



Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques



Josefine Kalbitz ^{a,*}, Julia Ostner ^{a,b,1}, Oliver Schülke ^{a,1}

^a Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg August University Göttingen, Germany

^b Research Group Primate Social Evolution, German Primate Centre, Göttingen, Germany

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In multimale multifemale primate groups, the strength and stability of affiliative relationships have been shown to affect an individual's long-term fitness such as offspring survival and longevity. Studies investigating the fitness benefits of close social relationships and the underlying mechanisms have mainly focused on the philopatric sex. The strong relationships of philopatric chimpanzee males and baboon females share important characteristics with human friendships in that increased strength of affiliative relationships is associated with increased equitability in service exchanges and relationship stability. So far, it has remained unclear whether the strong relationships of dispersing males share these characteristics as well and can thus be labelled as social bonds. Here we provide results on the variation in affiliative relationship strength and its relation to equitability and relationship stability from two wild groups of male Assamese macaques, *Macaca assamensis*, at Phu Khieo Wildlife Sanctuary, Thailand collected over 2 and 7 years, respectively. Our analyses of almost 9000 h of focal animal data show that males formed differentiated affiliative relationships and that the strength of a relationship affected how likely males returned a grooming service within a single bout and how equally males were responsible for the maintenance of close proximity. Partner stability among the three strongest relationships was higher than among weaker relationships which suggests that top partners were not retained simply because of a lack of alternatives. Together, these results suggest that dispersing male Assamese macaques form differentiated affiliative relationships that increase in equitability and stability with increasing relationship strength. This is the first study showing long-term partner stability in males as the dispersing sex. Our results thus add to the growing body of literature indicating that nonhuman animals form close social relationships similar to human friendships.

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Living in a social group entails costs and benefits for each individual. On the one hand, close proximity to and daily repeated interactions with conspecifics within a group increase feeding and mating competition, the risk of disease transmission and, in some species, the risk of infanticide (Altizer et al., 2003; Krause & Ruxton, 2002; Lukas & Clutton-Brock, 2014; Ostner, Heistermann, & Schülke, 2011; Palombit, Seyfarth, & Cheney, 1997; van Schaik & Aureli, 2000; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; Wittig & Boesch, 2003). On the other hand, animals can derive benefits from sociality such as lower predation risk, better access to food resources, more effective territory defence and increased access to mating

partners (Connor, 2000; Frère et al., 2010; Silk, Alberts, & Altmann, 2003; Silk et al., 2009; Weidt, Hofmann, & König, 2008). In gregarious species within-group variation in sociality may be associated with variation in coalition formation (Langergraber, Mitani, & Vigilant, 2007; Pope, 1990; Schülke, Bhagavatula, Vigilant, & Ostner, 2010), co-feeding tolerance, (Huchard et al., 2010) and buffering against environmental and social stressors (McFarland & Majolo, 2013; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). This in turn may lead to increased reproductive success and longevity for individuals (Archie, Tung, Clark, Altmann, & Alberts, 2014; Brent et al., 2013; Frère et al., 2010; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk et al., 2010a).

One mechanism linking partner preferences within a social group and fitness is the formation of social bonds that serve as reliable alliances in competitive situations and help to attain and maintain high social status which in turn regulates access to resources and safety (Connor, Smolker, & Richards, 1992; Heesen,

* Correspondence: J. Kalbitz, Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, Georg August University Göttingen, Kellnerweg 6, 37077, Göttingen, Germany.

E-mail address: jkalbit@gwdg.de (J. Kalbitz).

¹ Equal contribution as last authors.

Macdonald, Ostner, & Schülke, 2014; Ostner & Schülke, 2014). If bonds evolved for alliance formation, selection favoured an individual's ability to form a few very strong affiliative relationships (Hinde, 1976) for the exchange of support (Ostner & Schülke, 2014) rather than an individual's overall level of affiliation. Thus, differentiation into weaker and stronger affiliative relationships is crucial (Massen, Sterck, & deVos, 2010; Ostner & Schülke, 2014; Silk, 2002). Furthermore, strong affiliative relationships may be more equitable and longer lasting than weaker ones which makes them similar in kind to human friendships (Lehmann & Boesch, 2009; Massen et al., 2010; Mitani, 2009; Ostner & Schülke, 2014; Silk, 2012). Consequently, strength, equitability, and stability have been suggested as defining characteristics of a social bond (Ostner & Schülke, 2014).

In the past three decades, several studies have investigated characteristics of affiliative relationships separately. First, variation in the strength of social relationships, which emerges by biased allocation of affiliation towards specific group members, has been described for a broad range of animal taxa, for example guppies, *Poecilia reticulata*, and sticklebacks, *Gasterosteus aculeatus* (Croft et al., 2005), great tits, *Parus major* (Aplin et al., 2013), mice, *Mus domesticus* (Weidt et al. 2008), bats, *Myotis bechsteinii* (Kerth, Perony, & Schweitzer, 2011), feral goats, *Capra hircus* (Stanley & Dunbar, 2013), nonhuman primates (Aureli, Fraser, Schaffner, & Schino, 2012), kangaroos, *Macropus giganteus* (Carter, Macdonald, Thomson, & Goldizen, 2009), male bottlenose dolphins, *Tursiops truncatus* (Parsons et al., 2003), female African elephants, *Loxodonta africana* (Archie, Moss, & Alberts, 2006) and giraffes, *Giraffa camelopardalis* (Carter, Seddon, Frère, Carter, & Goldizen, 2013). Affiliation is often biased towards maternal and paternal kin and individuals similar in age or dominance rank (e.g. female giraffes, Carter et al., 2013), female yellow baboons, *Papio cynocephalus* (Silk, Altmann, & Alberts, 2006), female vervet monkeys, *Chlorocebus aethiops* (Cheney, Seyfarth, & Smut, 1986), female macaques, *Macaca* spp. (Cheney et al., 1986; Schülke, Wenzel, & Ostner, 2013; Widdig, Nürnberg, Krawczak, Streichl, & Bercovitch, 2001) and male chimpanzees, *Pan troglodytes schweinfurthii* (De Waal, 1991; Mitani, 2009).

Second, of the goods and services that are exchanged within dyads allogrooming is perhaps the best studied behaviour. In several species grooming is often reciprocated in the sense that the more grooming an individual provides to a partner the more it receives from the same individual in return (Connor, 1995; Fruteau, Lemoine, Hellard, van Damme, & Noë, 2011; Gomes, Mundry, & Boesch, 2009; Kaburu & Newton-Fischer, 2015; Lewis, Harris, Prigmore, & Wanless, 2007). So far, the relationship between grooming equitability and the strength of the partners' affiliative relationship, the second characteristic of social bonds, have only been investigated in a few studies (e.g. bonnet macaques, *Macaca radiata*, Adiseshan, Adiseshan, & Isbell, 2011; chimpanzees, Mitani, 2009; savanna baboons, Silk, Alberts, & Altmann, 2006; chacma baboons, *Papio ursinus*, Silk et al., 2010b). In humans, affiliative physical contact (e.g. cuddling) is an important predictor of the value of a relationship. Here friends touch each other more often than partners with a weaker affiliative relationship (Dunbar, 2010). Hence, it is important to study similar behaviours such as grooming in animals (Massen et al., 2010). Finally, empirical data on the relative temporal stability of affiliative relationships, the third characteristic of social bonds, are scarce. In philopatric male chimpanzees (Mitani, 2009) and female chacma baboons, stronger affiliative relationships were more stable over time than weaker ones (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012), albeit partner choice for their strongest relationship was not consistent among female chacma baboons of a different population (Henzi, Lusseau, Weingrill, Schaik, & Barrett, 2009). In female yellow baboons, mothers, daughters and maternal sisters formed the

strongest and also most enduring relationships suggesting that stronger relationships were also more stable (Silk, Alberts, et al., 2006). The same pattern has been observed in male chimpanzees. Here both the strength of an affiliative relationship and its stability were positively related to grooming symmetry (Mitani, 2009) which suggests that stronger relationships were also more stable. In contrast, stronger affiliative relationships were not more stable than weaker ones in dispersing female chimpanzees. Females' preferences for association partners were much more stable than preferences for grooming partners (Lehmann & Boesch, 2009). It remains to be shown whether the long-term stability of affiliative relationships varies with their strength in the dispersing sex in which group membership and dominance relationships are more fluid.

We have previously shown for the dispersing sex with a smaller sample of 12 adult individuals observed over 2 years that affiliative relationships of male Assamese macaques, *Macaca assamensis*, are differentiated in strength and that in general the amount of grooming given is correlated with the amount of grooming received across all possible dyads (Schülke et al., 2010). The strength of affiliative relationships also predicted cooperation in agonistic within-group coalitions against other males. This coalitionary support helped males attain and maintain higher social status in the future and ultimately translated into increased paternity success (Schülke et al., 2010; Sukmak, Wajjwalku, Ostner, & Schülke, 2014). Our previous analyses did not, however, answer the question whether stronger affiliative relationships differ in their grooming symmetry and stability from weaker relationships, and hence fulfilling the three characteristics of social bonds. Here, we investigated whether the affiliative relationships formed by the dispersing sex of Assamese macaques qualify as social bonds. Our study is based on almost 9000 h of focal animal data collected over 7 consecutive years to test whether dispersing male Assamese macaques form strong, equitable and stable social relationships that qualify as social bonds.

METHODS

Study Site and Subjects

This study was carried out in the Phu Khieo Wildlife Sanctuary (PKWS; 16°5'–35'N, 101°20'–55'E) which is part of the ca. 6500 km² interconnected and well-protected Western Isaan forest complex in northeast Thailand (Borries, Larney, Kreetiyutanont, & Koenig, 2002). The hilly forest comprises dense, mostly evergreen vegetation and harbours a diverse community of predators (Borries et al., 2002). Behavioural data were collected on two fully habituated multimale multifemale groups. All adult males of the AS group were followed from 2006 until 2013. Data from the AO group were collected from May 2012 until September 2013. Both groups were observed almost daily. The AS group had on average \pm SD 51.4 \pm 4.7 group members, 10.1 \pm 1.9 males and 13 \pm 1.9 females, and the AO group had 45.1 \pm 2.0 members, 10.6 \pm 0.5 males and 10.6 \pm 0.5 females. Changes in group composition occurred due to immigration, emigration and death. Across the entire study period 17 individual adult males lived in the AS group and 10 in the AO group.

Data Collection

All adult males, from both groups, were subject to 30 min focal animal sampling, yielding a total of 8952.82 h (AS: 7200.40 h; AO: 1752.42 h) of focal animal data. For a more detailed overview on observation hours per male and per period see the Appendix (Tables A1 and A2). An effort was made to equally distribute focal sampling across males and for each male across time of the day. By

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