not affect the frequency of the interactions. This is in agreement with the most of the previous studies of Barbary macaques that also found that male dominance rank was not correlated with the number of triadic interactions received or with the number of triadic interactions initiated (Taub 1980; Paul et al. 1996 but see also Kümmerli and Martin 2008). On the contrary, in Tibetan macaques, higher-ranking males were more frequently chosen as recipients in bridging compared to lower-ranking males (Ogawa 1995); and in bonnet macaques male dominance rank was significantly negatively correlated with the number of triadic interactions received but unrelated to the number of triadic interactions initiated (Silk and Samuels 1984). These studies however did not control for the identity of males, and thus their results may be biased in this respect.

The second prediction, the importance of rank distance, was not supported by our results. The rank difference between the initiator and receiver (either in actual or absolute value) did not affect the frequency of triadic interactions. This suggests that when choosing a partner for the interaction males did not consider the extent of the rank difference. Although the rank distance has been discussed in number of studies only a few have directly tested its effect on male-infant-male interactions (Paul et al. 1996; Kümmerli and Martin 2008). These studies concluded that rank distance is a significant predictor of the initiator`s choice, however, contrary to our study, they used categories for the rank distace (small, medium, large). It is possible that males consider just these wide categories, and are unable to consider the rank distance on the continuous, finer scale used in our study; It is also possible that a combination of choice rules are used simultaneously (e.g. choosing either closest rank or highest ranking individual), or that the decision-making process is dependent on the context of the interaction. Moreover, the low number of males in our study group and the changes in rank that ocurred can also influence the results, possibly weakening the general trends.

Types of interaction

Our results generally support the relationship management hypothesis, but only in context of interactions where the initiator is also the holder of the infant. Previous studies have suggested that interactions may be categorised according to whether the male initiating the interaction is a holder or non-holder (Collins 1986; Ogawa 1995; Paul et al. 1996; Zhao 1996), and that the effect of rank may differ for those categories. It has been found that only interactions initiated by a holder may be characterized by the prevalence of interactions going up the hierarchy (Paul et al. 1996), and interactions initiated up the hierarchy may be typical for those initated by holder (Taub 1980). However, the potential differences in the underlying patterns were rarely thoroughly tested and no explanation for the importance of interaction type was offered. The failure to find an effect of rank in interactions initiated by a non-holder might seem to contradict the agonistic buffering hypotheses and relationship management hypothesis (Deag 1980; Paul et al. 1996) . Agonistic buffering hypothesis describes “the deliberate use of a baby as a "buffer" in a situation where an approach without the buffer would lead to the increased likelihood of an aggressive response by a dominant male” (Deag 1980), and thus deliberately focuses mainly on interactions initiated by holder. Although formulated to broaden the relevant context of the male-infant-male interactions and explain both types of interactions (initiated by holder and non-holder), the relationship management hypothesis assumes that males should mainly approach higher ranking individuals regardless of who holds the infant (Paul et al. 1996).

We suggest that the pattern may reflect the different ways in which males can profit from initiating male-infant-male interactions. Subsequently, interactions initiated by holders and non-holders may have different explanations.

First, bonding with any even lower ranking male may be profitable (e.g. in the context of coalition formation; Widdig et al. 2000; Bissonnette et al. 2009). As infants are limited resources (Kümmerli and Martin 2008), and carrying infants may be costly (Henkel et al. 2010), males may use the infant more “strategicaly” and will be more likely to initiate interactions with high ranking individuals. In contrast non-holders may initiate interactions with others independent of their rank. A high ranking male may use his position to initiate interactions as a non-holder because he is unlikely to be refused.

Second, male-infant-male interactions may reduce stress (Cohen and Wills 1985). In nonhuman primates, high levels of stress have been found in subordinate (Abbott et al. 2003; Sapolsky 2005) as well as in dominant males (Virgin and Sapolsky 1997; Gesquiere et al. 2011), therefore any male may profit from interactions with other individuals. It has been suggested that social contact may moderate stressful situations, but is also generaly rewarding in any context, because the hormonal response underlaying stress reduction may benefit an individual’s health (Cohen and Wills 1985; Hennessy et al. 2009). The effect of stress reduction may be more important for interactions in which an initiator approaches a holder. The effect of stress reduction may be more important for interactions in which an initiator approaches a holder than when he is a holder himself, because the contact with the infant before the male-infant-male interaction may partly reduce the initiator’s stress already. It seems that when holding an infant, males use male-infant-male interactions for relationship management with high ranking individuals. However, the approach of a male-infant dyad may be motivated by a general need to interact with familiar individuals. To support this, further studies should focus on the changes in hormonal levels of males involved in male-infant-male interactions and other types of infant handling.

CONCLUSION

Our study provided support for the relationship management hypothesis. By controlling for individual IDs and the duration of body contact between the infant and both involved individuals we confirmed that males choose partners for male-infant-male interaction depending on the relative rank of the potential receiver. However, we found that this only applied to interactions initiated by the holder. This may suggest that the relationship management hypothesis is unsuitable as anexclusive explanation for male-infant-male interactions. We suggest that the motivation to manage relationships may be paramount when considering interactions that are initiated by an infant holder, but that other explanations – including stress reduction via social buffering –may be applied for interactions in which a non-holder initiates an interaction by approaching an existing male-infant dyad.

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MANUSCRIPT III

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Triadic awareness predicts partner choice in male-infant-male interactions in Barbary macaques

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ABSTRACT

Social knowledge beyond one's direct relationships is a key in successfully manoeuvring the social world. Individuals gather information on the quality of social relationships between their group companions, which has been termed triadic awareness. Evidence of the use of triadic awareness in natural contexts is limited mainly to conflict management. Here we investigated triadic awareness in wild Barbary macaques (*Macaca sylvanus*) in the context of bridging interactions defined as male-infant-male interactions whereby a male (initiator, holder) presents an infant to another male (receiver, non-holder) in order to initiate an affiliative interaction with that male. Analyses based on 1,263 hours of focal observations on ten infants of one wild social group in Morocco supported the hypothesis that males use their knowledge of the relationship between infants and other adult males when choosing a male as a partner for bridging interactions. Specifically, (i) the number of bridging interactions among holder-infant-receiver triads was positively affected by the strength of the infant-receiver relationship and (ii) when two males were available as bridging partners, a male was more likely to be chosen as the receiver the stronger his social relationship with the infant relative to the other available male. This demonstrates that non-human primates establish triadic awareness of temporary infant-male relationships and use it in a naturally occurring affiliative context. Our results contribute to the discussion about the mechanism underlying the acquisition of triadic awareness and the benefits of its usage, and lend support to hypotheses linking social complexity to the evolution of complex cognition.

Keywords

Triadic awareness – social cognition – infant handling – bridging – male-infant-male interactions – Barbary macaques

INTRODUCTION

Nonhuman primates living in stable social groups develop agonistic and affiliative relationships with group members of the same and other age-sex classes (e.g. Cheney et al. 1986; van Hooff and van Schaik 1994; Silk et al. 2006). These social relationships are established by social partners who individually recognize each other and repeatedly interact with one another over time; allowing past interactions to be predictive of future ones (Hinde 1976). This implies that individuals possess knowledge about their own relationships, that they use to modify their own behaviour towards others, and that it may also allow them to predict the behaviour of others. This capacity helps the individual to avoid aggression (e.g. De Waal 1986; van Hooff and van Schaik 1994), to increase fitness (e.g. Silk 2007a, b; Silk et al. 2009; Schülke et al. 2010) and contributes to the stability and cohesion of the group (e.g. Sterck et al. 1997; Lehmann et al. 2007). It has been suggested that the challenges of social life might drive the evolution of complex social knowledge, so-called triadic awareness defined as knowledge about the relationships among other individuals without assuming actual awareness. The capacity to recognize who outranks whom, who is closely bonded with whom, who is likely to support whom or intervene against whom, and to adjust one's behaviour accordingly, has been documented in apes (e.g. Tomasello and Call 1997; De Waal 2007), Old World (Cheney et al. 1986; Cheney and Seyfarth 1999), New World monkeys (Perry et al. 2004; but see also Ferreira et al. 2006), other mammals (Engh et al. 2005; Connor 2007; Johnson 2010) and in birds (Peake et al. 2002; Seed et al. 2007).

Evidence for triadic awareness of non-human primates mainly comes from experiments. Male hamadryas baboons *Papio hamadryas* use knowledge of the quality of male-female relationships when deciding whether to challenge a male for access to females (Bachmann and Kummer 1980). Adult vervet monkeys *Cercopithecus aethiops* react to play-backs of juvenile distress vocalizations by looking at the juvenile's mother, indicating triadic awareness of kin relations (Cheney and Seyfarth 1980). Female longtail macaques *Macaca fascicularis* demonstrate their ability to recognize kinship relationship in a discrimination task (Dasser 1988). Triadic awareness of rank relationships has been inferred from playback experiments using artificial sequences of calls of group members: e.g. in chacma baboons *Papio ursinus* calls mimicking interactions that are discordant with the current dominance relations between parties elicit stronger reactions in group members than calls in accordance with the hierarchy (Cheney et al. 1995; Kitchen et al. 2005).

Another set of studies used observational data on social behaviour in natural contexts to assess triadic awareness of others' dominance, kin and affiliative relationships. Individuals engaging in agonistic conflicts solicit support and target solicitations more often from group mates who outrank their opponent (e.g. Silk 1999) and from individuals with whom they are more closely bonded than their opponents (Perry et al. 2004). Support is likely to be offered to the higher ranking of the opponents (Schino et al. 2007), who is more likely to succeed in the conflict and/or represents a more powerful ally in prospective future conflicts (e.g. Bissonnette et al. 2009). After the conflict individuals may discriminate against the opponent's kin or affiliates; the aggressor directs reconciliatory behaviour at the opponent's close relatives (Judge 1991) or avoids affiliative interactions with them in expectation of retaliation (Call et al. 2002), while the victim may redirect aggression towards the opponent's kin (Aureli et al. 1992; Judge 1982; Smuts 1985; Cheney and Seyfarth 1989).

Although these patterns imply the use of triadic awareness, it has been pointed out that some of them may be also the result of alternative, simpler mechanisms, such as recruitment of allies based on an individual's own affiliative or dominance relationship, or simple rules of the recruitment of the highest-ranking available individual (Silk 1999; Perry et al. 2004; Range and Noë 2005), that do not require triadic awareness. This ambiguity may partly arise from the relative rarity of the interactions suitable for the research question: supporter recruitment only demonstrates the use of triadic awareness if the invitee recruits the higher ranking from both opponents and is not ranking in between them at the same time. Elegant experiments have been designed to rule out such alternative mechanisms and may more effectively demonstrate the cognitive capacity for triadic awareness. Nevertheless, these experiments are less informative about the use of this cognitive capacity in natural context, which limits the interpretations of its biological relevance (De Waal 1991; Schino et al. 2006; Schino et al. 2007). For example, playback experiments, which simulate situations that never or rarely happen (e.g. dominant individual being threatened by subordinate one), cannot demonstrate the development of social cognition as a response to selection pressure, also because the relative frequencies as played out in different social contexts cannot be assessed.

Studying triadic awareness under natural conditions should therefore complement experimental research. New observational studies should focus on underexplored social contexts that provide a more complete understanding of whether and how individuals use triadic awareness in different situations of their daily lives. Here we focus on a frequently occurring behaviour that may allow for an assessment of how triadic awareness is used in a natural affiliative context, specifically a type of polyadic infant handling so called bridging interactions (Ogawa 1995a) in male Barbary macaques.

Infant handling is broadly defined as non-maternal manipulation of an infant by individuals other than the infant's mother and may include different positive, neutral and negative interactions between the infant and its non-maternal caretaker, irrespective of the caretakers' sex and age class (Hrdy 1976; Hrdy 2007). Infant handling is found across different taxa (see Riedman 1982 for a review; Clutton-Brock 2002) with pronounced interspecific variation in intensity and type of interactions (Woodroffe and Vincent 1994; Hrdy 2007). In several species of Old World monkeys, males engage in a specific type of polyadic infant handling, variously called bridging interactions (Ogawa 1995a), triadic male-infant interactions (Taub 1980), male-infant-male interactions (Zhao 1996), or agonistic buffering (Deag and Crook 1971). During these interactions, two males simultaneously manipulate one infant, exhibiting a typical series of ritualized behaviours including teeth chattering, lifting the infant above their heads, and inspection of the infant's genitals (Deag 1980). Bridging has been reported in several papionin primates: Barbary *Macaca sylvanus* (Deag and Crook 1971), Tibetan *M. thibetana* (Ogawa 1995a), stumptail *M. acrtoides* (Estrada and Sandoval 1977), longtail *M. fascicularis* (de Waal et al. 1976), Assamese *M. assamensis* (Bernstein and Cooper 1998) and bonnet macaques *M. radiata* (Silk and Samuels 1984), yellow *Papio cynocephalus* (Collins 1986), olive *P. anubis* (Smuts 1985) and chacma baboons *P. ursinus* (Busse and Hamilton 1981), sooty mangabeys *Cercocebus atys* (Busse and Gordon 1984), gray-cheeked mangabeys *Cercocebus albigena* (Chalmers 1968) and geladas *Theropithecus gelada* (Dunbar 1984).

Dyadic infant handling and bridging interactions are often unequally distributed among infants and potential handlers. Males differ in their general interest in infant handling and also in preferences for particular infants (e.g. Taub 1980). In some baboon species, these preferences may to some extent reflect the likelihood of paternity (Nguyen et al. 2009; Moscovice et al. 2010). In macaques, male preferences for infants appear mostly unrelated either to paternity or to past mating (Paul et al. 1992; Ménard et al. 2001; but see Ménard et al. 1992; Ostner et al. 2013) but may reflect the male's social relationships with the mother and may be predictive of future mating opportunities (Ménard et al. 2001; Smuts and Gubernick 1992). Males also choose the male partner in the bridging interaction non-randomly (e.g. Estrada and Sandoval 1977; Dunbar 1984; Ogawa 1995a). Males initiate more bridging interactions with relatively higher ranking males than with lower ranking males (Paul et al., 1996; Silk and Samuels 1984; Collins 1986; Deag 1980), and/or with males who are relatively close to their own rank (Stein 1984; Paul et al. 1996). It has also been suggested that the male initiating the bridging interaction preferentially uses the infant that is preferred by the receiver to increase the chances of a successful interaction, indicating that males recognize affiliative relationships between other males and infants (Ogawa 1995b). This suggestion implies the use of triadic awareness in bridging interactions. Patterns of interactions in accordance with this mechanism have been found in Barbary macaques (Paul et al. 1996), but the element of partner choice has not yet been systematically studied.

Barbary macaques live in multimale-multifemale groups. Males emigrate from their natal group after reaching sexual maturity, while females remain in the natal group with their offspring. They are seasonal breeders with a mating season in autumn and a birth season in spring (reviewed in Fooden 2007). Females mate with numerous males (Small 1990) and paternal kinship is not recognised (Ménard et al. 2001; Kuester et al. 1994; but see Ménard et al. 1992). Despite such promiscuity selecting against male care for offspring (see van Schaik and Paul 1996), infants may spend exceedingly large proportions of time being carried, cradled and groomed by males, whereas aggression or abuse by males are rare (e.g. Deag 1980; Paul 1999). Most interactions are initiated and maintained by males, but the contact seems voluntary and infants can be responsible for its start or termination (BK personal observation). Male infant handling bouts have been reported to generally last up to 20 minutes (Deag and Crook 1971), but may take even up to over an hour (BK personal observation), and are often alternated with bridging interactions.

In this study we investigated the relationship between the strength of the infant-male affiliative relationship and the distribution of bridging interactions initiated by the adult male holding the infant. We predicted that the stronger the relationship between the infant and another male the higher would be his chance of being picked as a partner for a bridging interaction by the infant holder. This implies triadic awareness on the part of the infant holder who initiates the interaction (Ogawa 1995b). Unlike the previous study (Ogawa 1995b) we assumed that an infant holder (initiator) chooses a receiving male based on the infant he has instead of searching for an infant that fits his pre-selected male partner (receiver). This assumption is more plausible for Barbary macaques because bridging interactions are often preceded by extended dyadic infant carrying and handling episodes. More specifically we predicted that the number of interactions of each holder-infant-receiver triad would be positively related to the strength of the affiliative relationship between the infant and the receiver of the interaction. We also predicted that the stronger a male's relationship with the infant is relative to a second available male (the closest bystander), the more likely he is to be chosen as the receiver of the interaction.

METHODS

Field site and subjects

This study was conducted on one group of wild Barbary macaques inhabiting the cedar and oak forest of the Ifrane National Park in the Middle Atlas Mountains of Morocco (33-240°N, 005-120°W). Permission to conduct the research in the park was granted by the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco.

The data were collected by BK during two field seasons corresponding with two following birth seasons (April–August 2013, April–September 2014). The study group (Green Group) was well habituated to the presence of human observer and all members were individually recognizable. In both seasons the group consisted of 7 adult (5 years old and older) males and 6 adult females (older than 5 years). There were 19 juveniles in 2013 and 20 in 2014. All adult females gave birth in both seasons resulting in 6 infants in each season (5 female, 1 male in 2013; 3 female, 3 male in 2014).

Data collection

Behavioural data were collected using handheld HP iPAQ 114 series pocket PCs loaded with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, U.S.A.). We used continuous focal sampling (Altmann 1974) with infants as focal subjects. In both seasons, the data collection started when at least 4 infants were born. We observed all infants until the end of the field season, except one male infant (born in 2014), who disappeared approximately two months after his birth. Infants were followed during observation sessions lasting 2 hours, during which we recorded all social interactions between the focal infant and other group members. We pseudorandomized the order in which we observed infants to ensure that all infants were observed equally often at the different times of the day. The data collection on the 12 infants yielded a total of 1,430 hours of observation. We excluded two infants that never interacted with adult males from the analyses. Thus the analyses were based on 1,263 hours of focal observation of 10 infants (hours of focal data per infant mean ± SD = 126.3 ± 12.5)

We defined dyadic infant handling as an interaction between an adult male and an infant. During the interaction the adult male and infant were in body contact that included cradling, dorsal carrying, ventral carrying, grooming, resting in body contact and “contact crawling” defined as an infant crawling in body contact with a male or playfully climbing over a male’s body (see Thierry et al. 2000; Deag 1980 for a more detailed description of the behaviours). We also included polyadic interactions if they involved only one adult male and one or more females or non-adult males (e.g. a male manipulates an infant together with a juvenile individual or the mother of the infant). For each dyadic infant handling interaction, we recorded the start and end time, and the identity (ID) of the male involved.

We defined bridging as an interaction involving (at least) two adult males who simultaneously manipulated one infant, exhibiting a series of ritualized behaviours including teeth-chattering or lip smacking, inspection of the infant’s genitalia, lifting the infant above their heads (Deag 1980). We scored the start of the interaction once both males (being already in body contact with the infant and to each other) displayed teeth chattering in a way typical for bridging behaviour. We classified the initiator as the male that approached the other to start the body contact, and the receiver as the male being approached. For interactions in which males approached at the same time, the initiator was classified as unknown. The male who was in body contact with the infant before the bridging interaction started was classified as the infant holder. We scored the end of the interaction once the males stopped being in mutual body contact with one another. A new independent bridging interaction was scored after a >2min break in body contact between males.

We sorted bridging interactions into three types (see also Paul et al., 1996; Zhao 1996; Ogawa 1995a): 1) interactions initiated by a male that is in dyadic interaction with the infant (initiator = holder) and that approached another male without an infant (receiver = non-holder); 2) interactions initiated by a male without an infant (initiator = non-holder) that approached a male that was already interacting with an infant (receiver = holder); 3) other cases, i.e. interactions with unknown initiator, interactions initiated by both males, and interactions that were not preceded by dyadic handling between the infant and any of the males participating in the following bridging interaction. Only interactions belonging to the first category (bridging initiated by the infant-holder) were considered suitable for the analysis of triadic awareness in this study because the other two options could not reliably discriminate the target of the interaction (infant or adult male) or the role of the initiator. In the second field season we expanded the data collection to obtain additional information about the choice of male partner and recorded the ID of the nearest male present within 10 meters at the beginning of a bridging interaction and classified him as a bystander.

We used an *ad libitum* method (Altmann 1974) to record all dyadic agonistic interactions. For each season we entered the recorded data into a winner-loser dominance matrix and built a hierarchy based on the standardized normalized David's score (Schmid and De Vries 2013).

Data analysis

We used a composite sociality index (CSI; Silk et al. 2006) to assess the strength of dyadic affiliative relationships between infants and males. The CSI was based on: 1) the duration and 2) frequency of body contact (including ventral carrying, cradling, grooming and also infant directed polyadic behaviour that involved one male and female or juvenile individual/s), and 3) the duration of crawling body contact as defined above. The three behaviours were highly correlated in row-wise matric correlations ($rho_{rw,av}$ ranged from 0.80 to 0.88) run with MatMan 1.1.4 (De Vries et al. 1993). For each dyad, we divided the value for each behaviour by the average across all dyads this infant formed with all males in the group and averaged the resulting relative value of all three behaviours. Thus, the index expresses the relative strength of the bond of the infant-male dyad compared to bonds this infant had with all males. Any infant-male interaction was excluded, if being a part of bridging according to the definition, so that these two variables were independent from one another.

To test the predictions of our hypothesis, that holders choose receivers based on the strength of the relationship the receiver has with the infant we used two generalized linear mixed-effect models (GLMM) using the lme4 package (Bates et al. 2015) in R 3.1.1 (R

Core Team 2014). Fitted models were assessed for over-dispersion and model stability (see Quinn and Keough 2002).

To test prediction 1, that the number of interactions of each holder-infant-receiver triad is predicted by the strength of the bond between the infant and receiver, we used a GLMM with assumed Poisson distribution and the number of bridging interactions among each holder-infant-receiver triad as the response variable (N=654; for more information about the distribution of interactions see Table S1 in Online Resource 1). The logarithm of the total observation time of each infant was entered as an offset term (which standardized the number of bridging interactions for durations of focal observation). We included as the two predictors of interest the CSI between holder and infant (CSIh), and the CSI between infant and receiver (CSIr) and as the random factors the identities of the infant, initiating holder and receiver to avoid pseudo-replication, and a factor distinguishing each unique holder-infant-receiver triad to account for over-dispersion. We also included several variables, one by one, to control for the effects of birth season (2013 or 2014), the David`s score of the receiver (DSr), and the rank distance between holder and receiver, computed as an absolute value of the rank difference between holder and receiver (|ΔDShr|), We dropped these controls if they did not improve the Bayesian Information Criterion (BIC, Schwartz et al. 1978) of the model by >2.

To test prediction 2, that the holder bases the choice of receiver between two available males on their CSI with the infant we used a GLMM with assumed binomial distribution. The binomial response was scored as one if the male was selected to be the receiver and zero if the male remained a bystander to the bridging interaction (two lines for each interaction; N=224). We entered as predictor of interest the difference between the CSI of the infant-receiver and the infant-bystander dyad (ΔCSIrb) with positive values indicating the selection of the male with the stronger relationship with the infant, and negative values indicating the selection of the male with the weaker relationship with the infant. Similar to the first model, we included as random factors in our null model the identities of the infant, the holder, the receiver and the bystander and the identity of the interaction. We also controlled for the effect of the rank distance between the holder and the involved male (receiver or bystander), calculated as an absolute difference of their David’s score (|ΔDShm|), and the rank distance between receiver and bystander, calculated as a difference between their David’s score (ΔDSrb), by assessing the BIC of the model as these controls were included one by one.

Our final models include the predictors of interest, all random effects and those controls that improved the BIC. Collinearity of the selected predictors was assessed by variance inflation factor (VIF<10; Bowerman and O’Connell 1990). Significance of our predictors of interest was determined by comparing a model with the predictor to a reduced model without this predictor using anova function.

RESULTS

Distribution of interactions

In 2013 we assessed the rank of 7 adult males based on 124 interactions. The David's score ranged from -14.5 to 11.8 (median = 0.8) with 3 (14.3%) dyads with unknown and 1 (4.8%) with a two-way relationship. In 2014 the David's score was based on 114 interactions and showed the same range as in the previous season (median = 0.7) with 2 (9.5%) dyads with unknown and 4 (19%) dyads with two-way relationship. The change of David's score between seasons (in absolute values) ranged between 0 and 9.4 (median = 5.4) for each male. All males engaged in dyadic infant handling and bridging interactions. The ten infants that were included in the analysis spent between 3.7% and 26.3% of focal observation time in dyadic infant handling interactions with males (mean ± sd = 16.2 ± 7.2). The durations of dyadic infant-handling interactions (continuous body contact uninterrupted by bridging interaction) varied between 0.03 and 84.5 minutes (mean ± sd = 2.7 ± 5.2). The values of infant-male CSI based on these dyadic interactions ranged between 0 and 5.8 (median= 0.4; see Fig. S1 in Online Resource 2).

The dataset included 1,873 male bridging interactions (between 10 and 368 for each infant, mean ± sd = 187.3 ± 122.1). Of these, 654 (between 6 and 148 for each infant, mean ± sd = 65.4 ± 46.2) were initiated by a male holding the infant and were used for testing the first prediction. These interactions were distributed among 155 holder-infant-receiver triads (from 420 possible). The distribution of interactions is shown in Fig. 1 and Table S1 in Online Resource 1. We recorded the ID of the bystander for 209 of these interactions. A bystander was present in 112 cases (between 4 and 38 cases for each of 6 infants followed during the second season) which we used to test prediction 2. The dataset included interactions with all males participating as holders (range = 5 to 36), receivers (range = 9 to 36) and bystanders (range = 12 to 18). For more details about the distribution of interactions see Fig. 2 and Table S2 in Online Resource 1.

Fig. 1

Distribution of bridging interactions each infant (in separate panels) experienced with different holder-receiver dyads. The size of each point corresponds to the squared rate of bridging interactions among each triad (adjusted by the time of observation for each infant).

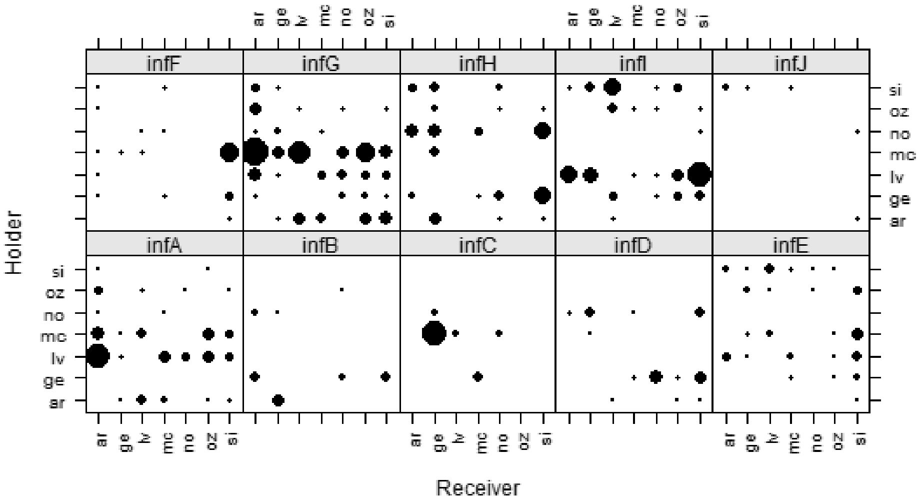
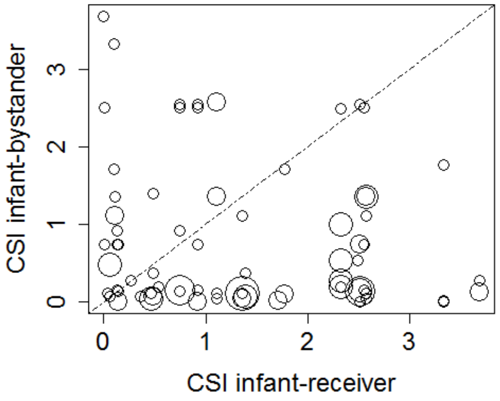


Fig. 2

Relationship between the strength of the social relationship (measured as composite sociality index, CSI) between the infant and the receiver (CSIr) and between the infant and the bystander (CSIb). Data points below the diagonal indicate that the receiver had a higher CSI with the infant than the bystander. The size of data points indicates the number of interactions among same infant-receiver-bystander triad. In 72% of cases the holder chose the male with the stronger bond with the infant as a partner for a bridging interaction.



The model selection results for the model testing prediction 1 are summarized in Table S3 in Online Resource 1. The CSI between infant and holder (CSIh), and between infant and receiver (CSIr) both increased the model's quality. Season, rank of the receiver (DSr), and the difference between rank of the holder and receiver (|ΔDShr|) did not improve either the null model or the models with CSIh and/or CSIr. We thus fitted our final model only with CSIh and CSIr as predictor variables. The frequency of bridging interactions among the holder-infant-receiver triad significantly increased with increasing CSIh and increasing CSIr (ranging between 0 and 5.8; see Table 1 and Fig. 3, 4). The model predicted that an increase of CSIh by 1.0 increased the expected frequency of interaction 2.3–3.1 times, and each increase of CSIr by 1.0 increased the expected frequency of interactions 1.7–2.3 times (95% CI). There was no substantial collinearity between the two predictors (VIF=1.21).

The model selection results for the model testing prediction 2 are summarized in Table S4 in Online Resource 1. The rank distance between holder and involved male (receiver or bystander; |ΔDShm|) and between receiver and bystander (ΔDSrb) did not improve the null model. Adding the difference between the CSI of the infant-receiver and the infant-bystander dyad (ΔCSIrb) improved the model (Table 2, Fig. 5) and was retained as the only predictor in the final model. An increase of ΔCSIrb (ranging between -3.68 and 3.68) by 1.0 increased the probability that a male was selected 1.7–2.7 times (95% CI).

Table 1

Result of the final model for GLMM predicting the frequency of bridging interactions between two males and a specific infant with social relationship strength between infant and holder (CSIh) and social relationship strength between infant and receiver (CSIr) as predictors

N=654	Estimate	SE	95% CI	
Intercept	-4.550	0.526	-5.679	-3.500
Relationship strength infant-holder CSIh	0.972	0.074	0.831	1.122
Relationship strength infant-receiver CSIr	0.677	0.072	0.537	0.820

Fig. 3

Effect of the strength of the infant-holder relationship (CSIh) on the frequency of bridging interactions for a given holder-infant-receiver combination (per 24 hours due to low occurrence of interactions)

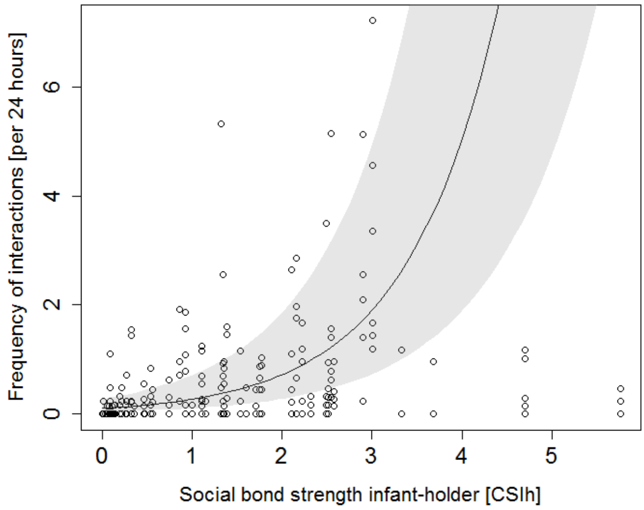


Table 2

Result of the final model for GLMM predicting the choice of a male as the receiver of a bridging interaction with a specific infant including the difference in social relationship between infant and receiver and the social relationship strength between infant and bystander (ΔCSIrb) as predictors

N=224	Estimate	SE	95% CI	
Intercept	0.000	0.152	-0.352	0.326
Difference in relationship strength ΔCSIrb	0.744	0.116	0.527	0.984

Fig. 4

Effect of the strength of the infant-receiver relationship (CSIr) on the frequency of bridging interactions for a given holder-infant-receiver combination (per 24 hours due to low occurrence of interactions)

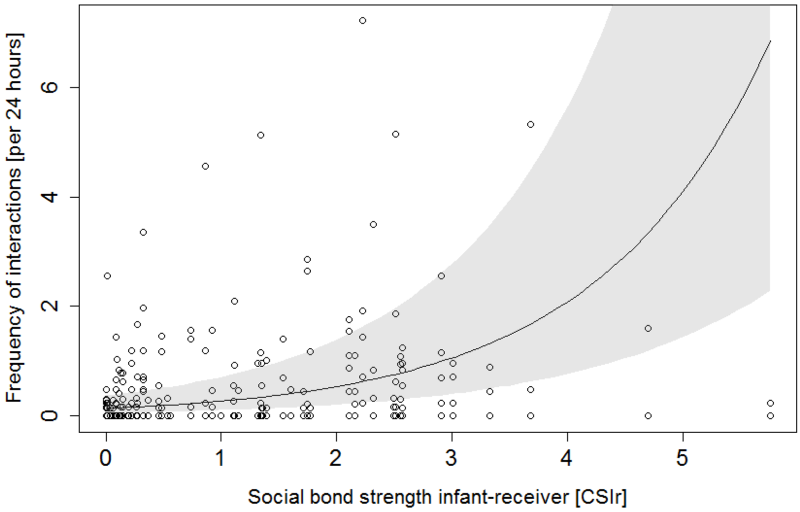
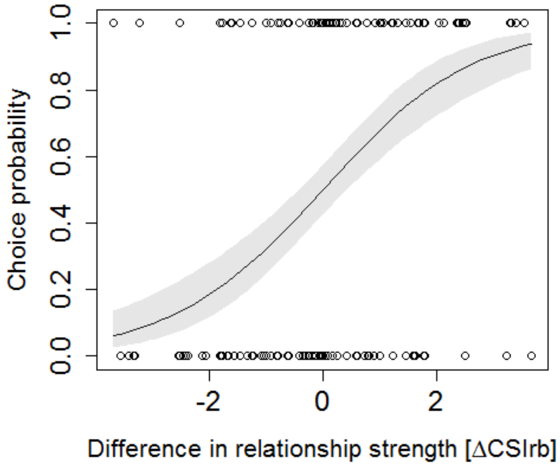


Fig. 5

Effect of the relative strength of a male's relationship with the infant (ΔCSIrb) on the probability that a male was chosen over a bystander as the partner for a male-infant-male bridging interaction



DISCUSSION

Our results support the hypothesis that males choose their partners based on the relative strength of the affiliative relationship the partner has with the infant. First, the number of bridging interactions of a holder-infant-receiver triad was predicted by the strength of the relationship between the infant and the receiver of the interaction after controlling for the effect of the relationship between the infant and its holder. Second, an infant-holder`s choice between two males in proximity of the interaction was predicted by the relative strength of their affiliative relationships with the infant. The stronger a male's relationship to the infant, relative to the strength of the other male's relationship, the more likely he was chosen as a receiver instead of being left as a bystander to the interaction. Neither relative nor absolute rank of the receiver was a significant predictor of the distribution of bridging interactions. These patterns in male bridging interactions indicate the use of triadic awareness. Males as initiators of the interactions use their knowledge of the relationships that other males have with an infant they are currently holding when choosing the receiver of the interaction. The use of triadic awareness in the context of infant handling has also been suggested in Tibetan macaques (Ogawa 1995b): in most bridging interactions that were initiated by infant holders, the receiver was provided with the infant he handled the most often, his "affiliated infant". These results led to the conclusion that the male holding an infant choses a specific infant based on his knowledge of the preferences of potential receivers. Similarly, our results suggest that Barbary macaque males use knowledge of the relationships between infants and other males when they select partners for bridging interactions. However, we based our study on a slightly different assumption and methodology than the previous study, and provide new details that were not previously considered.

We did not assume that holders chose specific infants based on the relationship that an available male (potential receiver) had with different infants (e.g. Ogawa 1995b for Tibetan macaques), but that the holder chooses specific males (as receivers) based on the infant he currently has access to. This adjustment is based on the patterns of infant handling in Barbary macaques, in which bridging interactions are typically preceded by, or alternate with, long dyadic handling periods between the infant and one of the males later involved in the bridging interaction (see Deag and Crook 1971). The low availability of infants leads to long handling episodes, making it rather unlikely that males would be able to find a particular infant (or be motivated to "give up" one infant for another) based on their choice of a receiver male. We suggest that males rather keep one infant for a long time and search for a suitable receiver. This is also in accord with the earlier study on Barbary macaques, which also assumes, that males take infants to specific males rather than to those who just happen to be close (Deag, 1980). This view is supported by our result that males were more likely to be chosen as receivers the stronger their relationship to the infant relative to the second available male. We cannot completely rule out however that both mechanisms – selection of particular infant and a particular receiving male depending on their relationships – act in concert. Future research should assess in more detail the availability of other potential receivers and other infants to quantify constraints on both mechanisms.

In our study we used a composite sociality index to measure the strength of infant-male relationships instead of using the frequency of interactions (Ogawa 1995b). Due to long periods of dyadic infant handling it is likely that males mainly consider the duration of the interactions between other males and infants when assessing infant-male relationship strength, rather than the number of separate interactions. Thus, a composite index that combines frequency and duration of different behaviours might be better suited for the assessment of infant-male relationships in this species. Our CSI quantified how strong the relationship was between a particular infant and male, relative to the average strength of the relationship between the specific infant and all other males. The distribution of CSI values shows that each infant realises a number of relationships that vary in strength, rather than affiliating almost exclusively with a single male. Thus, knowledge of third-party relationships may not be restricted to the ability to distinguish between two categories of individuals (affiliated vs. non-affiliated), but might reflect continuous variation in the strength of different relationships. Future studies could benefit from an investigation of the effect of the chosen method of relationship assessment on the results, and explain in more detail how males evaluate infant-male relationships (e.g. whether the duration or frequency of interactions factors most strongly in their assessment).

As mentioned in the introduction, some previous studies struggled to distinguish whether the individual used triadic awareness or acted based on an egocentric view of the world and the strength of his own relationships (see e.g. Perry et al. 2004). In order to address this problem we controlled the holder’s relationships with the infant and absolute and relative dominance rank of the receiver which may affect the holder’s choice of receiver, according to previous studies (Deag and Crook 1971; Paul et al. 1996). We suggest that the study of triadic awareness of infant-male relationships might be less vulnerable to the described problem of ambiguity, compared to the studies based on dominance relationships: where individuals are part of the same hierarchy they may base their knowledge of others’ dominance relationships either on monitoring the interactions of others (triadic awareness), or on comparing their own dominance relationships with each of other individuals (e.g. the individual who ranks in between two others may recruit the higher ranking from both opponents based on own position; Range and Noë 2005; Bissonnette et al. 2009). In the case presented here, however, it is clear that the relationship that other males have with an infant cannot be easily deduced from one’s own relationships. Holders, whose awareness we assess, have a relationship with the infant they hold; the strength of this relationship influences how often the infant is available for other males, but does not affect how the time is distributed among them. Infant-male relationships also differ from the relationships that females establish amongst each other. In male dispersal species female relationships are strongly affected by maternal relatedness (Hamilton 1964; Ruiter and Geffen 1998; Silk et al. 2006), which allows one to predict certain aspects of a female’s behaviour from the behaviour of her relative to some degree. Unlike females in matrilinearly structured societies the more individualistic males can also be expected to be independent of each other in developing preferences for certain infants. Thus an understanding of a certain infant-male relationship needs to be based on the monitoring of the interactions of that dyad.

The considerable difference between infant-male and most other affiliative relationships is their ephemerality. Infant handling is very seasonal; male interest in infants peaks shortly after birth and rapidly decreases (see Berghänel et al. 2011). As a consequence of such seasonality, relationships are transient and males have very little time to assess the quality of others’ infant-male relationships and to implement this knowledge during bridging interactions. The fact that males establish triadic awareness of quickly emerging and quickly fading relationships indicates their ability to update their knowledge of others’ relationships quite quickly.

Seasonality of infant handling also implies that males invest in monitoring third party relationships despite the fact that the information is quickly outdated and needs to be gathered again every year. In light of these investments it seems relevant to ask how males benefit from using knowledge about third party relationships during bridging, and how these interactions are linked to dyadic infant handling. It has been suggested that bridging interactions mainly serve to establish and maintain bonds among males (Deag and Crook 1971; Paul et al. 1996). The agonistic buffering hypothesis (Deag and Crook 1971) proposes that when holding an infant, males can approach higher ranking males without being attacked and have a chance to improve and/or re-establish disturbed relationships and reduce stress. The relationship management hypothesis (Paul et al. 1996) emphasizes that bridging gives males the opportunity to interact peacefully in general, not only after a conflict, and that the interactions may contribute to male-male bonding that is profitable in various ways (Kümmerli and Martin 2008) even long term, e.g. via coalition formation (Widdig et al. 2000; Young et al. 2014a). Being provided with his preferred infant the approached male may be more likely to establish an affiliative relationship with the holder, which may become beneficial in terms of coalitionary support as shown in the study species (Berghänel et al. 2011; Young et al. 2014a). The infant preferred by the receiver may be a more effective “buffer” against aggression because the approached male may tend to avoid a conflict that could harm his favourite infant. If males handle infants to regulate their relationship with the mother (e.g. Ménard et al. 2001; Smuts 1985) the receiver should also avoid aggression towards the infant-holder because it could disrupt his own relationship with the infant’s mother (Ogawa 1995b). This means, that the choice of receiver might also be influenced by the holder’s previous experience with aggression by specific male when holding specific infant. However, in our study, the rate of observed aggression was too rare to be responsible for observed patterns of the receiver choice suggesting that the choice is rather based on observed male-infant interactions.

The use of triadic awareness may also be guided by mechanisms including hormonal regulation and stress reduction. According to the social buffering hypothesis (not to be confused with the agonistic buffering hypothesis) any affiliative interaction with a closely bonded individual may decrease the physiological stress response, which consequently increases individual health (Cohen and Wills 1985; Hennessy et al. 2009). The hormonal response to social contact (social buffering) depends on the emotional state of the interacting individuals (Kikusui et al. 2006). Hence, the strength of the relationship between the infant and the receiver may predict not only the behavioural responses of the receiver, but also his hormonally regulated attitude towards the initiator (which also feeds back on the hormonal response of the initiator). This suggests that choosing a receiver based on the infant's relationships may drive a hormonally mediated positive loop (Nagasawa et al. 2015) that benefits both individuals. Future research will have to show how levels of physiological stress, aggression-related hormones, and bonding-related hormones are linked (see e.g. Wingfield et al. 1990; Young et al. 2014b).

Conclusion

Our results indicate that Barbary macaque males recognise the affiliative relationships between infants and other males, and make use of this triadic awareness when choosing male partners for bridging interactions. The capacity to monitor, memorise, and act upon the social relationships of others has already been documented, but previous studies usually focused on different types of relationships and different contexts of use. Here we provide evidence for the use of triadic awareness that is not related to aggression and is based on temporary and dynamic affiliative infant-male relationships.

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

Our study was observational and non-invasive. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study were in accordance with the standards of the International Primate Society for the use of non-human primates in research.

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Electronic Supplementary Material 1: Tables

Table S1

Distribution of 654 analyzed bridging interactions: Representation of bridging interactions of different dyads, proportion from all possible combinations, variability in numbers of interactions for those dyads that performed the behavior

N=654	Number (%)	max	mean	sd
Infant-holder	52 (74%)	81	12.58	15.95
Infant-receiver	57 (81%)	51	11.47	10.99
Holder-receiver	41 (97%)	59	15.95	13.40
Male-male	21 (100%)	72	31.14	18.01

Table S2

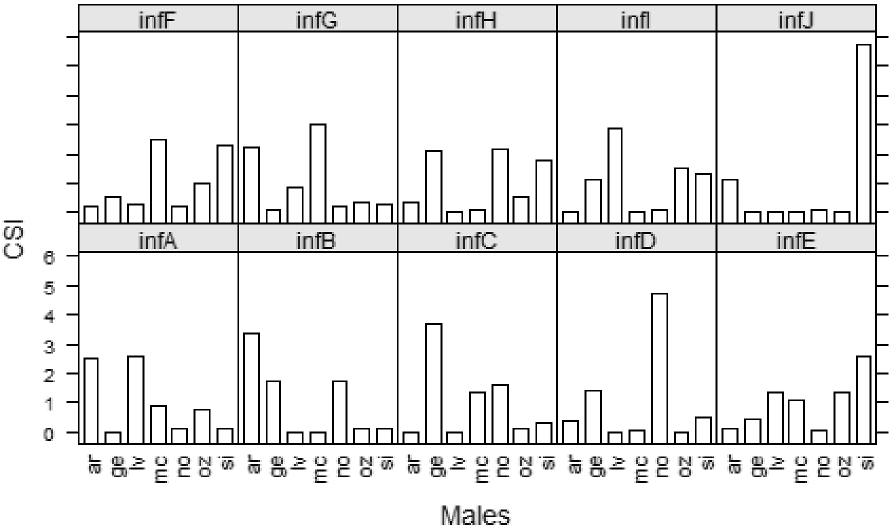
Distribution of 112 analyzed bridging interactions with bystanders: Representation of bridging interactions of different dyads, proportion from all possible combinations, variability in numbers of interactions for those dyads that performed the behavior

N=112	Number (%)	Max	mean	sd
Infant-holder	22 (52%)	20	5.18	4.75
Infant-receiver	29 (69%)	14	3.80	3.39
Infant-bystander	34 (81%)	9	3.13	2.21
Holder-bystander	37 (88%)	7	2.85	2.08
Holder-receiver	32 (76%)	13	3.56	3.32
Receiver-bystander	39 (93%)	6	2.78	1.75

Electronic Supplementary Material 2: Fig S1

Fig. S1

Distribution of the strength of the relationship (measured as composite sociality index, CSI) between infant-male dyads



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MANUSCRIPT IV

Waters S., El Harrad A, Amhaouch Z, Kubenova B (2016). **Releasing confiscated Barbary macaques to improve national awareness of the illegal pet trade in Morocco**. In Global-reintroduction Perspectives: 2016, Case-studies from around the globe. IUCN, pp 216-220

Releasing confiscated Barbary macaques to improve national awareness of the illegal pet trade in Morocco

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INTRODUCTION:

The Barbary macaque (*Macaca sylvanus*) is found in fragmented populations in Morocco and Algeria. Barbary macaques are unique within *Cercopithecidae* for their extensive non-maternal care *(*Kümmerli & Martin, 2008*)*. Infants are targets of interest for both sexes and all age classes, especially during the first weeks after birth. The promiscuity of the species makes it unlikely that infant handling is a paternal investment. In spite of that, infants may spend a high proportion of time in males' care and some males seem to have preferences for particular infants.

The Barbary macaque is listed on Appendix II of CITES and Endangered on the IUCN Red List (Butynski et al 2008). The main cause of its decline is attributed to infant capture for the pet trade from the Middle Atlas population (Menard et al 2013) and, less intensively, from other populations over its distribution. The capture, keeping and selling of Barbary macaques is illegal in Morocco but the law is infrequently enforced. In 2009, a conservation project inclusive of local people was initiated in Bouhachem forest in northern Morocco. The forest is in a remote mountainous area with non-habituated Barbary macaque groups and a supportive local human population (Waters 2014).

GOALS & SUCCESS INDICATORS:

Main Goals:

- Goal 1: Implement confiscation protocols to discourage the open sale and exploitation of Endangered Barbary macaques in Tangier-Tétouan region, Northern Morocco
- Goal 2: Use social media to increase public awareness regarding the conservation and welfare implications of the illegal trade in Barbary macaques.
- Goal 3: Ensure the welfare of confiscated macaques within the limitations of the situation in Morocco, where there is only one officially recognised centre to house all confiscated wildlife.
  Goal 4: To alleviate pressure on the above centre, release confiscated infant macaques into wild Barbary macaque groups if they meet basic behavioural and psychological criteria.

- Goal 5: Communicate news of releases on social media

Success Indicators of Project determined before initiation of project:

- Indicator 1: All Barbary macaques openly on sale or used as tourist photo props in Tangier-Tetouan region confiscated and owners fined.
- Indicator 2: Public awareness increased
- Indicator 3: Adult and imprinted macaques transferred to the only officially recognised centre for confiscated wildlife in Morocco.
- Indicator 4: Confiscated macaques meeting physical and psychological criteria released into wild macaque groups
- Indicator 5: Increased reporting of illegally held macaques by the Moroccan public using social media/ or a contact number provided on social media.

DESCRIPTION OF MAIN STAGES OF RE-INTRODUCTION PROJECT:

Feasibility:

In 2012, the Moroccan conservation NGO, Barbary Macaque Awareness & Conservation (BMAC), signed an MOU with the Direction Rif Haut Commissariat Eaux et Foret et la Lutte contre la Desertification (DRHCEFLCD), to collaborate in the confiscation of Barbary macaques openly on sale or exploited for tourism in Tangier-Tétouan region. BMAC was given responsibility for the care of confiscated macaques whilst DRHCEFLCD prepared relevant permits and arranged a place for the confiscated individuals. This was the Rabat Zoo which was forced to close its doors to further confiscations in September 2013 due to being over capacity. The Moroccan public was responding to news of confiscations by reporting other illegally held macaques. Thus we believed it important to continue the momentum and decided to try releasing suitable confiscates into relatively undisturbed wild groups in Bouhachem

Implementation:

Five macaque confiscations took place with two adult females transferred to the Rabat zoo. Two female infants were confiscated by customs in Tangier and may have been infants reported as poached from a macaque group habituated for research in the Ifrane National Park (INP) in the Middle Atlas Mountains. BMAC staff transferred the infants to INP but, on release, the infants fled the scene due to their fear of the macaque males in close proximity. After extensive searching only one female was found. This female was rehydrated and fed and the following day placed in an improvised "howdy" cage, which was placed close to the study group. She could see and hear macaque group members but they could not touch her. The reaction of the males was particularly strong when they heard the infant and they also reacted against the researchers who were following the group. The researchers moved the cage when the group moved in order to maximize the familiarization period between it and the infant. This procedure continued for four days. To enable better communication between the infant and the group, the infant was placed in a larger wire cage. Various forms of communication between the infant and other group members – including greetings and reciprocal teeth chattering and invitations to follow - were observed. Moreover, the infant started reacting to the group's departures with distress calls.

On the 4th day of the soft release, the decision to release the infant was made because the infant seemed used to the group and the group appeared to be losing interest in the infant. The next day, the cage door was opened. After ~30 seconds, the infant calmly left the cage and was picked up by a sub-adult female, who took her into the centre of the group. Later, she started being handled by one male, who had had the strongest reaction to her when she was still in the cage. He became her main caretaker or "adoptive male".

To date, we have released two other confiscated macaques, a ~8-month male and an 18-month female into two different groups in Bouhachem, but without the use of a "howdy" cage because the individuals did not demonstrate fear of conspecifics. The male was immediately carried off into the forest by adult males who were very aggressive towards the BMAC team members trying to back away from the infant. The female was released because there was no suitable accommodation for her. Luckily she met the physical and psychological criteria and joined a wild group of her own volition when she heard them whilst on training walk to find wild foods in the forest.

Post-release monitoring:

The infant in INP was monitored for a year post-release. The infant was handled most frequently by males, but levels of interest in her differed among individuals. The infant spent most time in the proximity and "care" of her "adoptive" male. His interest seemed to play a crucial role in the infant's survival, as he carried her when the group was travelling, protecting her against potential danger and aggression and also staying with her overnight.

Female infant in cage surrounded by wild macaques © BMAC

Females' behavior towards the infant was mainly neutral or negative, but their aggression was mainly non-contact (display) and never led to serious injury. However, the infant was attacked three times by sub-adult males, when she was about 16 months. One sub-adult female was often observed providing the infant with positive care, including grooming. The rare interactions between the infants and other non-adults included negative, neutral and positive behavior. Play displays were observed very occasionally, never lasted long, and the released female never initiated play or played much with other infants.

Female with her adoptive male post-release
© B. Kubenova

The lack of play and low activity could be caused by earlier deprivation but also by lack of energy. The absence of milk seemed to result in the infant's dehydration during summer months, whereas malnutrition was obvious during winter, when the infant seemed unable to gain weight. This female was observed for ~18months but, since the winter of 2014, we have no further information about her status.

<u>MAJOR DIFFICULTIES FACED</u>:

- We are unable to quarantine confiscated macaques due to a lack of suitable facilities
- If infants have spent prolonged time in captivity, the behaviour of the adult males inspires a fear and flight response from the infants on release.
- Behavioural backwardness – possibly caused by maternal deprivation causing retarded social development
- Risk of undernourishment and dehydration. The possibility of supplemental provisioning is limited when wild groups are used.
- It is impossible to ascertain the fate of confiscated macaques released into non-habituated macaque groups due to lack of funding for post-release monitoring equipment.

<u>MAJOR LESSONS LEARNED</u>:

- Due to the adult male Barbary macaques' caretaking behavior, it is possible to release confiscated infants into wild groups of the species even when it is not the infant's natal group.
- If infants demonstrate extreme fear of adult males then a soft release in a "howdy” cage which can be moved with an habituated macaque group enables the infants to gain confidence and initiate contact themselves with group males that may adopt the infant on its release.
- Adult males' enthusiasm for handling the infants decreases as the infants grow.
- The best candidates for release are infants that have not endured prolonged captivity and are more than 8 months old so have been weaned.

SUCCESS OF RE-INTRODUCTION PROJECT:

Success or Failure	
Highly Successful	
Successful	X (in the case of the female released in Ifrane National Park and in terms of raising public awareness)
Partially Successful	
Failure	

Reason(s) for success/failure:

- The use of social media to publicise the confiscations increased public awareness in the region and beyond. For example, the second photo prop macaque was confiscated after BMAC received 20 calls in 30 minutes from the public reporting the first appearance of the animal and its handler at a coastal resort close to Tétouan. See Waters & El Harrad (2013) for further information.
- The success in releasing confiscated infants into wild macaque groups can be attributed to the alloparental behavior of adult male Barbary macaques.
- We are very aware that we are unable to adequately address all health and welfare concerns of released animals due to our lack of funding and facilities. We hope to rectify this situation in the near future.
- We are unable to confiscate adult macaques because they are habituated to humans and are unsuitable for release. A rescue centre for confiscated wildlife is needed in Morocco so that the law regarding Endangered Barbary macaques can be enforced.

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CURRICULUM VITAE

Education

Since 2012	Doctoral studies in Zoology, Faculty of Science, University of South Bohemia, Czech Republic
2009 - 2011	Doctoral studies in Anthropology, Faculty of Science, Charles University in Prague, Czech Republic (without degree.)
2007 – 2009	Master in Anthropology of Past Populations, Faculty of Philosophy and Arts, University of West Bohemia, Czech Republic
2003 – 2007	Bachelor in Social and Cultural Anthropology, Faculty of Philosophy and Arts, University of West Bohemia, Czech Republic

Research Experience / Fieldwork

03-10/2013, 04-10/2014	Data collection for the PhD project, The National Parc of Ifrane, Morocco
05-12/2011	Research assistant of The Barbary Macaque Project, The National Parc of Ifrane, Morocco
01-04/2011	Assistant Project Director of The Semliki Chimpanzee Project, Semliki Reserve, Uganda
06-07/2008	Data collection for master's thesis, Pilsen / Liberec /Ostrava, Czech Republic

Scholarships

11/2013–03/2014, 11/2014, 06-08/2015, 11-12/2015, 02-03/2016, 06/2016, 11/2016
Scholarship, research group Primate Social Evolution, Göttingen, Germany

Membership

Since 11/2013	Member of the research group Primate Social Evolution, Göttingen, Germany
Since 04/2016	Member of Leibniz-ScienceCampus Primate Cognition, German Primate Center & Georg August University of Göttingen, Germany

Funding awards

2015	Christian-Vogel Fond for Field Research, small research grant of the German Society for Primatology, main investigator
2014	Grant Agency of the University of South Bohemia, main investigator
2013	Award of the German Academic Exchange Service DAAD

Teaching

2015	Primatology (undergraduate course), Faculty of Humanities, Charles University in Prague, Czech Republic

2015 Consultant of the master thesis: Stability in hand preferences in Lion-tailed macaques, University of South Bohemia in České Budějovice, Czech Republic

Presentations

2016 PhD workshop of the Leibniz-ScienceCampus, Akademie Waldschlösschen, Germany. Oral presentation: Infant handling in male Barbary macaques: mate-then-care or care-then-mate? October 19-21.

2016 8th European Conference on Behavioural Biology (ECBB2016), Vienna, Austria. Oral presentation: Who likes you the most? Triadic awareness predicts partner choice in male–infant–male interactions in Barbary macaques, July 12-15.

2016 Graduate Meeting: Animal Behaviour, Animal Behaviour Section of the German Zoological Society, Biological Station Gülpe (University of Potsdam), Germany. Oral presentation: Triadic awareness predicts partner choice in male-infant-male interactions in Barbary macaques, May 03-05.

2016 3rd European Student Conference on Behaviour & Cognition, University of St Andrews, Scotland. Oral presentation: What does infant handling reveal about social cognition in Barbary Macaques? March 17-18.

2015 42nd Conference of the Czech and Slovak Ethological Conference, České Budějovice, Czech Republic. Oral presentation: Infant handling and social cognition in Barbary Macaques (in Czech), November 4-6.

2015 10 Years of Barbary Macaque Conservation Conference of the Morocan Primate Conservation foundation, Azrou, Morocco.

Oral presentation: Infant handling in Barbary macaques: How can new findings contribute to conservation? September 7.

2015 Seminar of the Section of Biological Anthropology, Department of Anthropology, University of West Bohemia, Pilsen, Czech Republic. Invited seminar talk: On the way to field primatological research, March 11.

Publications

Kubenova B, Konecna M, Majolo B, Ostner J, Smilauer P, Schülke O (2017)

Triadic awareness predicts partner choice in male–infant–male interactions in Barbary macaques. Anim Cogn 1–12.

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