



## Stable heterosexual associations in a promiscuous primate



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Close associations between adult males and females are rare among group-living, nonmonogamous mammals but may mark the transition from life in promiscuous bisexual groups to groups of pairs or pair living. Although heterosexual friendships have been described in baboons, these are short-term affairs serving as protection against infanticide and thus tightly linked to the presence of vulnerable infants. Long-term association may be adaptive in situations of low male monopolization potential where it pays to invest in a particular female partner instead of spreading the effort among many females. Using long-term data, we investigated male–female and male–infant associations in wild Assamese macaques, *Macaca assamensis*. Group-wide and individual male–female associations were stable for at least 2 or 3 years. Association during the mating season but not before the mating season predicted male mating success, lending support to the ‘friends with benefits’ but not the ‘mating effort’ hypothesis. Mating success in turn predicted male–female association at birth as well as male–infant association before weaning. In support of the ‘paternal care hypothesis’ paternity was an independent predictor of male–infant association beyond weaning age, creating potential for true paternal care. We thus postulate that particular demographic and life history circumstances may favour male–female friendships by creating a positive feedback between male–female–infant associations driven by paternal care and male–female associations promoted by increased mating access to drive the evolution of long-term male–female bonds.

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The evolution of differentiated heterosexual associations of adult individuals (sometimes also called ‘friendships’; Strum 1974; Smuts 1985; Silk 2002) is unexpected among promiscuous group-living mammals because sex differences in parental investment and potential reproductive rates are expected to drive males to invest in more than one female and her offspring (Trivers 1972; Clutton-Brock 1989; Clutton-Brock & Parker 1992; Kvarnemo & Ahnesjö 1996). Primates, particularly species of the cercopithecine subfamily, macaques and baboons, are unusual in this respect. Within their large multimale–multifemale groups particular males and females may form temporary associations and spend an atypically large amount of time together (Smuts 1985; Palombit 1999, 2000). Recent conceptual work on and phylogenetic reconstruction of primate social evolution suggests that primate pair living and the human pair bond evolved from life in promiscuous multimale–multifemale groups (Chapais

2008; Shultz et al. 2011). Our study on a cercopithecine primate investigated how this important shift might have been accomplished.

For females, the adaptive benefits of heterosexual friendships have been extensively studied in baboons (e.g. Ransom & Ransom 1971; Seyfarth 1978; Altmann 1980; Anderson 1983; Smuts 1985; Palombit et al. 1997, 2000; Weingrill 2000). In chacma baboons, *Papio ursinus*, lactating females maintain close associations with adult males during the most vulnerable period of an infant’s life as a counterstrategy to male infanticide, which accounts for 37% of infant mortality in this species (Palombit et al. 1997, 2000; Palombit 1999, 2000, 2009). These bonds are short term in nature though, as they are neither exhibited during gestation nor extended beyond lactation (Palombit 2000, 2009), and are terminated abruptly after the infant dies (Palombit et al. 1997). In yellow, *Papio cynocephalus*, and olive baboons, *Papio anubis*, for which the risk of infanticide is much lower (Palombit 2000; Henzi & Barrett 2003), females with male friends benefit directly from protection against harassment from conspecifics and indirectly by reduced harassment of their offspring (Lemasson et al. 2008; Nguyen et al. 2009). Yellow baboon males protect genetically related juveniles in conflicts with group

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members (Buchan et al. 2003) and the presence of a father in the group beneficially accelerates the maturation of juveniles (Charpentier et al. 2008). An early study suggests that male–female associations in olive baboons may be stable over longer periods (Smuts 1985), but as most studies on male–female associations have usually focused on the 8–12 weeks before and after parturition (Palombit et al. 1997; Nguyen et al. 2009; Huchard et al. 2010), we lack the relevant data to evaluate comprehensively the stability and possible benefits of longer-term heterosexual bonds spanning mating periods, gestation and beyond early lactation.

For males, the evolutionary value of heterosexual associations is less clear (Palombit 2000). Male reproductive effort can be dissected into mating effort and parental effort, two investments that may have to be traded off against each other (Wingfield & Moore 1987; Ellison 2003). The ‘paternal care hypothesis’ proposes that heterosexual bonds develop as a by-product of the male associating with the female’s infant for which the male provides paternal care (Taub 1980a, b; Charpentier et al. 2008; Moscovice et al. 2009, 2010) and as such the hypothesis does not make any specific predictions about male–female relationships prior to the infant’s birth. Males are expected to associate with infants (and their mothers) based on the likelihood of paternity (based on either genetic paternity or past mating success; Moscovice et al. 2009, 2010) and it seems likely that males use cues of past mating or association history with the infant’s mother during the preceding mating season as an approximation of paternity probability. Alternatively, male–female associations may evolve as a form of male mating effort, where males ingratiate themselves to females in order to enhance their mating success (van Schaik & Paul 1996). The classical ‘mating effort hypothesis’ suggests that males may benefit from associating with adult females (and the female’s offspring irrespective of the male’s relatedness to the infant) by increasing future mating success with this female (Smuts 1985).

The original formulation of the idea that ‘low ranking males (...) may behave in such a way that females will prefer them over other higher ranking individuals’ (Seyfarth 1978, page 242) does not invoke such a temporal contingency as a necessary condition. Thus, we propose the ‘friends with benefits hypothesis’ as a variant of the classical ‘mating effort hypothesis’ also aiming at enhancing a male’s mating success by forming a bond with a specific female. In contrast to the ‘mating effort hypothesis’ the ‘friends with benefits hypothesis’ does not assume strict temporal contingency, that is male–female associations enhancing future mating success. It also does not consider all male–female association during the mating season as reflections of male mate guarding. Support for the ‘friends with benefits hypothesis’ comes from two seasonally breeding rhesus macaque, *Macaca mulatta*, groups in which male monopolization potential is low and male mating success and paternity are predicted by the strength of rather symmetric heterosexual social bonds during the mating season (Kulik et al. 2011; Massen et al. 2012). Although subordinate males will not be able to fend off higher ranking competitors and thus will not truly ‘mate guard’ a female, subordinate males may use a strategy of staying close to a particular female and mating as often as possible instead of sneaking copulations from every receptive female in the group. These associations may not be recorded as consortship activity because subordinate males may try to keep a low profile to avoid attacks from dominants. For males, the strategy of concentrating their mating effort to one or a few females, that is of investing in a specific female instead of aiming for maximal promiscuity, will pay off in situations in which male monopolization potential is low owing to high reproductive synchrony

among many females and/or male inability to assess female fertility status reliably, which creates perceived synchrony (Fürtbauer et al. 2011a; Ostner et al. 2011). A mutual bond may form over the course of a mating season and may carry over into nonreceptive phases of the female reproductive cycle, and be potentially maintained by the female in expectation of future benefits (see above), leading the way to stable heterosexual associations.

While the ‘paternal care hypothesis’ has received wide support from studies in three baboon species (Palombit et al. 1997; Lemasson et al. 2008; Huchard et al. 2010; Moscovice et al. 2010) and other primates (Lehmann et al. 2006), predictions of the classical ‘mating effort hypothesis’ have not been met in yellow baboons (Nguyen et al. 2009) and free-ranging Barbary macaques, *Macaca sylvanus* (Paul et al. 1996), and the finding that male–female friendships in baboons are temporally tightly linked to the period of infant dependency can be interpreted as further evidence against the hypothesis (reviewed in Palombit 2000). In wild Barbary macaques, chimpanzees, *Pan troglodytes*, and olive baboons, however, male–infant or male–female association was positively related to future mating success (Smuts 1985; Ménard et al. 2001; Langergraber et al. 2013).

In this study, we aimed to investigate the long-term nature of heterosexual associations and to explore their evolutionary basis by testing predictions from all three hypotheses in Assamese macaques, *Macaca assamensis*, a species characterized by frequent and intense male–infant interactions (Maestripieri 1998). Previous research points to important contrasts to the well-studied baboons in terms of male reproductive strategies because (1) sexual swellings of female Assamese macaques are not indicative of ovulation, (2) female receptivity during the short mating season is extended and (3) ovulation is concealed (Fürtbauer et al. 2011a) leading to low mating and paternity skew (Schülke et al. 2010; Ostner et al. 2011). The distributions of male mating and reproductive success in this species are predicted by dominance rank but high female reproductive synchrony resulting from seasonal breeding and extended receptive phases (Fürtbauer et al. 2011b) yields low skew in mating (17% alpha male mating success; Ostner et al. 2011) as well as reproductive success (29% alpha male paternity; M. Sukmak, W. Wajjwalku, O. Schülke & J. Ostner, unpublished data). Females have preferred mating partners, allocating most matings to a few, not necessarily high-ranking, males. A male of any rank may be the main mating partner of a female, focusing his efforts on individual females instead of maximizing his mating success with many females (Fürtbauer et al. 2011a).

Moreover, Assamese macaques differ from baboons because (1) infants are often separated from their mothers for extended periods during their first year of life when the risk of infanticide is highest (A. Berghänel, O. Schülke & J. Ostner, unpublished data), and (2) male tenure in the group is long relative to individual maturation time (in chacma but not in yellow baboons more than half of the fathers are gone by the time an infant reaches 6 months of age (Clarke et al. 2009) whereas in Assamese macaques only 13% of infants lose their father within their first year of life; J. Ostner & O. Schülke, unpublished data). This demographic stability may not only provide the opportunity for extended male–immature bonds, but in conjunction with a relatively short interbirth interval (Fürtbauer et al. 2010; Heesen et al. 2013), and thus renewed reproductive opportunities for males, may also give rise to long-term male–female bonds.

At 4.5 years our study was longer than previous studies and provided long-term association, mating and paternity data to test all three hypotheses described above. We also hoped to add new insights on the evolution of intersexual friendships in larger

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