

# Male social relationships among wild Assamese macaques (*Macaca assamensis*)

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I hereby declare that I have written this thesis independently and with no other aids or sources than quoted.

Göttingen,

Josefine Kalbitz



This thesis is dedicated to

N'D.



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# Summary

General socioecological theories predict that in multi-male multi-female mammalian groups, males and females compete over resources of different nature. While females mainly compete over generally sharable food, males compete over the non-sharable fertilization of each female and the formation of strong affiliative relationships with specific partners might have evolved as a strategy to minimize the costs of this competition. Lifetime co-residency in the same social group enables individuals from the philopatric sex to form strong, equitable and long-lasting affiliative relationships between group members, the so called social bonds.. Social bonds in philopatric females are mainly linked to kinship, which influences an individual's dominance rank position and hence the access to resources. The emergence of social bonds between males is more striking pertaining to the high level of competition over non-shareable fertile females which may hamper the likelihood of the formation of affiliative relationships among males. However, if two males gain mutual benefits from affiliating with each other, for instance if affiliation leads to an increase in the formation of cooperative coalition to outcompete other males and get higher dominance rank positions and the associated reproductive benefits, social bonds might arise. This type of relationship between bond and coalition formation is found in philopatric male chimpanzees. Here social bond formation may serve as an adaptive strategy to maximize the efficiency of these cooperation. In species in which males are not philopatric, the reduced co-residency time represents an additional potential obstacle to the formation of social bonds between males, beside the nature of male-male competition itself. The question therefore remain whether in female philopatric species males still form affiliative relationships with each other of the same nature than philopatric males or females. Yet, it remains unclear so far whether the affiliative relationships between dispersing males share these characteristics as well and can thus be labelled as social bonds. In addition, the proximate behavioural mechanism underlying the formation of affiliative relationships has received less attention in both, philopatric and dispersing living individuals.

The overall aim of my thesis was thus, first to shed light on whether three characteristics of social bonds (differentiation in strength, equitability and partner stability)

## Summary

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are found between males of the dispersing sex and second to assess whether a behavioural proximate mechanism other than grooming might underlie bond formation and maintenance. To address these aims, I studied two habituated groups of wild Assamese macaques (*Macaca assamensis*, a species in which females are philopatric and males disperse) at the Phu Khieo Wildlife Sanctuary in North-eastern Thailand. I used data collected for seven years on the AS group and for 1.5 years on the AO group. First, I assessed whether male Assamese macaques form differentiated affiliative relationships by using the composite sociality index (CSI) to examine the distribution of the frequency and duration of spatial proximity, body contact and grooming across all male-male dyads. Further, I investigated whether the strength of a male-male affiliative relationship affected the likelihood of immediate grooming reciprocation. Further, I calculated a grooming symmetry index (GSI) for each male dyad to investigate whether the strength of affiliative relationships had an effect on grooming equitability. In addition, I assessed the most crucial characteristic of social bonds (and so far the most understudied in the dispersing sex), by examining the stability of affiliative relationship over time. I calculated the partner stability index (PSI) of each male with their top 3 preferred affiliative partners and with the following three partners (number 4, 5, 6) to assess whether stronger affiliative relationships were more stable across years than weaker ones. Finally, I investigated whether male Assamese macaques use male-infant-male interactions (MIMIs, a specific macaque behaviour known to appease the social partners and reduce the likelihood of aggression), as a proximate behavioural mechanism to form and maintain social bonds. I first investigated whether subordinate males benefited from engaging in MIMIs with a higher ranking male upon approach. Second, I assessed whether the strength of male affiliative relationship affected the frequency at which they engaged in MIMIs. Finally, I investigated whether MIMIs may play a role in bond formation by testing if the current rate of MIMIs increased the time two males spent in close proximity in the future and thus had more opportunity to bond.

My analyses of about 9000 h of focal animal data show that males form social bonds. Male-male affiliative relationships were highly differentiated with the majority of male dyads sharing weaker affiliative relationships than average and few male dyads sharing stronger affiliative relationships. The stronger an affiliative relationship between two males was, the more likely they reciprocated a grooming act. In those bouts where grooming was

reciprocated; males sharing a stronger affiliative relationship were more balanced in their exchange of grooming than those males sharing a weaker affiliative relationship. Partner stability among the three strongest relationships was higher than among weaker relationships, which suggests that top partners were not preserved simply because of a lack of alternatives. Regarding the proximate mechanism underlying social bonds, I found that the overall frequency of MIMIs increased with the strength of the dyadic affiliative relationships between males. Further, subordinate males could increase their proximity time with higher-ranking males on average by 50% if they engage in a MIMI upon approach irrespective of the affiliative relationship strength with the male partner. The latter result, increase in proximity time irrespective of affiliative relationship strength, together with the finding that the stronger a male dyads affiliative relationship the more males engage in MIMIs, indicates that male Assamese macaques use this behaviour to maintain their affiliative relationships. In contrast, I did not find support for a role of MIMIs in bond formation since the frequency of MIMIs did not affect the time a male dyad spent in proximity in the consecutive year. However, this result may, may have been caused by a lack of newly immigrating males establishing new bonds during the study period.

In summary, my results suggest that male Assamese macaques, the dispersing sex in this species, are able to form social bonds with a similar structure as the bonds reported in the philopatric sex of some other mammalian species and possibly maintain those bonds not just via grooming, but also via male-infant-male interactions. Male Assamese macaques form risky rank-challenging coalitions to rise in rank and get the associated benefit of priority of access to fertile females ultimately leading to a higher reproductive success. In this context, forming social bonds with specific individuals might be mandatory in order to benefit from a reliable coalitionary partner and thus be successful in rank-changing coalition. My findings contribute greatly to our understanding of the pattern of affiliative relationships among individual of the dispersing sex in multi-male multi-female mammalian groups by showing for the first time that social-relationships are not only differentiated across dyads but also extremely stable over time. My specific study on MIMIs provide some insight into alternative mechanisms to grooming which might be involved in bond maintenance and possibly bond formation in social groups. Altogether my results are therefore contributing to the general debate on which behaviours influence social dynamics in group living mammals.



# Zusammenfassung

Bei Säugetieren, bei denen die Gruppen aus mehreren Männchen und Weibchen bestehen, konkurrieren die Weibchen hauptsächlich um den Zugang zu Futter und die Männchen tendenziell um den Zugang zu fertilen Weibchen. Die Bildung von starken sozialen Bindungen innerhalb einer Gruppe könnte als adaptive Strategie fungieren, um die durch ständige Konkurrenz entstehenden Kosten zu minimieren. Solche sozialen Bindungen sind gekennzeichnet durch ausgeprägte affiliative Beziehungen, Ausgeglichenheit im Geben und Nehmen, sowie Partnerstabilität. Ein relativ stabiles soziales Umfeld von Individuen des philopatrischen Geschlechtes ermöglicht es ihnen enge, ausgeglichene und langfristige, affiliative Bindungen miteinander aufzubauen. Soziale Bindungen zwischen philopatrisch lebenden Weibchen sind stark durch Verwandtschaftsbeziehungen geprägt, welche auch die Dominanzbeziehungen unter den Weibchen beeinflussen und damit letztlich den Zugang zu einer Ressource. Affiliative Beziehungen oder das Entstehen von sehr engen sozialen Bindungen unter den Männchen stellt sich etwas komplizierter dar, auf Grund des hohen Konkurrenzkampfes um die nicht teilbare Ressource (fertile Weibchen). Durch diesen Konkurrenzkampf ist die Wahrscheinlichkeit, dass sich affiliative Beziehungen unter den Männchen herausbilden können, stark eingeschränkt. Wenn nun jedoch zwei Männchen durch eine gemeinsame affiliative Beziehung einen gegenseitigen Vorteil erhalten, zum Beispiel durch das Bilden von Koalitionen, um eine höhere Rangposition in der Gruppenhierarchie zu erreichen, was ihnen wiederum den Zugang zu Weibchen erleichtert und ultimativ auch den Reproduktionserfolg erhöht, können sich sehr enge soziale Bindungen unter den Männchen herausbilden, wie es zum Beispiel bei männlichen Schimpansen beschrieben worden ist. Inwieweit sich jedoch aus affiliativen Beziehungen langfristige soziale Bindungen auch bei Individuen des abwandernden Geschlechtes ausbilden können, ist bisher weitestgehend ungeklärt. Zudem hat man den proximalen Verhaltensmechanismen, die der Bildung und Aufrechterhaltung von sehr engen sozialen Bindungen zu Grunde liegen, sowohl beim philopatrischen als auch beim abwandernden Geschlecht bisher wenig Aufmerksamkeit gewidmet.

Das Hauptziel dieser Arbeit bildete die Untersuchung von drei Komponenten von engen sozialen Bindungen (Variation in der Beziehungsstärke, Ausgeglichenheit im Geben und Nehmen, sowie Partnerstabilität) bei adulten Männchen des abwandernden Geschlechtes. Zusätzlich untersuchte ich die Fragestellung, ob eine andere Verhaltensweise neben der Fellpflege als proximaler Mechanismus der Formation und der Aufrechterhaltung von sehr engen sozialen Bindungen zu Grunde liegt. Hierfür habe ich zwei habituierte freilebende Assam-Makaken Gruppen im Phu Khieo Wildlife Sanctuary im Nordosten Thailands beobachtet. Für meine Analysen nutzte ich einen 7-jährigen Datensatz der AS Gruppe und einen 1,5 jährigen Datensatz der AO Gruppe. Als erstes habe ich die Variationen in der Stärke jeder dyadischen Beziehung beleuchtet. Hierfür berechnete ich für jede Dyade einen sozialen Index (CSI) aus der Frequenz und Dauer drei verschiedener Verhaltenskomponenten (räumliche Nähe, Körperkontakt und Fellpflege). Basierend darauf analysierte ich, inwieweit die Stärke einer affiliativen Männchen-Beziehung Auswirkung auf das Durchführen und Empfangen der Fellpflege hat. Hierbei untersuchte ich den Einfluss der Beziehungsstärke auf die Wahrscheinlichkeit, dass eine Fellpflegeaktion eines Partners sofort erwidert wird. Zusätzlich habe ich für jede Dyade einen Fellpflegeindex (GSI) berechnet. Dieser Index gibt Aufschluss, inwieweit das Durchführen und Empfangen der Fellpflege innerhalb eines Fellpflegezyklus ausgeglichen ist. Weiterhin habe ich eine der wichtigsten Komponenten, welcher enge soziale Bindungen ausmacht (und die bisher am wenigsten untersuchte Komponente beim abwandernden Geschlecht), betrachtet, indem ich einen Partnerstabilitätsindex (PSI) für jedes Männchen mit dessen drei stärksten Beziehungspartnern, sowie für jedes Männchen und dessen weniger engen Beziehungspartnern (Partner Nummer 4, 5 und 6) berechnet habe, um die Frage zu klären, ob adulte Männchen die Partner mit denen sie stärkere affiliative Beziehungen pflegen über Jahre hinweg beibehalten, jedoch nicht jene Partner, mit denen sie eine weniger intensive Beziehung pflegen. Zum Abschluss untersuchte ich, inwieweit das Verhalten, bei dem adulte Männchen eine gemeinsame Interaktion mit einem Kind durchführen (MIMI, ein typisches Verhalten bei Makaken), als ein proximaler Verhaltensmechanismus fungiert, der der Formation enger sozialer Bindungen zu Grunde liegt und diese aufrechterhält. Hier habe ich untersucht, ob subordinate adulte Männchen einen Vorteil haben, wenn sie eine MIMI mit dem höherrangigen Männchen kurz nachdem sie sich bis auf 1.5m angenähert haben,

durchführen. Als nächstes habe ich überprüft, ob adulte Männchen dieses Verhalten nutzen, um ihre affiliativen Beziehungen aufzufrischen, indem ich untersucht habe inwieweit die Stärke der Männerbeziehung Einfluss auf das Auftreten von MIMIs hat. Schlussendlich, interessierte mich die Funktion des MIMI Verhaltens auf die Formation von engen sozialen Bindungen, und ich analysierte hierfür, ob die Anzahl der durchgeführten MIMIs in einem Jahr, Auswirkung auf die Zeit der räumlichen Nähe im Folgejahr und damit auf die Stärke der affiliativen Beziehung hat.

Meine Auswertungen von etwa 9000 Beobachtungsstunden, zeigen, dass einige adulte männliche Assam-Makaken sehr enge soziale Bindungen miteinander bilden. Die Männerbeziehungen variierten hinsichtlich ihrer Stärke; die meisten der Beziehungen waren tendenziell schwach und nur einige Männchen bildeten sehr enge soziale Bindungen untereinander aus. Die Beziehungsstärke hatte weiterhin Auswirkung auf die Wahrscheinlichkeit ob eine Fellpflegeaktion vom Partner sofort erwidert wurde. Je stärker eine Beziehung zwischen den Männchen war, desto wahrscheinlicher wurde das Fellpflegeverhalten vom Partner sofort erwidert. In Zyklen, in denen die Fellpflege sofort erwidert wurde, war das Durchführen und Erhalten des Fellpflegeverhaltens umso ausgeglichener, je stärker die affiliative Beziehung einer Männchen-Dyade war. Männchen, die eine starke Beziehung untereinander aufwiesen, pflegten diese über Jahre hinweg. Männchen hingegen, die nur eine schwache Beziehung pflegten, wechselten häufiger ihre Partner. Letzteres macht deutlich, dass die Stabilität in der Partnerwahl nicht nur auf eventuell mangelnde Partneralternativen zurückzuführen ist.

Bezüglich der proximalen Mechanismen die engen sozialen Bindungen zu Grunde liegen, habe ich einen Zusammenhang zwischen Beziehungsstärke und der Durchführung von MIMIs gefunden. Je stärker die affiliative Beziehung zwischen zwei Männchen war, desto häufiger führten die Männchen MIMIs durch. Weiterhin konnte ich zeigen, dass subordinate Männchen im Durchschnitt 50 % länger in räumlicher Nähe bei eines höherrangigen Männchens verbleiben konnten, wenn sie mit diesem eine MIMI nach dem Aufeinander-Zugehen, durchgeführt haben, unabhängig von der Stärke ihrer affiliativen Beziehung. Diese beiden Ergebnisse verdeutlichen sehr eindringlich, dass männliche Assam-Makaken dieses Verhalten zum Aufrechterhalten der Beziehung nutzen. Die Funktion des MIMI Verhaltens bezüglich der Formation von affiliativen Beziehungen konnte ich nicht bestätigen, da die

## Zusammenfassung

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Anzahl der MIMIs in einem Jahr keine Auswirkungen auf die Zeit in räumlicher Nähe im Folgejahr hatte. Dies kann jedoch daran liegen, dass die Beziehungen zwischen den Männchen schon vor Beginn der Datenaufnahme etabliert wurden und während der gesamten Beobachtungszeit keine neuen Männchen in die Gruppe eingewandert sind, bei denen die Bildung neuer Beziehungen mit residenten Männchen hätte beobachtet werden können.

Zusammenfassend zeigen meine Ergebnisse, dass männliche Assam-Makaken (das abwandernde Geschlecht dieser Art), in der Lage sind enge soziale Bindungen untereinander zu entwickeln, wie es auch beim philopatrischen Geschlecht verschiedener Säugetierarten berichtet wurde. Diese engen sozialen Bindungen werden nicht nur durch die Fellpflege, sondern auch durch die spezielle Interaktion zweier Männchen mit einem Kind aufrechterhalten. Es ist bekannt, dass die adulten Männchen dieser Art mit favorisierten Partnern Koalitionen formen, um einen höheren Rang zu erwerben und damit einen besseren Zugang zu fertilen Weibchen erhalten und folglich auch einen höheren Reproduktionserfolg. Derartige Koalitionen sind kostspielig, wobei ein vertrauensvoller Partner Voraussetzung für solche riskanten Aktionen zu sein scheint. Meine Ergebnisse tragen dazu bei, das Muster von affiliativen Beziehungen bei Säugetieren in Gruppen mit mehreren Männchen und mehreren Weibchen besser zu verstehen und geben weiteren Aufschluss über die proximalen Verhaltensmechanismen bei der Aufrechterhaltung und möglicherweise auch bei der Formation von affiliativen Beziehungen unter den Männchen. Damit erweitern die Resultate meiner Arbeit die generelle Thematik, welche Verhaltensweisen die Dynamik von Sozialbeziehungen in gruppenlebenden Säugetieren beeinflusst.

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# Chapter 1

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## General Introduction

Mammalian societies, including humans, are complex socio-ecological systems shaped by a species' social organisation (i.e. group size, sex ratio and cohesion of social groups), mating system (e.g. polygynous: one male is mating with several females; polyandrous/polygynandrous: one female is mating with several males; promiscuous: a male is copulating with several females and vice versa) and social structure (i.e. social relationships among individuals) (Hamilton, 1964; Kappeler, 2012; Kappeler and van Schaik, 2002). Due to food abundance, predation and the distribution of mates, the variation in society structures across and within species can be enormous. Most mammalian species live solitarily (Lukas and Clutton-Brock, 2013) and males and females segregate in their spatial habitat use as well as socially, primarily due to intra-sexual competition and female avoidance of male harassment (e.g. several carnivore, Sandell, 1989; reviewed in Wolf et al., 2005). A smaller portion of mammalian species, including humans, live in social groups (Lukas and Clutton-Brock, 2013) ranging from unstable aggregations of individuals such as several grazing ungulates (e.g. impalas, *Aepyceros spp.*, Leuthold, 2012) to stable gregarious groups (e.g. plain, *Equus quagga*, and mountain zebras, *Equus zebra*, Klingel, 1967; lesser kudu, *Tragelaphus imberis*, Leuthold, 1974) and to highly structured social groups as reported in several primate species (humans, Hruschka, 2010, and non-human primates, see Mitani et al., 2012).

Both, close spatial proximity and social interactions among individuals within a group (Smuts et al., 1987) can lead to fitness costs such as disease transmission, food and mating competition or infanticide (e.g. Crockett and Janson, 2000; Greenwood, 1980; Clutton-Brock, 2009; Lloyed and Rasa, 1989). However, benefits of group living outweigh those costs (Krause and Ruxton, 2002; Silk, 2007a). Benefits comprise lower predation risk (e.g. dilution effect and cooperative defence against predators, Garay, 2009), better food exploitation and defence (Mosser and Packer, 2009), mutual parasite removal (e.g. through grooming, Mooring and Hart, 1992), better access to mating partners but also cooperative hunting (e.g. social carnivores, Macdonald, 1983; chimpanzees, *Pan troglodytes*, Boesch, 1994; Boesch, 2002) or cooperative breeding (e.g. *Callitrix spp.*, Digby et al., 2007; Goldizen, 1987; meerkats, *Suricata suricata*, Clutton-Brock et al., 2006), ultimately resulting in enhanced individual lifespan and reproductive rate (Gilby et al., 2013; Silk et al., 2010b; Snyder-Mackler et al., 2012). To optimize those benefits relative to costs, group living promotes the

evolution of specific behavioural strategies (Boesch et al., 2006; Koenig, 2002; Sterck et al., 1997; van Hooff and van Schaik, 1994). One key strategy to optimize the benefits to cost ratio of group living might be the establishment of affiliative relationships and in particular the formation of social bonds (Ostner and Schülke, 2014).

Social bonds are affiliative relationships between specific group members which are strong compared to other dyadic relationships, equitable in their exchange of services, cooperative and long-lasting (Ostner and Schülke, 2014). The short-term and long-term benefits gained by having social bonds can be tremendous. Individuals support each other in fights, cooperate to gain better access to resources (Gilby et al., 2013; Schülke et al., 2010; Young et al., 2014b), transfer information (Kerth and Reckardt, 2003; Pennisi, 2001; Price et al., 2015; Seyfarth et al., 1980) and huddle to regulate their body temperatures under harsh climatic conditions and to reduce social stress (Fraser et al., 2008; McFarland and Majolo, 2013; Pretzlaff et al., 2010; Young et al., 2014a). Having a close long-term partner enhances an individual's longevity (Silk et al., 2010b), its infant survival (Silk et al., 2009) and reproductive success (Gilby et al., 2013; Schülke et al., 2010; Silk et al., 2010b).

Given the importance of social bond formation as fitness enhancing strategy, in the following section of the introduction I will lay out how affiliative relationships develop in mammalian species and how they are influenced (section 1.1). Following on from this, I will discuss some behaviour involved in the establishment and maintenance of affiliative relationships (section 1.2). I will then discuss one fundamental precondition for affiliative behaviours to take place: spatial proximity (section 1.2.1), some key specific signals used to increase proximity time and possibly enhance the bonding process (section 1.2.2) and finally one key behaviour involved in the bonding process in several species: grooming (section 1.2.3). Afterwards, I will explain the dynamic of affiliative relationships (section 1.3) and the possible underlying mechanism driving bond formation and maintenance. Later I will briefly introduce the well-studied pattern of female-female affiliative relationships (section 1.4) and will discuss in more detail the intriguing evidence for male-male social bonds (section 1.5). Towards the end of the first chapter I will introduce the study species and highlight why adult male Assamese macaques (*Macaca assamensis*) provide an excellent model taxon for fostering our understanding of social bonds in dispersing males (section 1.6). Finally, I will

outline the overall aims of my thesis, the objectives and approaches of each study undertaken to achieve these aims (section 1.7).

### 1.1. Affiliative relationships in multi-male, multi-female groups

Affiliative relationships between group members are established by recognizing each other, by spending time in spatial proximity and by exchanging socio-positive behaviours (e.g. groom, lick, rub, touch or embrace) (Hinde, 1983). They are established over time in which interactions are based on previous interactions (Cords, 1997). Affiliative relationships are found in a wide range of mammalian societies (e.g. giraffes, Carter et al., 2013; bottlenose dolphins, *Tursiops truncatur*, Connor, 2000; elephants, *Loxodonta Africana*, Archie et al., 2006b; several non-human primates species, Silk, 2002; and humans, Hruschka, 2010). Those relationships can emerge between individuals of similar or different age classes as well as between closely or distantly ranked individuals (reviewed in Seyfarth and Cheney, 2012a). The repetition of several different interactions within a given dyad allows each partner to acquire positive and negative experiences with the other one which determines the affiliative relationships. The variation of affiliative interactions between individuals is one important characteristic to identify social bonds.

The grounding of establishing and maintaining social relationships with specific partners is spatial proximity and socio-positive behaviours which is in turn often influenced by kinship, dominance rank relationships and age similarity (e.g. non-human primates, Kapsalis, 2004; spotted hyenas, *Crocuta crocuta*, Holekamp et al., 1997; sperm whales, *Physeter macrocephalus*, Gero et al., 2008). Below I will briefly describe close spatial proximity, behavioural signals to appease the counterpart and grooming.

### 1.2 Behaviours to establish and maintain affiliative relationships

#### 1.2.1 Proximity

Spatial proximity is by far the most common behaviour used to quantify the pattern of affiliative relationships in a social group (Whitehead & Dufault 1999). Beside the benefits individuals gain from being close to each other, it has been shown that individuals prefer to

be close to some specific individuals but be distant to others (e.g. house mice, *Mus domesticus*, Weidt et al., 2008; bats, *Myotis bechsteinii*, Kerth et al., 2011; feral goats, *Capra hircus*, Stanley and Dunbar, 2013; bottlenose dolphins, Connor, 2000; giraffes, *Giraffa camelopardalis*, Carter et al., 2013; elephants, Archie et al., 2006b; Wittemyer et al., 2005; Grey eastern kangaroos, *Macropus giganteus*, Carter et al., 2009; spider monkeys, *Ateles geoffroyi*, Ramos-Fernandez et al., 2009; chimpanzees, Langergraber et al., 2009; Mitani, 2009; white-faced capuchins, *Cebus capuchinus*, Schoof and Jack, 2014; Assamese macaques, *Macaca assamensis*, Macdonald et al., 2014; Ostner et al., 2013; blue monkeys, *Cercopithecus mitis*, Cords, 2002) and can derive benefits from such selectivity. Proximity data is a reliable factor to measure the strength of dyadic relationships since it allows species comparison which is less possible with species specific socio-positive behaviours. Dyads with higher frequencies and longer durations of close proximity are considered as stronger affiliative relationships compared to dyads that hardly spent time together (Massen et al., 2010a; Silk et al., 2013). Those structured affiliative relationships can be found in several stable groups (e.g. baboons, Silk et al., 2006b; Silk et al., 2010a; macaques, Massen et al., 2010a; Ostner et al., 2013) and also groups with fission-fusion dynamic such as elephants (Archie et al., 2006b; Chiyo et al., 2011), dolphins (Connor, 2000), giraffes (Carter et al., 2013) or chimpanzees (Foerster et al., 2015; Langergraber et al., 2009) where individuals range in subgroups of temporally varying composition. On top of benefiting from the collective vigilance and increase in foraging time (e.g. Wrangham, 1980), being in proximity with certain individuals enhances the likelihood to interact socially and therefore to invest into relationship formation and maintenance.

The groups in most mammalian species are structured by a dominance hierarchy between individuals within a group (e.g. wolves, Peterson et al., 2002; primates, e.g. de Waal, 1986; Flack and de Waal, 2004; Ostner et al., 2008; Schino, 2001; elephants, Archie et al., 2006a) which may hamper spatial approaches of subordinate individuals to higher ranking individuals and thereby the formation and maintaining of affiliative relationships. In several species, some specific behavioural signals have evolved to circumvent this obstacle and allow low-ranking individuals to spend more time in proximity to higher ranking ones.

### 1.2.2 Behavioural signals promoting proximity and sociality

In many species, approaching a higher ranking individual without any sign of appeasement or submission might increase the risk of receiving aggressions (Gerald et al., 2009; Ogawa, 1995a; Petit and Thierry, 1994; Setchell and Wickings, 2005). To reduce intra- and inter-group aggression, natural selection favoured species specific olfactory, acoustical and visual signals (Hebets and Papaj, 2005). In mammals, these signals are mainly acoustic and visual such as body postures, facial expressions, vocalizations and gestures (Call and Tomasello, 2007; East et al., 1993; Fischer and Hammerschmidt, 2002; Fox, 1969; Gadziola et al., 2012; Gros-Louis et al., 2008; Maestripieri, 1997, 2005; Tomasello and Zuberbühler, 2002). For instance, male mandrills develop a rank-dependent red colouration allowing dominance relationship to be clearly signalled. Males with differences in the intensity of their red coloration are rarely in physical conflicts with each other whereas males similar in colouration attack each other to a higher degree (Setchell and Wickings, 2005). When clear physical dominance signals are lacking, some species (e.g. *Macaca spp*: Bauer et al., 2013; Ogawa, 1995c; Zhao, 1996; *Papio spp*: Busse and Hamilton, 1981; Ransom and Ransom, 1971; geladas, *Theropithecus gelada*, Dunbar, 1984) have developed specific behaviour to buffer against aggression from higher ranking individuals. Some species have developed submissive body posture (e.g. presenting genitals or sexual crouch in gibbons, *Hylobatidae*, Baldwin and Teleki, 1976) or facial expressions (e.g. bared teeth face in macaque species, Hesler and Fischer, 2007) whereas baboons (Busse and Hamilton, 1981; Ransom and Ransom, 1971) and geladas (Dunbar, 1984) use their infants as a social tool during agonistic encounters. If young adult male geladas approach a new harem, they often carry a male juvenile of the harem leader on their back or present it directly to the harem leader to appease the leader and avoid possible aggression (Dunbar, 1975). Male macaques, on the other hand, handle infants mainly in affiliative context (e.g. Barbary macaques, *M. Sylvanus*, Deag, 1980; Deag and Crook, 1971; Taub, 1980; stump-tail macaques, *M. arctoides*, Estrada and Sandoval, 1977; Tibetan macaques, *M. tibetana*, Ogawa, 1995b). These male-infant-male interactions (hereafter called MIMI) are mainly described to function as “agonistic buffers” between two adult males reducing the likelihood of receiving aggression from a high ranking male when in close proximity (Deag, 1980; Deag and Crook, 1971; Kuester and Paul, 2000; Paul et al., 1996; Smith and Peffer-Smith, 1982). Since MIMIs increases the time

spent in close spatial proximity it is quite likely that MIMI is an important behaviour facilitating bond formation and maintenance (Kuester and Paul, 2000; Paul et al., 2000), a hypothesis that has not been formally tested.

### *1.2.3 Grooming*

Grooming is a widespread socio-positive behaviour in mammals (e.g. Clutton-Brock et al., 1976; Cords, 2000; Dunbar, 1988; Feh and de Mazières, 1993; Goosen, 1987; Hart and Hart, 1992). The primary function of grooming is to remove ecto-parasites (Barton, 1985), yet grooming also reduces heart rates (Boccia et al., 1989; Feh and de Mazières, 1993), mediates physiological positive and negative stress levels (Shutt et al., 2007; Wittig et al., 2008) and lowers social tensions among group members (Schino et al., 1988). Self-grooming in Sika deers, *Cervus nippon*, for instance, is influenced by the habitat's tick density but not allo-grooming which suggests allo-grooming might play a crucial role in social activities (Yamada and Urabe, 2007). Grooming seems to be a substantial component of affiliative relationship formation in many mammalian species, and particularly in primates (Dunbar, 1988; Smuts, 1985). When grooming others for either parasite removal or relationship maintenance the groomer might bear some costs (e.g. decreased vigilance, Maestriperi, 1993) and the receiver gain some benefits (e.g. ecto-parasites removal, Zamma, 2002). In that sense grooming may be considered as an altruistic behaviour from one individual towards the other. Among kin dyads (e.g. primate species, Schino, 2001), the investment costs to an individual are outweighed by the inclusive fitness benefits gained through their genetic relatedness with the recipient (Hamilton, 1964). However, kin selection is not the only driving force of grooming exchanges since unrelated individuals also groom each other (e.g. chimpanzees, Mitani, 2009; female chacma baboons, Barrett and Henzi, 2002; Silk et al., 2010a; male bonnet macaques, *M. radiata*, Adiseshan et al., 2011; male white-faced capuchins, *Cebus capuchinus*, Schoof and Jack, 2014). Here reciprocal altruism plays a crucial role in rendering this process evolutionarily stable; the costs individual A is investing to serve individual B with some goods needs to be reciprocated (Trivers, 1971). Grooming can be exchanged for grooming itself but also for other commodities such as infant handling (Tiddi et al., 2010), better food access (de Waal, 1989a) or coalitionary support (Seyfarth, 1977).

The equitability in the reciprocation of goods and services between partners can be short-term (e.g. de Waal, 2000; Hemelrijk, 1994; Koyama et al., 2006), but also equitable in the long-term (e.g. Gomes and Boesch., 2009; Romero and Aureli, 2008; Schino et al., 2009). However, reciprocity should withstand short-term inequality (Silk, 2002; Surbeck and Hohmann, 2015). How balanced the exchange of commodities between dyad partners is, is an important characteristic to identify social bonds, since it gives some indication of the relationships' quality.

### 1.3 Dynamics of affiliative interaction patterns

Besides the rate of interactions, there is also a growing body of evidence, particularly in non-human primates, that the equability of service exchanges within a dyad sheds light on the quality of a dyadic affiliative relationship making it one of the important characteristics to identify social bonds (Ostner and Schülke, 2014). The exchange of services is often more reciprocal within dyads sharing strong affiliative relationships than dyads sharing weaker relationships (Massen et al., 2010a; Mitani, 2009; Silk et al., 2006a). Reciprocity is also influenced by the degree of kinship; individuals reciprocate favours more often if the partner is related to themselves (e.g. macaques, Schino, 2001; yellow baboons, *P. cynocephalus*, Silk et al., 2006a), of dominance rank similarity (e.g. Chacma baboons, *P. ursinus*, Seyfarth, 1977; bonnet macaques, *M. radiata*, Silk, 1994; and white faced capuchins, *C. capucinus*, Manson et al., 2004) and/or of age similarity (e.g. male chimpanzees, Mitani, 2009; female yellow baboons, Silk et al., 2006a; female chacma baboons, Silk et al., 2010a).

Besides the facts that dyads sharing stronger affiliative relationships are more balanced in their exchange of grooming than other dyads, a few studies could also show that dyads with a strong and equitable affiliative relationship are also the relationships which last the longest. Evidence suggests that in some species those social bonds may last beyond 10 years (Langergraber et al., 2009; Lehmann and Boesch, 2009; Mitani, 2009; Silk et al., 2006a; Silk et al., 2012; Silk et al., 2010a; Stanley and Dunbar, 2013).

While Silk and colleagues brought to light the existence of social bonds (i.e. strong, equitable and stable) and of their benefits (Silk, 2001, 2002; Silk et al., 2006a,b; Silk et al., 2010a,b; Silk et al., 2009) some researchers alert that the dynamic of primates' interactions

may also be based on current individual needs rather than on the status of their affiliative relationships within the group (e.g. grooming partner instability according to infant availability, see Barrett and Henzi, 2002). The trade of valuable commodities such as grooming for infant handling (Barrett and Henzi, 2002), meat sharing for mating opportunities (Gomes and Boesch, 2009), grooming for coalitionary support (e.g. Borgeaud and Bshary, 2015; Schino, 2007) or grooming for itself (Schino and Aureli, 2008) might be linked to a demand/supply dynamic influenced by social and environmental contexts to gain immediate benefits (“Biological market theory”, Noë and Hammerstein, 1994).

Notwithstanding, analyses of the distribution of the services exchanged between individuals suggests that those exchanges may not be based only on current needs. In many non-human primates, those dyads grooming each other the most, are those who support each other more often in coalitions whereby the grooming interaction and the occurrence of the coalition are not necessarily temporal contingent (e.g. Schino, 2007) and the partner recruited for the coalition is not necessarily the more dominant of the present bystanders (which would be the prediction of the social market theory). The time delay in giving and receiving also holds in chimpanzees for the exchange of grooming for coalition formation, grooming for itself, but also meat sharing for coalitionary support (Mitani, 2006; Schino, 2007). Berghänel and colleagues (2011a) found that male Barbary macaques form, maintain and reinforce their affiliative relationships in the non-mating season when the rate of affiliations is higher and aggressions are lower compared to the mating season when males compete over access to females. In this study, partner choice for coalition formation in the mating season was not based on the rate of male-male affiliation (in the mating season), but on males’ relationship management during the preceding non-mating season. This temporal separation of affiliation and coalition formation contradicts the immediate demand/supply dynamic (Berghänel et al., 2011a).

On the proximate basis, one fundamental underlying mechanism of social bonding can be of physiological nature, mediated by neurochemical mediators such as endorphins and oxytocin (Crockford et al., 2015; Machin and Dunbar, 2011). Beside stress alleviation, oxytocin increases prosocial behaviour and build up trust between individuals, thereby enhancing the bonding process (Heinrichs et al., 2009; Olff et al., 2013). Similarly, affiliative interactions (e.g. embrace, grooming) leads to an endorphin release followed by an

activation of the neural reward system in association with a feeling of pleasure (Curley and Keverne, 2005; Machin and Dunbar, 2011). Following the endorphin peak generated by a specific interaction, endorphin levels rapidly decrease thereby motivating individuals to continue engaging in the same affiliative behaviour with the same individuals in order to experience the feeling of pleasure associated with endorphin release. This mechanism in itself, coupled with oxytocin reward system can lead to the formation, maintenance and reinforcement of affiliative relationships (Machin and Dunbar, 2011). The variations in frequency and duration of socio-positive interactions among dyads (Hinde, 1976) and the underlying mechanism I just described seem to lead to a specific partner selection over time (de Waal, 1986, 1989b) and establish specific affiliative relationships among specific individuals.

### 1.4 Affiliative relationships among females

In most gregarious mammalian species females remain in their natal groups with their female relatives (e.g. lioness, *Panthera leo*, Packer et al., 1991; elephants, Archie et al., 2006b; old world monkeys, reviewed in Silk, 2006c). Among these philopatric living females, kinship has an enormous impact on their affiliative and dominance rank relationships (Hamilton, 1964). Most research on the influence of kinship on affiliative relationships comes from studies on multi-male multi-female and multi-level primate groups such as baboons, geladas or macaques. Here kin biased affiliations are most pronounced within mother-daughter dyads. Affiliations are also found between maternal and paternal siblings but less strong than those of mother-daughter dyads (Silk et al., 2006a; Silk et al., 2006b). Those dyads spend more time in close spatial proximity, exchange the most affiliations (Borries et al., 1994; Chapais and Berman, 2004; Cheney and Seyfarth, 2008; Cords and Nikitopoulos, 2015; Kapsalis, 2004; Perry et al., 2008; Schülke et al., 2013; Seyfarth, 1980; Silk, 2006c; Silk et al., 1999) and form coalitions against others (reviewed in Kapsalis, 2004). Kin biased partner preferences and preferences towards same age classes or same sex individuals of adjacent ranks, lead to differentiated affiliative relationships (e.g. female crested macaques, *M. nigra*, Duboscq, 2013; female yellow baboons, Bentley-Condit and Smith, 1999; Silk et al.,

2006b; female chacma baboons, Silk et al., 2010a; female rhesus macaques, *M. mullata*, Widdig et al., 2001; geladas, Tinsley Johnson et al., 2014).

The partner preferences towards related individuals seem to hold even if females disperse. Genetically related adult female mountain gorillas, *Gorilla gorilla berengei*, for instance, spent more time resting and feeding in close proximity, groomed and supported each other more and aggressed each other less than non-related dyads (Stewart and Harcourt, 1987). Around puberty female gorillas disperse either together with their full or half-sisters or if they migrate on their own, they prefer to join those groups containing females who originally belonged to their natal groups (Stewart and Harcourt, 1987; Watts, 1994). Female chimpanzee also associate and groom with close kin, they do as well with unrelated females but still favour related females over non-related ones (Foerster et al., 2015; Langergraber et al., 2009).

Due to the extensive co-resident time among philopatric females and the migration with kin in some species where females disperse, long-lasting social bonds can emerge between some female dyads and last over extensive time periods (up to 10 years reported in yellow baboons, Silk et al., 2006a). Whereas bonded females compete over access to a food patch against other females which can be shared later on among the cooperative partners, males compete over access to fertile females where the benefit of siring an offspring cannot be shared (van Hoof & van Schaik, 1994). This fundamental difference brought researchers also to focus on studying bonding and cooperative process in male-male relationships.

### **1.5 Affiliative relationships among primate males**

From an evolutionary standpoint, group level cooperation in multi-male groups can be explained by common benefits group males gain if protecting their females against outsider males. Males communally defend their group and territory (e.g. chimpanzees, Furuichi and Ihobe, 1994, squirrel monkeys, *Saimiri oerstedii*, Boinski, 1994; and muriquis, *Brachyteles hypoxanthus*, Strier, 1994) and thus reduce the risk of group take overs (Fedigan and Jack, 2004; Ostner and Kappeler, 2004; Snyder-Mackler et al., 2012). In addition, the number of males in a group can increase female reproductive rate possibly by defending a larger territory and enhancing female's access to food (Richter, 2014). In contrast the within

group cooperation observed in several primate species, often in the form of coalitional support to access fertile females, is harder to explain since the benefit obtained (the fertilisation of a single female) cannot be shared (van Hooff, 2000; van Hooff and van Schaik, 1992; van Hooff and van Schaik, 1994). In most mammalian species, physical characteristics such as canine size, body weight and body size determine males' dominance rank positions (e.g. bighorn sheep, *Ovis Canadensis*, Pelletier and Festa-Bianchet, 2006) and thus the priority of access to females. Physically weaker males or lower ranking males might need to find alternatives to compete over females. Due to the male-male competition the development of affiliative and cooperative relationships among males is, evolutionarily speaking, more puzzling than the group level cooperation (van Hooff, 2000; van Hooff and van Schaik, 1992; van Hooff and van Schaik, 1994). Since male-male cooperation within a group is not a universal phenomenon but is limited to certain species, biologists try to understand the variation in male-male cooperation and male-male affiliation observed across species. Those researchers highlighted that the occurrence and frequency of affiliative interactions between males depend on the degree of within-group competition, which determines the feasibility and benefits derived from male-male cooperation (Noë, 1992; Noë, 1994; Pandit and van Schaik, 2003; van Schaik et al., 2006). In those species in which males form coalitions the fitness benefit can be either direct by allowing immediate access to fertile females or indirect by allowing participant to join agonistic conflicts against higher ranking males resulting in a rise in dominance rank for both coalitional males which in turn gain access to fertile females (Muller and Mitani, 2005). However, the formation of coalitions is a risky task since the defection of a potential ally might result in the loss of a conflict or even in life threatening injuries. Males thus may have developed some ways to insure the participation of partners in conflicts via the formation of social bonds with specific male group members. A trustful partner might enable even small males to gain high rank positions despite their lack of large body size or physical strength (e.g. male chimpanzees, Foster et al., 2009). The long co-residence in philopatric males with their relatives enables males to engage in repetitive affiliations and thus to form social bonds through which affiliative partners develop into reliable cooperative partners.

Male philopatry does not necessarily guarantee high rates of affiliations between males (e.g. Wolly monkeys, *Lagothrix spec.*, Strier, 1994; red colobus, *Ptilinopus badius*,

Starin, 1994). Dispersal and male competition may prevent male-male affiliations with non-kin (Muller and Mitani 2005; Mitani, 2006) but cooperative interactions and differentiated affiliations between non related males which are similar in age have been reported in some species with male dispersal (Adiseshan et al., 2011; Hill, 1994; Schülke et al., 2010). For instance, male Barbary macaques form coalitions against other males, particularly in the competitive mating season with high rates of aggression (Berghänel et al., 2011a). Their partner choice is not random but rather based on dyads affiliative relationship strength (Young et al., 2014b). Similarly, male Assamese macaques favour coalition partners with whom they share a strong relationship; which even helps a male-male dyad to achieve a higher dominance rank position in the future (Schülke et al., 2010). As has been previously found in chimpanzees (where males are philopatric), body condition (i.e. body size and physical strength) is not the key factor with which males compete and take over higher ranking positions (Foster et al., 2009). The alpha positions in male Assamese macaque were kept (so far) by the physically weaker males (Schülke et al., 2014), but the strength of the affiliative relationship with the beta male seem to have a huge influence on an alphas tenure. Affiliations between specific males predicted a males' future rank position but this benefit was derived from the quality rather than the quantity of relationships with other males. In this species, the strength of a social bond to a specific partner was the determining factor of a male success rather than the number of social male partners per se (Schülke et al., 2010).

Social bonds might not just be important for individuals staying throughout their lives in their natal groups, but may also be an adaptive strategy for migrating males. Social bonds may help to offset the cost of male-male competition within a group on the one hand, and reduce the costs of dispersal (van Noordwijk and van Schaik, 2004) in species where related males disperse together (e.g. white face capuchins) on the other hand.

So far social bonds have been mainly reported in philopatric females where the strongest bonds are established between mothers and daughters. Social bonds among males are more striking due to their competitive nature. Notwithstanding, those special relationships are described in some philopatric males where they feature the same social bond characteristics as philopatric females (e.g. male chimpanzees, Mitani, 2009). While social bonds in the philopatric sex last over years, reliable coalition partners are constantly

available. Affiliative interactions; thus the formation of social bonds, and the reliability of social partners might be more threatened in the dispersing sex since the partner could leave at any given time. The pattern of male-male affiliative relationships, the quality, and stability of affiliative relationships as well as the formation and maintenance of social bonds among dispersing males have so far received little attention but are crucial to understand the variation in social systems.

### 1.6 Study species and study groups

For this thesis I studied two groups of wild Assamese macaques, comprising 40 to 60 individuals with 6 to 12 adult males, 9 to 15 adult females as well as juvenile and infants, living at the Phu Khieo Wildlife Sanctuary in Northeast Thailand. I used data collected from 2006 until 2013 on the AS group. In August 2012 three adult males together with some females and their offspring split off the main group and were no longer observed on a regularly basis. During the main part of this observation period no male could successfully immigrate in the AS group. After I finished the nine month habituation of the AO group, I observed several group encounters between both groups and three young sub adult males from the AO group joined the AS group. I started data collection in May 2012 on the AO group and used data for this study until 2013.

In this species, females form social bonds with female (Macdonald, 2014) and also with male group members (Haunhorst et al., 2016; Ostner et al., 2013). In the mating season, from October to January (Fürtbauer et al. 2010), the highest ranking males engage in mate-guarding behaviour. Yet, a males' ability to monopolize several females is limited in male Assamese macaques since females fertile phase is overlapping in the time (Fürtbauer et al., 2011b) and males are not able to accurately assess that timing (Fürtbauer et al., 2011a). To achieve higher rank positions (and with it increasing their reproductive success), adult male Assamese macaque form coalitions (Schülke et al., 2010). Those coalitions are not randomly formed, but rather formed with specific partners with whom they affiliate the most. Such a partner preference in the migrating sex is puzzling since males face the risk losing a reliable partner at any given time. Male Assamese macaques therefore are a perfect species to investigate first, whether the patterns of affiliative relationships among males,

their relationship quality and stability resembles those of social bonds found in philopatric males and females. And secondly, how social bonds in the dispersing sex are established and maintained since they are not life-long together.

### **1.7 Study aims**

The general aim of my thesis is to contribute to the understanding of social bonds. To achieve this aim I analysed the structure, the equitability and the stability of affiliative relationships among dyads, as well as assessed the formation and maintenance of male-male relationships in the dispersing sex of Assamese macaques.

In my first study (Chapter 2), I investigated whether male Assamese macaques fulfil the characteristics of social bonds. First I analysed the structure of adult male-male dyads using the composite sociality index (CSI) and how strongly differentiated their relationships are.

Since male Assamese macaques leave their natal group they have to establish new social relationships also with unfamiliar individuals in the group they migrate into. It is therefore of high interest to verify whether the relationships structure of those migrating males resembles the one of philopatric individuals who have the opportunity to interact with each other since they are born. After describing the general affiliative relationships structure I analysed one of the main behaviours likely to mediate those relationships by investigating the dynamics of grooming exchanges and by determining whether those exchanges are based on the strength of the relationship between individuals. More specifically, I tested the prediction that the stronger a relationship is the more balanced are the grooming exchanges within a dyad. After, I shed light on the most striking social bond characteristic in the dispersing sex: partner stability. The key question here was to assess whether affiliative relationships among males can be as enduring as found among philopatric individuals. To address this question I used a unique long-term data set of about 9000 focal animal observation hours collected over a continuous seven year (group AS, 1.5 years group AO) time period which was so far the most problematic issue in analysing long-term stability in the dispersing sex.

In my second study (Chapter 3), I focus on the proximate mechanism involved in the establishment and maintenance of social bonds. Balanced grooming exchanges between bonded individuals require enough time to reciprocate favours in the short- and long-term which is given in individuals staying in their natal groups. Due to time constraints (feeding, bonding with females and infants) and the risk of migration, other behaviours than grooming or coalitionary support might be relevant for bond formation and maintenances. Therefore I looked into a macaque specific behaviour where two adult males handling an infant together (MIMI). I investigated the effect of relationship strength on the occurrence of MIMIs to assess the potential role of MIMIs in social bond maintenance. Building up on Ogawas (1995a) finding, that males engaging in MIMIs increase their time in close proximity, I explored whether MIMIs influenced the time males spend in close proximity after they approached each other and whether the potential effect of MIMIs on time in close proximity changes with social relationship strength of the dyad. Finally, I tested whether the current rate of MIMIs will increase the time two males spend in close proximity in the future and thus the quality of the future affiliative relationship.





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## Chapter 2

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

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### Abstract

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.

## **Introduction**

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 and Ruxton, 2002; Lukas and Clutton-Brock, 2014; Ostner et al., 2011; Palombit et al., 1997; Smuts et al., 1987; van Schaik and Aureli, 2000; Wittig and 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 et al., 2003; Silk et al., 2009; Weidt et al., 2008). In gregarious species within-group variation in sociality may be associated with variation in coalition formation (Langergraber et al., 2007; Pope, 1990; Schülke et al., 2010), co-feeding tolerance (Huchard et al., 2010) and buffering against environmental and social stressors (McFarland and Majolo, 2013; Young et al., 2014a). This in turn may lead to increased reproductive success and longevity for individuals (Archie et al., 2014; Brent et al., 2013; Frère et al., 2010; Schülke et al., 2010; Silk et al., 2010b). 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 et al., 1992; Heesen et al., 2014; Ostner and 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 and Schülke, 2014) rather than an individual's overall level of affiliation. Thus, differentiation into weaker and stronger affiliative relationships is crucial (Massen et al., 2010a; Ostner and 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 and Boesch, 2009; Massen et al., 2010b; Mitani, 2009; Ostner and Schülke, 2014; Silk et al., 2012). Consequently, strength, equitability, and stability have been suggested as defining characteristics of a social bond (Ostner and 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 et al., 2011), feral goats, *Capra hircus* (Stanley and Dunbar, 2013), nonhuman primates (Aureli et al., 2012), kangaroos, *Macropus giganteus* (Carter et al., 2009), male bottlenose dolphins, *Tursiops truncatus* (Parsons et al., 2003), female African elephants, *Loxodonta africana* (Archie et al., 2006b) and giraffes, *Giraffa camelopardalis* (Carter et al., 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 et al., 2006b; female vervet monkeys, *Chlorocebus aethiops*, Cheney et al., 1986; female macaques, *Macaca spp.*, Cheney et al., 1986; Schülke et al., 2013; Widdig et al., 2001; and male chimpanzees, *Pan troglodytes schweinfurthii*, de Waal, 1991; Mitani, 2009). Second, of the goods and services that are exchanged within dyads allo-grooming 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 et al., 2011; Gomes and Boesch, 2009; Kaburu and Newton-Fischer, 2015; Lewis et al., 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 et al., 2011; chimpanzees, Mitani, 2009; savanna baboons, Silk et al., 2006a; chacma baboons, *Papio ursinus*, Silk et al., 2010a). 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 and Shultz, 2010). Hence, it is important to study similar behaviours such as grooming in animals (Massen et al., 2010b). 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 et al., 2012), albeit partner choice for their strongest relationship was not consistent among female chacma baboons of a different population (Henzi et al., 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 et al., 2006a). 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 and 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 et al., 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 km<sup>2</sup> interconnected and well-protected Western Isaan forest complex in northeast Thailand (Borries et al., 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 multi-male multi-female 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 using continuous sampling (Martin and Bateson, 2007) we recorded frequencies and durations as well as the actor and receiver of all affiliative (grooming, body contact), submissive (bare teeth, give ground, make room) and aggressive (e.g. lunge, slap, bite) behaviours and approaches into and departures from a 1.5 m radius around the focal individual (referred to below as ‘close proximity’) (Ostner et al., 2008). In addition we recorded agonistic interactions between males other than the focal animal by ad libitum sampling (Altmann, 1974).

### *Data Analysis*

To make our results comparable to previous studies on relationship strength, equitability and stability we broke our data down into yearly periods (e.g. Silk et al., 2006a; Silk et al., 2006b). We defined one observation period as 1 year from the start of the mating season (October) until the end of the subsequent non-mating season (September) (Fürtbauer et al., 2010). The observation periods were not the same as in our previous analyses (Schülke et al., 2010). The first observation period of the AO group spanned 5 months only.

### *Dominance hierarchy*

For the purpose of this study, we calculated a dominance hierarchy for each observation period from decided dyadic agonistic interactions (Ostner et al., 2008) recorded during continuous and ad libitum sampling (Martin and Bateson, 2007). A winner/loser matrix of these interactions was used to calculate the standardized normalized David's score (nDS) using DomCalc (Schmid and de Vries, 2013). These David's scores were utilized to calculate a continuous measure of rank distances (Table A3).

### *Strength of Affiliative Relationships*

We investigated the strength of affiliative relationships between adult males by following Silk et al. (2006b) and computing the composite sociality index (CSI) for each male dyad each year. This index quantifies the extent by which each dyad deviates from the average male dyad in the same group during the same period (Silk et al., 2006b). We used as components both the frequency and duration of grooming, body contact and time spent in close proximity <1.5 m. The time a dyad spent in close proximity while also in body contact or grooming was deduced from the proximity time; similarly, time spent grooming was deduced from time spent in body contact. All components were highly correlated in row-wise matrix correlations with 10 000 permutations using Spearman rank correlations (mean  $\rho_{rw,ave} = 0.92 \pm 0.01$ ; range  $\rho_{rw,ave} = 0.88 \pm 0.97$ ). To control for partner availability, we divided per dyad each component by the number of hours each of the partners was

observed to give a frequency per hour of observation or duration in minutes per hour of observation. Then values for an individual dyad (*ij*) were divided by the mean value of this component across possible male-male dyads.

Then the CSI was calculated as follows:

$$\text{CSI} = \left[ \frac{\frac{\text{FP}_{ij}}{\text{FP}_{\text{ave}}} + \frac{\text{FB}_{ij}}{\text{FB}_{\text{ave}}} + \frac{\text{FG}_{ij}}{\text{FG}_{\text{ave}}} + \frac{\text{DP}_{ij}}{\text{DP}_{\text{ave}}} + \frac{\text{DB}_{ij}}{\text{DB}_{\text{ave}}} + \frac{\text{DG}_{ij}}{\text{DG}_{\text{ave}}}}{6} \right]$$

The first term represents the hourly frequency of time spent in close proximity (frequency in proximity, FP) per dyad (*ij*) divided by the average hourly frequency in close proximity ( $\text{FP}_{\text{ave}}$ ) across all dyads. The second and third term represent the ratio between dyadic frequency of body contact ( $\text{FB}_{ij}$ ) and of grooming ( $\text{FG}_{ij}$ ) and average frequencies of both parameters across all dyads ( $\text{FB}_{\text{ave}}$  and  $\text{FG}_{\text{ave}}$ ). The last three terms represent the hourly duration of close proximity ( $\text{DP}_{ij}$ ), body contact ( $\text{DB}_{ij}$ ) and grooming ( $\text{DG}_{ij}$ ) for each dyad (*ij*) divided by their averages ( $\text{DP}_{\text{ave}}$ ,  $\text{DB}_{\text{ave}}$  and  $\text{DG}_{\text{ave}}$ ) across all dyads. The values of the six terms are then summed and divided by the number of behaviours used, i.e. six in this case. The average CSI score across all dyads is by definition always one. Values  $\geq 1$  reflect dyads that share a stronger affiliative relationship, while values between zero and one (excluding one) suggest that the relationship is weaker (Silk et al., 2006b). Descriptive statistics for the CSI and the components are provided in the Results section. It has been shown in other primates that individuals close in dominance rank may form stronger relationships than individuals ranking further apart (Silk et al., 2006b). To assess whether dominance rank drives the pattern of social relationship strength in male Assamese macaques, we tested for a possible relationship between dyadic CSI score and dominance rank difference using a linear mixed model (LMM; Model 1). The response variable was the CSI value of each dyad in each year and the predictor variable was the nDS difference. Actor and receiver identity as well as group and period were included as random factors to control for non-independent repeated measures across the same individuals within the same periods.

*Equitability of affiliative relationships*

We assessed the equitability of affiliative relationships in several ways. We calculated the grooming symmetry index (GSI; Silk et al., 2006a) based on the duration of grooming given ( $G_{ij}$ ) and received ( $G_{ji}$ ) by each male within a dyadic grooming bout and across grooming bouts. A grooming bout can contain one or several grooming interactions if grooming is reciprocated immediately.

$$GSI = 1 - \text{abs} \left( \frac{G_{ij} - G_{ji}}{G_{ij} + G_{ji}} \right)$$

GSI of one indicates a perfect balance between grooming given and grooming received whereas a GSI of zero indicates that all grooming went only one way. Relationships with a more symmetric exchange of grooming are more equitable. Additionally, we assessed imbalances in responsibility for the maintenance of close spatial proximity of <1.5 m by calculating the Hinde index (HI; Hinde and Atkinson, 1970) of approaches into and departures from a 1.5 m radius.

$$HI = \left( \left( \frac{A_{ij}}{A_{ij} + A_{ji}} \right) \times 100 \right) - \left( \left( \frac{D_{ij}}{D_{ij} + D_{ji}} \right) \times 100 \right)$$

The HI ranges from 0 to 100 and increasingly high indices indicate an increasing imbalance in the relationship (Hinde and Atkinson, 1970). Since small deviations from zero may result from sampling, e.g. because odd numbers of approaches or departures always generate an imbalance, it has been suggested that one should refrain from interpreting the variation in values below 10 (Hill, 1987). We therefore excluded all dyads with HIs below 10 from further analyses.

To assess whether the strength of affiliative relationships affected within-bout grooming symmetry and the likelihood of grooming reciprocation, we built two models. First, we used a generalized linear mixed model (GLMM; Baayen, 2008) to examine whether the dyadic CSI affected the likelihood of grooming being reciprocated at all within a bout (irrespective of the amount of grooming returned). Thus, in this model (Model 2) the response was binomial: is grooming reciprocated within the same bout yes or no? To control for dominance rank distance effects (Schino, 2001), we included the absolute nDS difference

as a fixed control factor. Second, to assess whether the dyadic CSI affected the GSI within a grooming bout we ran an LMM (Model 3; Baayen, 2008) with GSI as the response, CSI score as the predictor and nDS difference as the fixed effect. In models 2 and 3, actor and receiver identity, dyad, observation periods and group were included as random factors to control for non-independence of repeated measures across the same individuals within the same periods. We were unable to run an LMM to investigate whether CSI and rank differences affect grooming symmetry across bouts as the assumption of normality of residual distribution and homogeneous residuals were not fulfilled (Quinn and Keough, 2002). We built a fourth LMM (Model 4) with the HI as a response and the dyadic CSI and nDS difference as predictors; actor, receiver, dyad, group and observation period were included as random factors to control for non-independent repeated measures across the same individuals within the same periods in the same group. The predictors in all models were z-transformed and the response log transformed to achieve a normal distribution. All models were run in R (version 3.0.2, R Core Team, 2013) using the function 'lmer' of the R package 'lme4' (Bates et al., 2015). For model validation we checked that the assumption of normality of residual distribution and homogeneous residuals were fulfilled by visually inspecting scatter plots of the residuals plotted against the fitted values and a qq-plot (Quinn and Keough, 2002). We checked for the stability of each model by excluding data points one by one from the data and comparing the estimates derived with those obtained for the full model (Quinn & Keough, 2002). We present the outcome of the models run with the full data set. For each model we first determined the significance of the full model against a null model comprising only the random factors and the intercept. All three models were significant (see Results). We then derived the P value for each predictor in each model using the R function 'drop1' (Barr et al., 2013). Variance inflation factors were calculated for each predictor by using the function 'vif' of the R package car (Fox and Weisberg, 2010). VIF values below five indicate that collinearity between the predictors is not a problem (Bowerman and O'Connell, 1990). In all our models VIFs were below 2.2.

*Stability of Affiliative Relationships*

To assess the overall stability of male social relationships over time, we compared the CSI scores per dyad between observation periods using Kendall's tau row-wise matrix correlations computed in MatMan 1.1.4. (de Vries et al., 1993) with 10 000 permutations. Each period was compared to the following period and the first to the last. Within the analysis the average Kendall's tau of adjacent periods was calculated based only on CSI values of dyads that were present in both periods, meaning dyads that were only present in one of the respective periods were not considered in this matrix correlation. To specifically test whether relationship stability differed between stronger and weaker affiliative relationships we used the partner stability index (PSI; Silk et al., 2006a) for all males present for at least two observation periods as follows:

$$\text{PSI} = \left( \frac{ns - u}{ns - s} \right)$$

where  $n$  is the number of periods the individual was present in the group,  $s$  is the number of top partners considered and thus always equals three in our analyses and  $u$  is the number of unique partners, i.e. different males that were among the individual's top three affiliation partners ordered by their CSI values across periods. Male partners had to be present continuously; no gap between periods was allowed. For a male that always had the same top three partners across periods the PSI equals one. If a male changed all its top three partners between periods the PSI equals zero. We determined whether male partner choice was stable over time, by comparing observed PSIs to expected PSI values based on random partner choice. The top three partners were randomly chosen 10 000 times from all males residing in the group and PSIs were calculated for each permutation (Silk et al., 2012) using Microsoft Excel 2010. Partner stability was considered different from random when the observed PSI score of a given male was higher than 95% of all the simulated PSI values. To test specifically whether the strength of affiliative bonds affected their stability we used a matched-sample test comparing across males an individual's PSI for his top three affiliation partners with the PSI for his weaker partners ranking fourth to sixth in affiliation strength. In addition, we ran a Pearson correlation of male partner stability and the sum of the CSI values

of a male's top three partners. We only included males that were resident in the group for at least 3 years.

### Results

The number of co-resident male dyads in the same group varied across observation periods between 21 and 66 (mean  $\pm$  SE =  $45.2 \pm 5.3$ ) due to male maturation, immigration, emigration and death.

#### *Variation in the Strength of Affiliative Relationships*

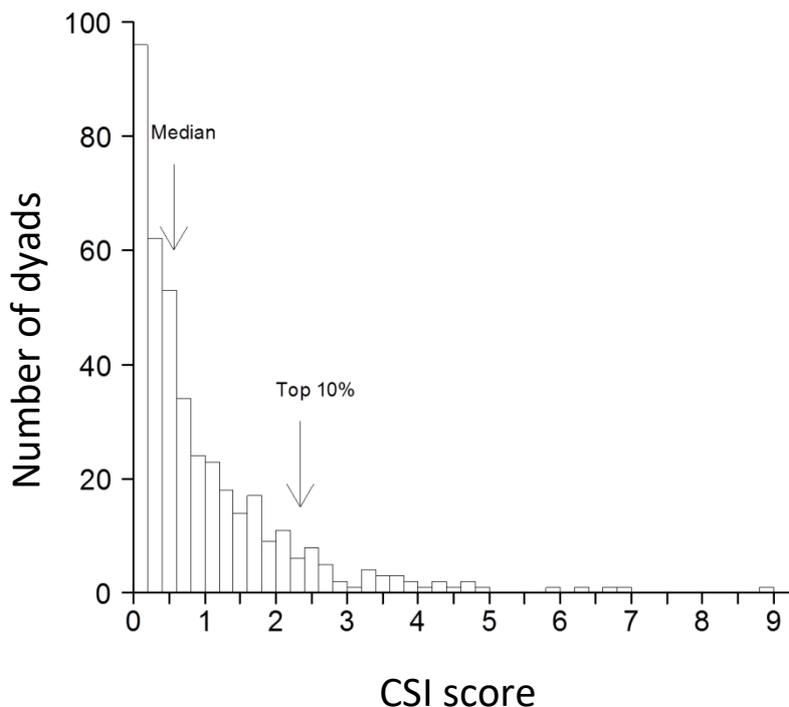
For a general description of relationship differentiation we computed one composite sociality index (CSI) for each co-resident dyad in each group across all years (N = 407 dyads). The distribution of these scores provides a measure of how evenly male affiliative behaviour was distributed across same-sex dyads. This distribution was strongly right-skewed which indicates highly differentiated social relationships between males (Figure 1.1). Most dyads formed weak affiliative relationships i.e. they had below average rates and durations of affiliative interactions. One-third of dyads (34%, N = 138) exhibited above average CSI values indicating strong affiliative relationships. The top 10% (N = 41) of values were above 2.34. The percentage of CSI values above 1 was 34% on average across all periods with a range between 21% and 44%.

Since the CSI is a dimensionless index we provide here some descriptive statistics of its components. Each male featured on average  $\pm$  SE  $3.2 \pm 0.21$  (range 0 - 8) relationships with CSI values above 1. Male dyads spent on average  $\pm$  SD  $25 \pm 36$  s/h (N = 407, range 0 - 263 s) in close proximity. Males sharing a closer than average affiliative relationship (CSI  $\geq 1$ ) spent  $52 \pm 48$  s/h (N = 138) in close proximity compared to  $10 \pm 12$  s/h (N = 269) in males with a weaker than average relationship (CSI  $< 1$ ). Across all possible male dyads, males spent on average  $\pm$  SD  $5 \pm 13$  s/h in body contact (N = 407, range 0 - 113 s) with closely affiliated males spending  $13 \pm 15$  s/h (N = 138) and weakly affiliated males spending  $2 \pm 3$  s/h (N = 269) in body contact. Finally, dyadic male-male grooming time averaged  $7 \pm 12$  s/h (N = 407,

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range 0 - 92 s) with closely affiliated males grooming  $17 \pm 16$  s/h (N = 138) and weakly affiliated males  $2 \pm 3$  s/h (N = 269).



**Figure 1.1:** Distribution of the strength of dyadic male-male affiliative social relationships measured as the composite sociality index (CSI). Data from both groups are pooled and one value is included for each co-resident dyad across the entire study period (*mean* = 1, *median* = 0.56, range: 0 - 8.83).

**Table 1.1:** Estimates $\pm$ SE, Z and P values for the LMM (Model 1) run to test the effect of rank differences on relationship strength

Response: Strength of Affiliative Relationships

No. of Dyads: 407

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Predictors	Estimate $\pm$ SE	T	P
Intercept	1.000 $\pm$ 0.087	11.520	< 0.001***
Rank Difference	-0.044 $\pm$ 0.010	-4.369	< 0.001***

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All statistical analyses were run on continuous measures of relationship strength. The dominance rank asymmetry between two males was negatively associated with the strength of their affiliative relationship (Model 1, Table 1.1). For this analysis we used the CSI score per dyad per period and controlled for potential differences between periods. The full model, with CSI as the response and rank differences as a predictor, was significantly different from the null model with the random factors ( $\text{Chi}^2 = 17.26$ ,  $P < 0.001$ ).

### *Equitability*

We observed 1845 grooming interactions (within 1198 grooming bouts) across both groups. Only 58 of 91 possible male dyads in the AO group and 132 of a possible 316 in the AS group engaged in grooming, indicating that male Assamese macaques were selective in their choice of grooming partners. The grooming interactions were directly reciprocated by the partner in only a quarter of all grooming bouts (294 of 1198, 24.62%). We found a significant and positive effect of the CSI score on the likelihood of reciprocating grooming during a given bout ( $N = 1198$ , Model 2, Table 1.2), indicating that the stronger the affiliative relationship between two males the more likely reciprocation occurred within a bout. Dominance rank distance did not significantly affect the likelihood of reciprocation (Table 1.2). The full model (GLMM) of grooming reciprocation was significantly different from the null model with the control variable and the random factors ( $\text{Chi}^2 = 16.75$ ,  $P < 0.001$ ).

**Table 1.2:** Estimates $\pm$  SE, Z and P values for the GLMM (Model 2) run to test the effect of affiliative relationship strength and dominance rank asymmetry on the likelihood of grooming reciprocation

Response: Likelihood of Grooming Reciprocation

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Predictors	Estimate $\pm$ SE	Z	P
Intercept	-1.546 $\pm$ 0.56	-2.775775	0.005**
CSI	0.518 $\pm$ 0.144	3.587	< 0.001***
Rank Difference	0.002 $\pm$ 0.115	0.025	0.979

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Across all grooming bouts in which grooming was reciprocated (N = 294 bouts, over 190 dyads) the GSI ranged from 0.01 to 0.99 (mean  $\pm$  SE = 0.6  $\pm$  0.02). The within-bout GSI was predicted by the CSI score and the dominance score difference between the partners (N = 294, Model 3, Table 1.3, Figure 1.2). The stronger the affiliative relationship between two males, the more balanced was their grooming exchange within a bout. Also, the closer males were in rank the more balanced were their grooming exchanges, independent from the CSI effect (Table 1.3). Variation inflation factors below 2.2 indicate that covariation between CSI and rank difference did not affect model outcome. The full model (LMM, Model 3) of grooming symmetry was significantly different from the null model ( $\text{Chi}^2 = 4.11$ ,  $P = 0.043$ ).

**Table 1.3:** The effect of affiliative relationship strength on the symmetry of the grooming relationship between the same males. Results for model 3 (LMM) are shown.

Response: Grooming Symmetry Index

No. obs. bouts      294

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Predictors	Estimate $\pm$ SE	T	P
Intercept	0.510 $\pm$ 0.025	20.310	< 0.001***
CSI	0.041 $\pm$ 0.018	2.288	0.041*
Rank Difference	-0.044 $\pm$ 0.017	-2.588	0.011*

**Table 1.4:** Estimates $\pm$ SE,  $T$  and  $P$  values for the LMM (Model 4) run to test whether the CSI and dominance score difference have an impact on the Hinde Index.

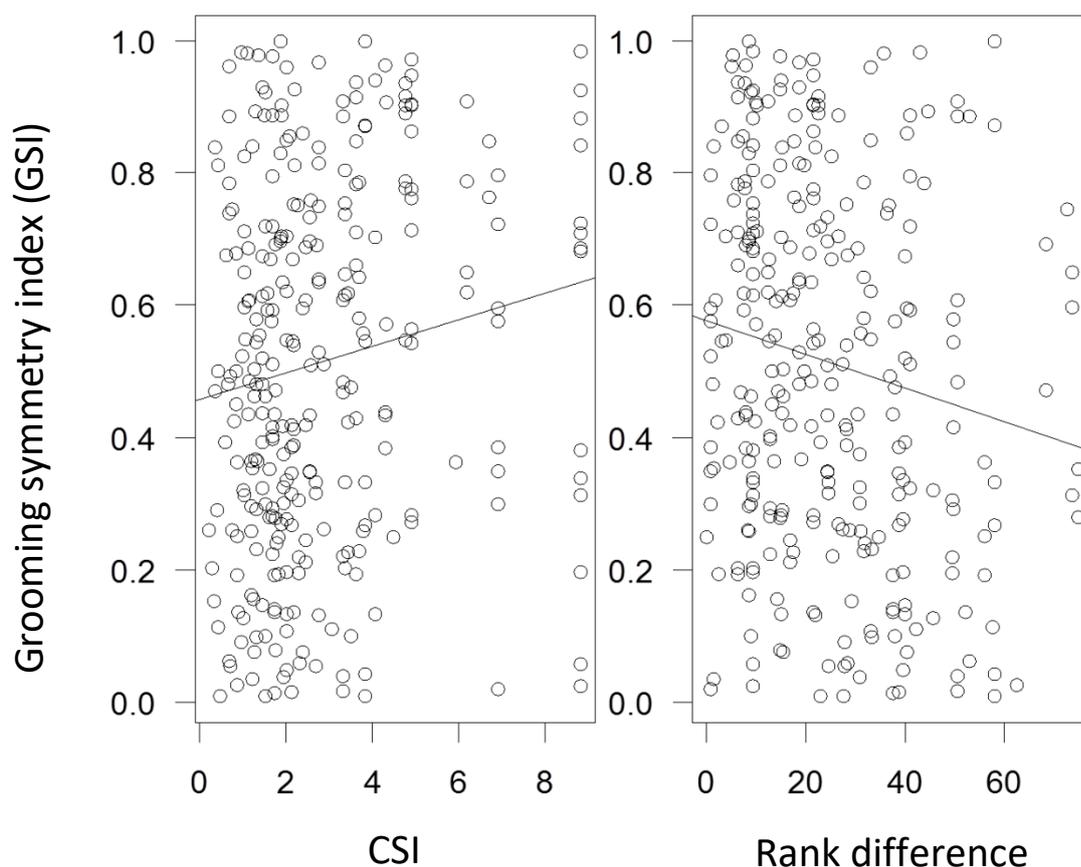
Response: Hinde Index

No. of observations      155

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Predictors	Estimate $\pm$ SE	T	P
Intercept	2.482 $\pm$ 0.035	71.93	< 0.001***
CSI	-0.072 $\pm$ 0.028	-2.51	0.017*
Rank Difference	0.058 $\pm$ 0.027	2.13	< 0.047*

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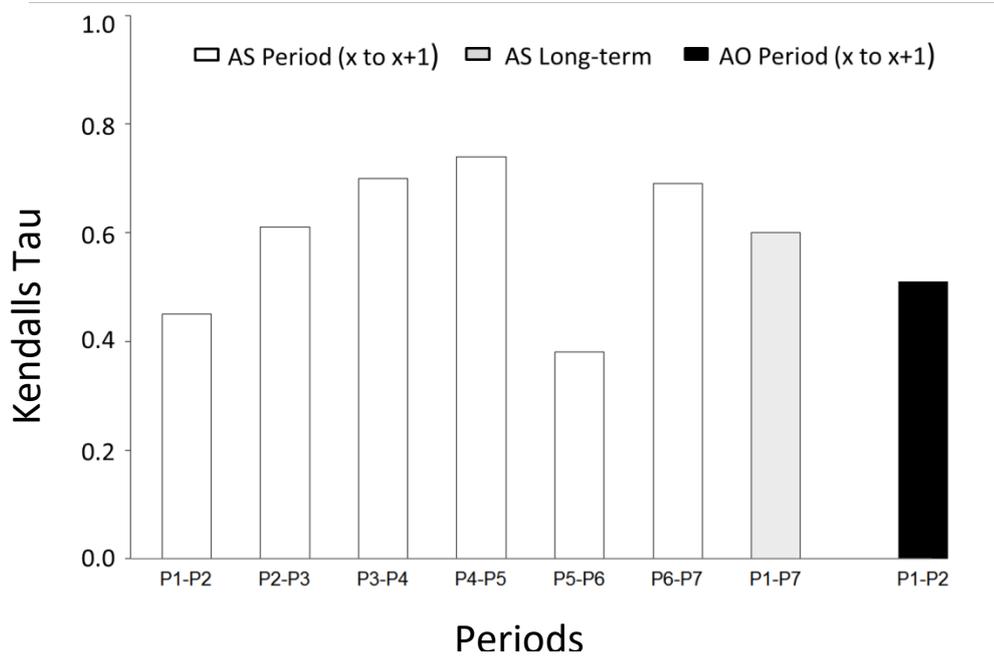


**Figure 1.2:** Within-bout grooming symmetry (GSI) as a function of strength of partners' affiliative relationship (CSI) and absolute dominance score difference. The plots show the prediction from the LMM and the raw data of 190 dyads formed by 26 males. In average  $\pm$ SD a male had  $7.3 \pm 3.0$  different grooming partners. Meaningful interpretation requires acknowledgement of all significant factors in the LMM.

Finally, an LMM (Model 4), examining whether the HI of a dyad was driven by relationship strength and dominance score differences was significantly different from the null model ( $\text{Chi}^2 = 12.48$ ,  $P < 0.002$ ). The higher the CSI score of a dyad the more balanced the responsibility for maintaining close spatial proximity was, independent of the effect of rank difference (Table 1.4).

### *Stability*

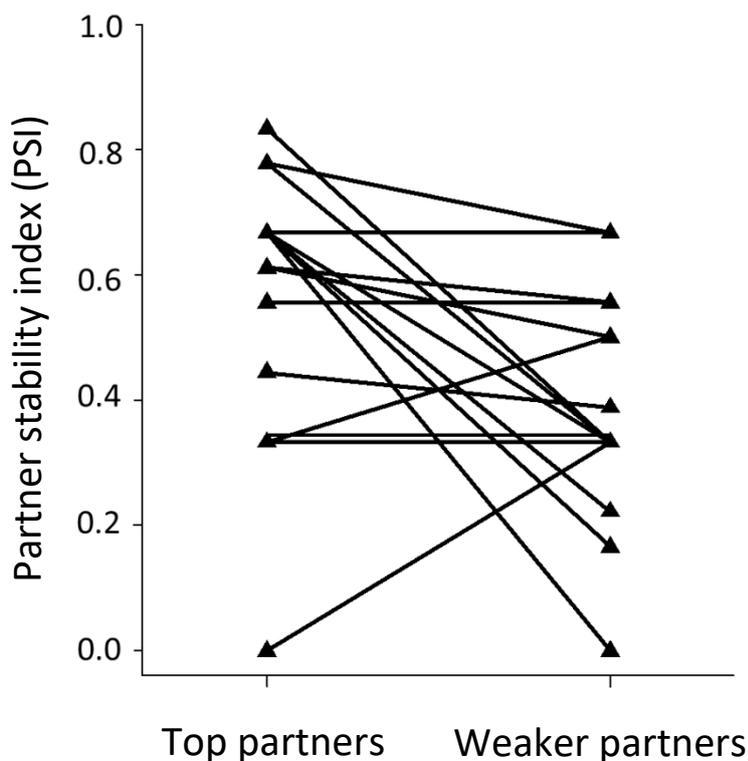
At the group level, patterns of affiliation were stable over time. CSI score matrices were correlated with each other from one observation period to the next (all row-wise, average Kendall's tau's between 0.38 and 0.74 and all  $P < 0.001$ ) and even from the first period to the last period, 7 years later ( $\text{tau}_{\text{rw,ave}} = 0.6$ ,  $P < 0.001$ ; Figure 1.3).



**Figure 1.3:** Group wide patterns of male affiliation are stable across time. Bars are average correlation coefficients from significant row-wise matrix correlations of CSI values comparing consecutive observation periods as well as the first to the last period (grey). The black bar is for AO group, all others for AS group.

Residence time of individual males varied between 1 and 7 years due to maturation, death and emigration. Of 17 adult males, 16 resided for at least two periods in the AS group and were thereby included in the analysis of partner stability. Since we observed the AO group for only 1.5 periods, this group was not included in this part of the analysis. The tendency of males to keep their preferred top three affiliation partners ranked by CSI was significantly higher than expected from random partner choice among all males of the group (Wilcoxon signed-rank test:  $V = 130$ ,  $N = 16$ ,  $P < 0.001$ ). Three-quarters of all males had a PSI score for their top three partners above 0.5. Across all 16 males the mean  $PSI \pm SE$  was  $0.57 \pm 0.05$  and ranged between 0 and 0.8 (Figure 1.4) in the AS group. Of these 16 males, nine kept at least one of their top three partners across their entire 2 - 7 - year residence time. Half of the males retained two of their top three partners. Partner stability was much lower for weaker partners ranking fourth to sixth in affiliation strength; only 37.5% of the males had a PSI score above 0.5 ( $PSI_{ave} \pm SE = 0.41 \pm 0.05$ , range 0 - 0.7,  $N = 16$ ; Figure 1.4). Thus, the strength of the affiliative relationship affected their stability. Males had significantly more

stable relationships with their top three affiliation partners than with their weaker partners (Wilcoxon signed-rank test:  $V = 65$ ,  $N = 16$ ,  $P = 0.045$ ). Differences in PSI between top and weaker partners were not related to male rank (Spearman  $\rho = 0.08$ ,  $N = 16$ ,  $P = 0.78$ ) nor to the number of years a male resided in the study group (Spearman  $\rho = 0.14$ ,  $N = 16$ ,  $P = 0.61$ ). In further support of the link between the strength and the stability of affiliative relationships, the PSI and the sum of CSIs for the top three affiliation partners were positively correlated among males from the AS group that were resident for at least three periods (Pearson correlation:  $r = 0.68$ ,  $P < 0.05$ ).



**Figure 1.4:** Stronger relationships (top three partners) were more stable than weaker ones (partners 4 to 6 ranked by CSI). A triangle displays the PSI values. Each line (total 16) connects the PSI values (1st, 2<sup>nd</sup> and 3<sup>rd</sup> partner on the left and 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> on the right) of one male.

## **Discussion**

Our study provides the first empirical evidence that males, the dispersing sex in Assamese macaques, form social bonds, defined as strong, equitable and long-lasting affiliative relationships. Adult males biased their affiliative behaviour towards a few male partners. The stronger an affiliative relationship between two males was the more likely they reciprocated a grooming act immediately and the more balanced was the grooming exchanged within a grooming bout. Furthermore, the stronger the affiliative relationship was the less biased was the responsibility for maintaining close spatial proximity and the more stable was the relationship over time. The degree of relationship differentiation we found in male Assamese macaques closely resembles that described for philopatric female baboons with the median CSI being close to 0.5 and only one third of relationships being stronger than the average (Silk et al., 2006b; Silk et al., 2010a). In contrast it is hard to detect what could be called a 'friendly' relationship in any pair of male baboons' (Noë, 1989, p. 219; cf. Silk, 1994) and males in many other species forming multi-male groups either affiliate rarely or in an undifferentiated manner (Ostner and Schülke, 2014; Young et al., 2014b). Males in our study formed fewer strong and more weak relationships than the female Assamese macaques in the same groups (Macdonald et al., 2014). This is similar to the differences described for dispersing female chimpanzees compared to their more sociable philopatric male group mates (Langergraber et al., 2009). As in the philopatric sex of several primates, dominance was an important feature structuring male relationships (Mitani, 2009; Schülke et al., 2013; Silk et al., 2006b; Widdig et al., 2001). The stronger affiliative relationships were the closer males were in rank. Our previous work suggests that rank similarity is the consequence rather than the cause of close affiliative relationships; close partners support each other in rank-changing coalitions effectively pulling each other to similar ranks (Schülke et al., 2010). Similarly, female philopatric primates form their strongest relationships with their closest maternal kin which they support in rank acquisition resulting in close affiliation partners occupying adjacent ranks (Chapais, 1992; Lea et al., 2014; Silk et al., 2004; Silk et al., 2006b). The degree to which kinship structures male Assamese macaque affiliative relationships remains largely unknown, but males sharing mtDNA haplotypes formed strong relationships as often as males with different haplotypes (Schülke et al., 2010). Expectations for the

equitability in exchanges between partners in stronger versus weaker affiliative relationships can go both ways (Massen et al., 2010a): either close partners exchange goods and services more equitably (Silk, et al., 2006a) or close relationships could withstand more short-term inequality (Silk, 2002; Surbeck and Hohmann, 2015). If the properties of males' social relationships reflect their tendency to participate in coalitions, as well as the roles that they play in those coalitions (Silk, 1994), grooming relationships may reflect the partners' willingness to reciprocate aid. In wild Barbary macaques, *Macaca sylvanus*, for example, the closer the affiliative relationships between males the more equitable their grooming exchanges and the less likely it is that a partner ignores the other's recruitment for agonistic support in an ongoing conflict with another male (Young et al., 2014b). In the present study grooming equitability was also related positively to the similarity of the partners' dominance ranks. The fact that relationship strength and rank difference had independent effects may result from grooming having different functions in different dyadic relationships. For partners with a strong affiliative relationship grooming may function to strengthen and maintain their bonds whereas it may be traded for other commodities (e.g. tolerance or reduced aggression, Fairbanks, 1980; Silk, 1982) in less closely bonded ones. The view that not all grooming serves the same function is supported by observations in chimpanzees in which grooming with a close partner is associated with increased peripheral oxytocin levels, while oxytocin levels remain unchanged when two non-bonded individuals engage in the exact same grooming interaction (Crockford et al., 2013). Furthermore, we found the affiliative relationships of male Assamese macaques to be rather stable. Half of the males retained two of three partners among their top three closest relationships throughout their residence time of up to 7 years. More specifically, the proportion of partners that was retained was higher for the three closest partners than for weaker relationships. This latter finding suggests that stability in top partner choice did not result directly from constrained partner availability due to small male group size. Interestingly, these findings mimic the situation in philopatric female baboons and male chimpanzees which is surprising because male Assamese macaques show natal and secondary dispersal (Ostner and Schülke, unpublished data). Relationship stability is a crucial characteristic of social bonds if social bonds evolved for alliances in competition for social status (Ostner and Schülke, 2014). If male coalitions evolved for their function in rank attainment instead of more directly

levelling the mating skew (van Schaik et al., 2006), coalitionary partner choice requires a certain level of stability. After rank changes caused by coalitions within a group, more powerful males may come to rank below physically weaker but cooperative males. These situations are potentially very risky but can be managed if successful coalition partners maintain their relationship over time and defend their social status via defensive/conservative coalitions (Ostner and Schülke, 2014; Young et al., 2014b). Together, our results show that male Assamese macaques form social bonds with a few co-resident males which serve as reliable partners in cooperative attainment and maintenance of social status. Several lines of evidence suggest that social bonds are represented in nonhuman primates and variation in affiliation is not always simply the consequence of repeated identical partner choices in small groups. In many primates the probability that former opponents reconcile after a conflict is increased for closely bonded partners (Aureli et al., 2012), males base their coalition partner choice on relationships established in the past (Berghänel et al., 2011a), individuals modulate their loud calls in reaction to the presence of bonded partners (Micheletta and Waller, 2012), females react with elevated glucocorticoid levels to the death of a partner compared to a non-bonded individual (Engh et al., 2006), and the stronger a male's social bonds the stronger the buffering effects they provide against increasingly strong stressors (Young et al., 2014a). Thus, we may be dealing with a phenomenon that is very similar to human friendships (Silk, 2002), which are also characterized by variation in relationship strength, equitability and stability (Allen-Arave et al., 2008; Gurven, 2006) and which may have evolved as within group alliances (DeScioli and Kurzban, 2009). Future research is needed on relationship characteristics in non-primate species to assess the generality of the phenomenon that animals establish relationships equivalent to human friendships.

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

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**Appendix**

**Table A1:** Total and average observation hours per period

Group_Period	Observation hours per period (mean±SD)
AS_P1	393 (35.67±4.19)
AS_P2	950 (86.36±16.37)
AS_P3	1816 (129.73±50.72)
AS_P4	779 (86.56±18.98)
AS_P5	887 (98.51±14.35)
AS_P6	1184 (118.40±45.04)
AS_P7	892 (127.43±5.06)
AO_P1	350 (38.91±14.54)
AO_P2	1397 (127±48.48)

**Table A2:** Total and average observation hours per male

Group	Male ID	Total No. of Observation hours per male(mean±SD)	Residence time in years
AS	Ach	782 (111.75±44.78)	7
AS	Bon	504 (126.03±34.94)	4
AS	Bru	672 (95.92±39.47)	7
AS	But	126	1
AS	Cha	628 (89.68±36.58)	7
AS	Cof	177 (59±39.77)	4
AS	Cut	396.18 (99.04±11)	3
AS	Jow	235 (78.44±31.06)	5
AS	Lim	652 (130.31±32.45)	4
AS	Pun	387 (96.67±66.66)	4

**Table A2** continue

AS	Roc	772 (110.30±44.35)	7
AS	Soa	228 (75.83±37.30)	3
AS	Soo	143 (47.56±30.58)	3
AS	Spu	322 (47.56±74.74)	3
AS	Tru	134 (66.97±29.75)	2
AS	Wal	709 (101.27±43.39)	7
AS	Wen	143 (71.5±39.83)	2
AO	Cof	11.25	1
AO	Dra	123	1
AO	Jow	197 (98.45±92.78)	1.5
AO	Kil	133 (66.71±59.67)	1.5
AO	Num	86 (43.14±40.76)	1.5
AO	Oka	149 (74.37±66.75)	1.5
AO	Qog	204 (101.85±73.73)	1.5
AO	Rom	208 (104.1±71.11)	1.5
AO	Tar	219 (109.45±77.85)	1.5
AO	Tok	214 (107.2±83.58)	1.5
AO	Woo	202 (101.13±79.01)	1.5

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

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**Table A3:** Characteristics of male dominance hierarchies used in this study.

Group	Period	No. of males	No. of conflicts	$h'$	Unknown relationships in %	DC	Two-way relationships in %	Ties in %
AS	1	12	247	0.83	13.6	0.96	6.1	1.5
AS	2	12	361	0.82	12.1	0.93	13.6	0.0
AS	3	11	357	0.94	3.6	0.81	29.1	1.8
AS	4	9	240	0.87	13.9	0.94	13.9	2.8
AS	5	9	164	0.86	8.3	0.92	13.9	2.8
AS	6	9	191	0.97	2.8	0.90	13.9	0.0
AS	7	7	165	1.0	0.0	0.95	14.3	0.0
AO	1+2	11	292	0.9	10.9	0.99	1.8	1.8

Period one and two of the AO group were combined,  $h'$  = corrected Landau's linearity index, DC = Directional Consistency Index.



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## Chapter 3

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# Triadic infant handling serves in bond maintenance in male Assamese macaques

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Behaviour (submitted)

### Abstract

While social bonds among males start to be better understood, the proximate behavioural mechanisms underlying their formation and maintenance have received less attention. We investigated the possible function of male-infant-male interactions (MIMIs) in male-male social bonding processes by analysing over 9000h of focal data collected on two groups of wild Assamese macaques. After engaging in a MIMI upon approach, subordinates stayed longer in close proximity of a dominant male irrespective of the males' affiliative relationship strength. Yet, the overall frequency of MIMIs increased with the strength of the dyadic affiliative relationship between males, suggesting that MIMIs function in relationship maintenance. We did not find support for a role of MIMIs in bond formation as the frequency of MIMIs did not affect the time a male dyad spent in proximity in the following year. Our results contribute to the general topic on behaviours influencing social dynamics in group living mammals.

## Introduction

The benefits associated with the formation of close affiliative relationships in gregarious species range from selective tolerance for access to resources (Huchard et al., 2010; Braun and Bugnyar, 2012), to coalition formation (Pope, 1990; Langergraber et al., 2009; Schülke et al., 2010; Fraser and Bugnyar, 2012), to cooperative hunting (Stander, 1992; Boesch, 1994), protection against harassment (Borgeaud and Bshary, 2015), food sharing and mating access (Cords, 1997; van Schaik and Aureli, 2000). This may lead to buffering against social and environmental stressors (McFarland and Majolo, 2013; Young et al., 2014a), and ultimately to increased reproductive success and longevity (Frère et al., 2010; Schülke et al., 2010; Silk et al., 2010b; Brent et al., 2013; Archie et al., 2014). Thus, the development of close affiliative relationships with specific group members may be an adaptive strategy in both, the philopatric and the dispersing sex as well as between sexes (van Schaik & Aureli, 2000; Silk, 2007a; Ostner and Schülke, 2014). In some primate species affiliative relationships are highly differentiated among group members (e.g. bonnet macaques, *Macaca radiata*, Adiseshan et al., 2011; yellow baboons, *Papio cynocephalus*, Silk et al., 2006b; bonobos, *Pan paniscus*, Hohmann et al., 1999; female black howler monkeys, *Alouatta pigra*, van Belle et al., 2014) and last over years (e.g. female yellow baboons, Silk et al., 2006a), male chimpanzees, *P. troglodytes*, Lehmann and Boesch, 2009; Mitani, 2009), Assamese macaques, *M. assamensis*, Haunhorst et al., 2016; Kalbitz et al., 2016). Furthermore, the equitability of affiliative relationships is positively associated with their strength (e.g. female chacma baboons, *P. ursinus*, Barrett et al., 1999; grey-cheeked mangabeys, *Lophocebus albigena*, Chancellor & Isbell, 2009; female yellow baboons, Silk et al., 2006a; vervet monkeys, *Chlorocebus pygerythrus*, Borgeaud and Bshary, 2015; male chimpanzees, Mitani and Watts, 2001). Close, stable and equitable relationships are labelled as social bonds (Ostner and Schülke, 2014).

The evolution of affiliative relationships between males is puzzling since male relationships are generally competitive, aggressive, and intolerant (van Hooff and van Schaik, 1992; Strier, 1994; van Hooff and van Schaik, 1994; van Hooff, 2000). Yet in the past twenty years a few studies on primate male-male relationships in species with male dispersal, revealed that males differentiate among group members and engage in reciprocal affiliative interactions and thus form social bonds (e.g. Barbary macaques, *M. sylvanus*, Young et al.,

2014b; Assamese macaques, Kalbitz et al., 2016; bonnet macaques, Silk, 1994; Costa Rican squirrel monkeys, *Saimiri oerstedii*, Boinski, 1994; chimpanzees, Mitani, 2009).

The structure, stability, and benefits of social bonds among males start to be better understood, whereas the behavioural, physiological and cognitive mechanisms underlying the formation and maintenance of bonds have received less attention. Close spatial proximity is the basic precondition to engage in exchanges of affiliative interactions and is regarded as an important component of relationship quality measures. Given the strict hierarchical social structures in most mammal groups (e.g. wolves, *Canis lupus*, Peterson et al., 2002; non-human primates, de Waal, 1986; Schino, 2001; Kapsalis, 2004; Ostner et al., 2008; elephants, *Loxodonta africana*, Archie et al., 2006a) low ranking individual often face a risk when approaching high-ranking individuals. Therefore, several behavioural patterns including facial expressions, vocalizations, body postures and gestures have evolved to appease the social counterpart (e.g. Maestripietri, 1997; Fischer and Hammerschmidt, 2002; Tomasello and Zuberbühler, 2002; Liebal et al., 2004; Maestripietri, 2005; Call and Tomasello, 2007; Gros-Louis et al., 2008). Appeasement can also be achieved by using infants as a “social tool” to reduce the risk of aggression from higher ranking males as observed in several cercopithecine species (macaques: Ogawa, 1995c; Zhao, 1996; Bauer et al., 2013; *Papio spp*: Ransom and Ransom, 1971; Busse and Hamilton, 1981; geladas, *Theropithecus gelada*, Dunbar, 1984). In male-infant-male interactions (hereafter MIMIs), the interaction between two males is mediated by the infant in the sense that upon approach both males focus their attention and actions on the infants by lifting the infant, teeth-chattering at it, uttering appeasing vocalisations like “grunts” and “girneys” (Blount, 1985; Fischer & Hammerschmidt, 2002), pulling on arms and legs, or inspecting its genitals during which males may make body contact themselves that may last beyond the duration of the MIMI (Deag and Crook, 1971; Deag, 1975; Ogawa, 1995a). The contexts in which males engage in MIMIs seem to differ between species (Paul et al., 2000). In baboons (Ransom and Ransom, 1971; Busse and Hamilton, 1981) and geladas (Dunbar, 1984) infants are typically handled by males during agonistic encounters, whereas MIMIs (“bridging behaviour”, Estrada and Sandoval, 1977; Ogawa, 1995b), “triadic infant interaction”, Taub, 1980) in macaques occur mainly in affiliative contexts (e.g. Barbary macaques, Deag and Crook, 1971; Deag, 1980;

Taub, 1980; Stumptail macaques, *M. arctoides*, Estrada and Sandoval, 1977; Tibetan macaques, *M. tibetana*; Ogawa, 1995b).

MIMIs have been suggested to function as “agonistic buffers” between two adult males reducing the likelihood of subordinates to receive aggression from a higher ranking male when in close proximity (Deag and Crook, 1971; Deag, 1980; Smith and Peffer-Smith, 1982; Paul et al., 1996; Kuester and Paul, 2000). Accordingly, MIMIs increase the chance of being in close proximity with a higher ranking male and with it the likelihood of engaging in affiliative contact (Ogawa, 1995a). Regulating proximity via MIMIs may therefore not only buffer males against aggression, but may also shape male-male affiliative relationships via initiating and/or maintaining social bonds (Kuester and Paul, 1992; Paul et al., 2000; Berghänel et al., 2011a). To better understand the proximate mechanisms involved in bond formation and maintenance we studied MIMIs in wild adult male Assamese macaques, a species in which some dyads of males form strong, long lasting affiliative relationships (Kalbitz et al., 2016) and rank-changing coalitions (Schülke et al., 2010). In our study, we first examined whether the occurrence of a MIMI had a positive effect on the time a subordinate spent in close proximity to a dominant male after an approach and how this effect may be modulated by the strength of the affiliative relationship between the males involved. We further predicted that if MIMIs function to maintain close affiliative relationships, the frequency of MIMIs should increase with the strength of the males’ affiliative relationship. To rule out that the correlation between MIMIs and relationship strength results from males engaging randomly in MIMIs with males that are spatially close, we controlled our analysis for the time the dyad spent within 5m spatial proximity. Finally, we predicted that if MIMIs function to establish close affiliative relationships, the frequency of MIMIs should predict how much time two males will spend in close proximity in the future.

Thus we addressed questions related to the agonistic buffering function of MIMIs (Ogawa, 1995a) but also consider them as a potential bonding mechanism (Paul et al., 2000). We predicted that if MIMIs only function as an agonistic buffer, time spent in close proximity after an approach should be more strongly affected by the occurrence of a MIMI the weaker the affiliative relationships between the males. In contrast, if MIMIs play a role in relationship formation and/or maintenance, we predicted that this behaviour increases the time two males spend in proximity; irrespective of their relationship strength.

### Methods

#### *Study Site and Subjects*

The study was carried out on two multi-male, multi-female groups of Assamese macaques living in closed, hilly, dense and mostly dry evergreen forest on which is subjected to a long dry and an intense monsoon season (Borries et al., 2002). The study site is located at “Huai Mai Sot Yai” in the Phu Khieo Wildlife Sanctuary (PKWS; 16°5′–35′N, 101°20′–55′E) which is part of the contiguous and well-protected ca. 6500 km<sup>2</sup> Western Isaan forest complex in north-eastern Thailand (Borries et al., 2002). Data were collected almost daily from October 2006 until September 2013 of all adult males of the group AS. On average±SD this group consisted of 51.4±4.7 group members, 13±1.9 adult females and 10.1±1.9 males. From May 2012 until September 2013 data were collected also from the group AO. This group consisted of on average±SD 45.1±2.0 members, 10.6±0.5 adult females and 10.6±0.5 males. The group composition varied due to immigration, emigration and death. Throughout the entire study period 10 different adult males lived in the group AO and 17 different adult males in the group AS. All individuals of both groups were well habituated and individually known by all human observers.

#### *Data Collection*

Using 30 min focal animal sampling, behavioural data were collected on adult male macaques of both groups, yielding a total of 8,954 hours (AS: 7,200 h; AO: 1,752 h). The identity of the focal individuals, their interaction partners as well as the individuals in close proximity (<1.5m) were recorded by using continuous sampling (Martin and Bateson, 2007). All occurrences of affiliative (grooming, body contact, triadic infant handling), submissive (bare teeth, give ground, make room) and aggressive (lunge, slap, chase, push and pull) behaviours as well as durations of body contact and grooming were recorded (Ostner et al., 2008). Agonistic interactions between males other than the focal animal were recorded ad libitum (Altmann, 1974). Instantaneous scan sampling was used to record all individuals within 5m of the focal individual every 10min (Martin and Bateson, 2007).

*Data Analysis*

For the purpose of this study, we calculated dyadic relationship strength (composite sociality index (CSI, Silk et al., 2006b) for one year blocks and defined each block as one observation period from the beginning of the mating season (October) until the end of the following non-mating season (September) (Fürtbauer et al., 2010). The first period of data on group AO spanned over a 5 month period only. The CSI was calculated from hourly rates of six affiliative behaviours (duration of close spatial proximity (DP), body contact (DB) as well as duration of grooming (DG) and frequency of close proximity (FP), body contact (FB) and grooming (FG)) using the formula:

$$CSI = \left[ \frac{\frac{FP_{ij}/h}{\overline{FP}_{ave}/h} + \frac{FB_{ij}/h}{\overline{FB}_{ave}/h} + \frac{FG_{ij}/h}{\overline{FG}_{ave}/h} + \frac{DP_{ij}/h}{\overline{DP}_{ave}/h} + \frac{DB_{ij}/h}{\overline{DB}_{ave}/h} + \frac{DG_{ij}/h}{\overline{DG}_{ave}/h}}{6} \right]$$

(for more details see Kalbitz et al., 2016). By definition the CSI group mean is 1 and the stronger the relationship the higher the CSI.

Additionally, we determined the dominance hierarchy across males for each observation period from decided dyadic agonistic interactions. We used a winner/loser matrix of these interactions (for more details see Kalbitz et al., 2016) to calculate the standardized normalized David's Score (nDS) (DomCalc, Schmid & de Vries, 2013). We used the differences in David's Scores between two males as a measure of rank distances.

To test the effect of MIMIs on immediate proximity time, we counted all observed MIMIs which occurred within the first 3 minutes after a dyad approached or until one male of the dyad departed before the 3rd minute. Therefore, we used a subset of the data where all approaches occurring within the last 3 minutes of the focal protocol were excluded. Descriptive statistic about proximity times and MIMI occurrence are given in the result section.

To assess the impact of MIMIs on the immediate proximity time between two males after a subordinate male approached a male higher in rank, we used a Linear Mixed Model (LMM, Model 1). Time spent in close proximity ( $\leq 1.5m$ ) was set as the response and MIMI as a categorical predictor (two levels, MIMI occurred or not). In order to investigate whether the effect of MIMI on proximity time is modulated by the strength of the males' affiliative

relationship, we added CSI score as a factor as well as the interaction between CSI and MIMI occurrence in the model. Rank distance was included as control fixed factor and the identities of the initiator and receiver, the dyads, the study periods as well as the social groups were included as random factors. To control for diverging observation time for each dyad we incorporated dyadic observation time as an offset term. Dyadic observation time was log transformed to fulfil the assumption of the LMM on symmetric distribution of the factors. For this analysis, we used only the data where males approached other males outranking themselves and we discarded data where both males approached simultaneously or where high ranking males approached lower ranking once.

To investigate whether the CSI affected the frequency of MIMIs we used a generalized linear mixed model (GLMM; Model 2) with a Poisson distribution. The number of MIMIs was set as the response and dyadic CSI values as predictor. We included proximity (time the focal individual spent within 5m distance with the other) as an offset term to create a rate of MIMI per dyad and the time they spent in 5m proximity. We incorporated dyads, male identities, social groups and the observation periods as random factors to control for non-independence of repeated measures across the same individuals within the same periods and the same groups. In addition, we used observation level random effects to account for overdispersion in count data following (Harrison, 2014). Both predictors were power-transformed 0.25 to achieve a normal distribution.

Finally, to test the long-term effect of MIMIs, we used another LMM (Model 3) to test the effect of MIMIs in a given year (predictor) on the time dyads spent in close proximity in the consecutive year (response). Current proximity time and current CSI values were included as fixed factors. Male identities, dyad and group were included as random factors. For this analysis we calculated the time male dyads spent in close proximity ( $\leq 1.5$  m). Here the proximity time following MIMI was not considered.

All models were run in R (version 3.2.2, R Core Team, 2015) using the function 'lmer' of the R package 'lme4' (Bates et al., 2015). We derived the *P* value for each predictor in all three models by likelihood ratio tests using the R function 'drop1' (Barr et al., 2013). To check that the assumptions of the models are fulfilled, we inspected visually the distribution of the residuals plotted against the fitted values (Quinn and Keough, 2002). For all three models the residuals were homogeneously distributed. Furthermore, we calculated for each

predictor the variance inflation factor by using the function “vif” of the R package car (Fox and Weisberg, 2010). VIFs in all our models were below 5 indicating that the collinearity between the predictors was not an issue (Bowerman and O'Connell, 1990). Finally, we checked for model stability by excluding data points one by one from the data and by comparing the estimates derived with those obtained for the full model to check for model stability. All models were stable.

## **Results**

The number of male dyads in each group varied across the years between 21 and 55 (mean  $\pm$  SE =  $39.8 \pm 5.4$ ) due to migration and death. Across the observation periods we recorded in total 919 MIMIs.

### *MIMIs and time spent in close proximity time*

Across all observation periods, 97.1 % of all possible male-male dyads, males approached each other at least once. In total, we recorded 16,550 approaches with an average  $\pm$  SE rate of  $0.22 \pm 0.01$  approaches per hour per dyad. 12.44% of all approaches were followed by a social interaction between the males. Out of the total number of approaches, 2.44% of the approaches were followed by an aggression and 10% (MIMI: 3.69%, grooming: 2.89%, mounting: 2.41%, embrace: 1.01%) by an affiliative social interaction. To test the impact of MIMIs on the immediate time spent in close proximity after the approach, we extracted all approaches where subordinate males approached, which resulted in a subset of 7,015 approaches. Here 13.46% of the approaches were followed by a social interaction; only 2.35% of the approaches were followed by an aggression whereas in 11.11% males engaged in an affiliative interaction (4.21% MIMIs). In Model 1, testing the impact of MIMIs on immediate time spent in close proximity, the interaction between CSI and MIMI was not significant ( $N = 7015$ ,  $t = -0.49$ ,  $p = 0.619$ ). Therefore we rerun the model without this interaction. The new model was significantly different from the null model ( $\text{Chi}^2 = 46.37$ ,  $P < 0.001$ ,  $R^2 = 0.64$ ) and showed that subordinate males who approached a male higher in rank spent significantly more time in close proximity if an approach was followed by a MIMI

(average  $\pm$  SE 186.7  $\pm$  15.94 sec (range: 2 – 1843 sec) than after an approach without a MIMI (average  $\pm$  SE 120.5  $\pm$  2.78 sec (range: 0 – 2524 sec), Table 2.1, Figure 2.1).

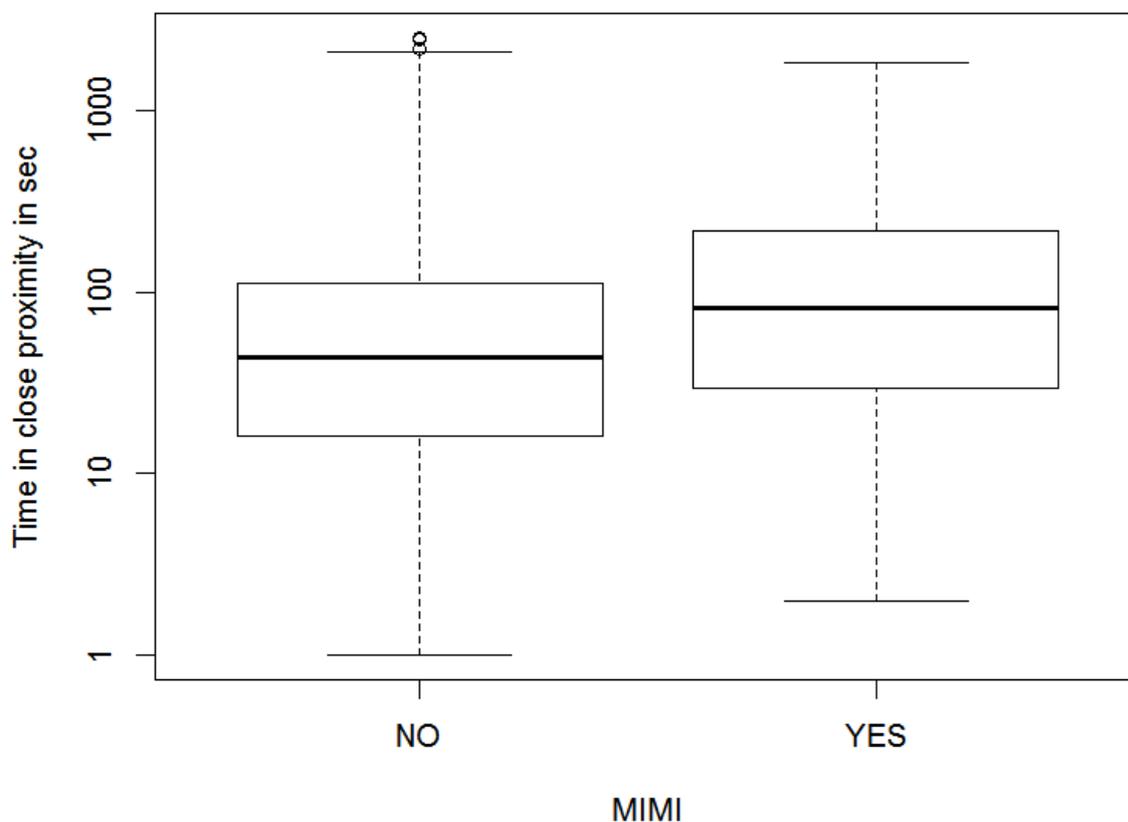
**Table 2.1:** Estimates  $\pm$  SE, Z and P values for the LMM (Model 1) run to test whether MIMI have an effect on current time spent in proximity after a subordinate male approached a dominant male

Predictors	Estimates $\pm$ SE	t	P
Intercept	-3.72 $\pm$ 0.28	-13.14	<0.001
MIMI after approach	0.18 $\pm$ 0.03	6.82	<0.001
CSI	-0.00 $\pm$ 0-01	-0.7	0.521
Rank Distance	0.00 $\pm$ 0.00	0.76	0.654

*Number of Observations = 7015; Number of Dyads = 186*

*Effect of relationship strength on MIMI frequency*

Model 2 was significantly different from the null model ( $\text{Chi}^2 = 85.44$ ,  $P < 0.0001$ ,  $R^2 = 0.39$ ). Dyadic relationship strength positively influenced the occurrence of MIMIs (N = 407 dyads, Model 2, Table 2.2, Figure 2.2). The stronger a relationship was, the more often males engaged in MIMIs. Each dyad handled an infant on average  $\pm$  SE 0.01  $\pm$  0.00 times per hour (range: 0 - 0.24), N = 407) with non-bonded dyads engaging in MIMIs on average  $\pm$  SE 0.01  $\pm$  0.00 times (range: 0 - 0.09, N = 269) and bonded dyads with a  $\text{CSI} \geq 1$  0.03  $\pm$  0.00 times (range: 0 - 0.24, N = 138). On average  $\pm$  SE each male had 4.73  $\pm$  0.26 (range: 0 -9) different MIMI partners which indicates that at least some males were highly selective in their partner choice for MIMIs.

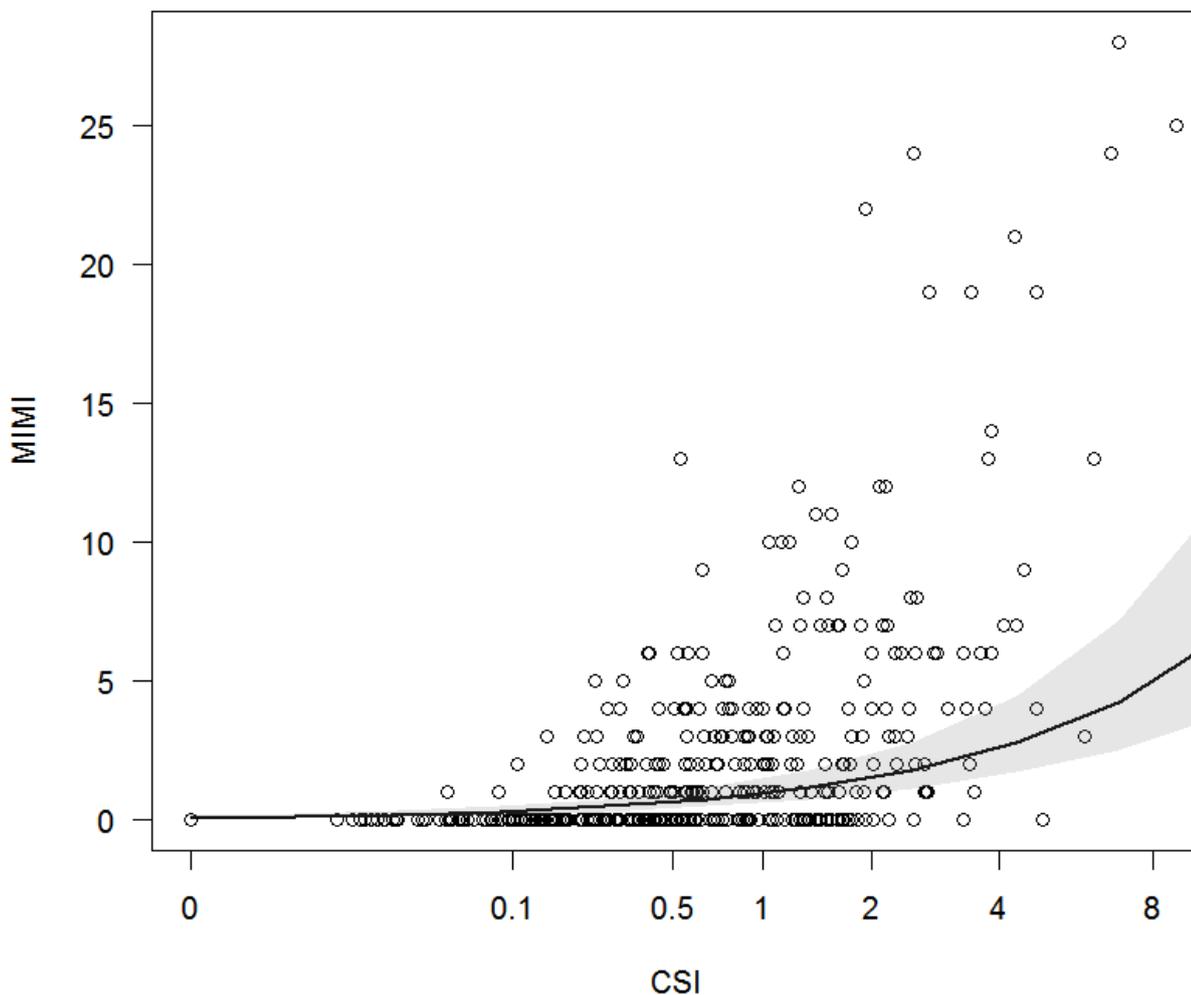


**Figure 2.1** The effect of MIMIs on time two males spent in close proximity after an approach by the subordinate in the dyad. The boxes indicate medians (thick line) and first and third quartiles. The whiskers indicate the 90<sup>th</sup> and 10<sup>th</sup> percentiles. The y-axis is plotted on a logarithmic scale for graphical convenience.

**Table 2.2:** Estimates ± SE, Z and P values for the GLMM (Model 2) run to test whether the strength of the affiliative relationship between two males (CSI) has an effect on how often they engage in MIMIs

Predictors	Estimates±SE	Z	P
Intercept	-4.08±0.37	-11.04	<0.0001
CSI	2.73±0.29	9.12	<0.0001

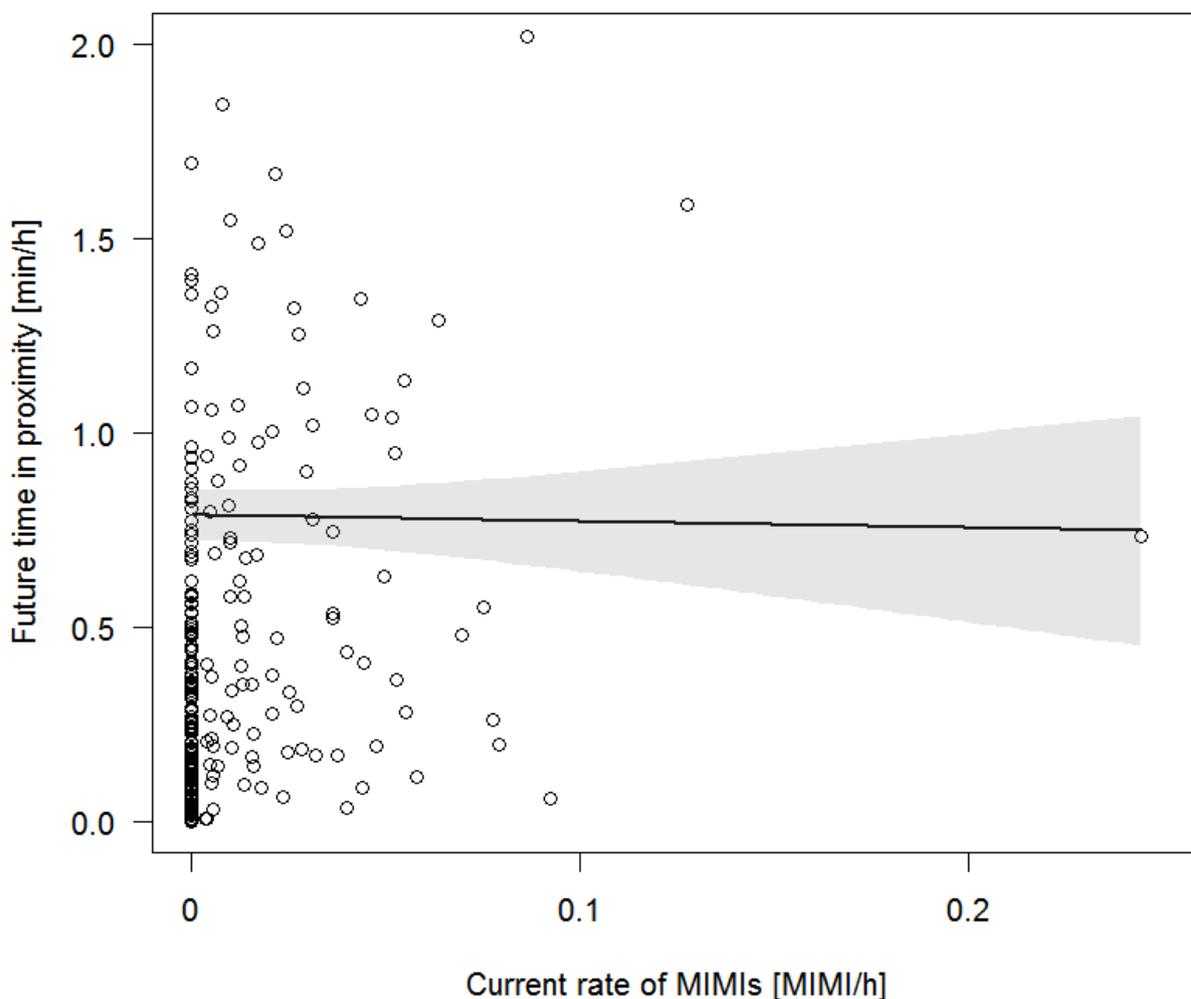
*Number of dyads = 407 across periods. (A dyad can occur in several periods)*



**Figure 2.2:** The occurrence of MIMIs as a function of relationship strength. The black line depicts the relationship between CSI and MIMI as predicted by Model 2. The circles represent the raw data of 407 dyads and the grey area the 95% confidence interval of the model. The x-axis is plotted on a double square root scale ( $\sqrt{\sqrt{x}}$ ).

*Long-term effect of MIMI on future time spent in close proximity*

We found no evidence that the current rate of MIMIs predicted future proximity of a dyad (N = 240, Model 3); Model 3 was not significantly different from the null model ( $\text{Chi}^2 = 0.0862, P = 0.7691, R^2 = 0.37$ ). Our dataset comprised a dyad which appeared as an outlier in that their rate of MIMI was almost twice as high as the rate of all the other dyads (see Figure 2.3). Rerunning Model 3 after removal of the outlier did not change the results.



**Figure 2.3:** The effect of current MIMIs on future proximity. The black line depicts the relationship between current MIMI and future time in proximity as predicted by Model 3. The circles represent the raw data of 129 dyads and the grey area the 95% confidence interval of the model.

### Discussion

The results of our study suggest that wild male Assamese macaques use male-infant-male interactions (MIMIs) to form and in particular to maintain their affiliative relationships rather than solely as an agonistic buffering mechanism. The closer two males were bonded the more often they engaged in MIMIs suggesting that infant handling might serve to maintain social bonds. Handling an infant upon approach to dominant males allowed subordinate males to subsequently spend more time in close proximity to higher ranking males and

possibly increasing the likelihood to engage in other affiliative interactions and thereby strengthening their affiliative relationship.

Our results that MIMIs increase the time male-male dyads spend in close proximity add to the findings of other macaque studies (Taub, 1980; Paul, 1984; Silk and Samuels, 1984; Ogawa, 1995a). Subordinate male Tibetan macaques are more likely to approach males higher in rank if they engaged in MIMIs (Ogawa, 1995a). Although most MIMIs in Tibetan macaques occurred in an affiliative rather than aggressive context, the increase in spatial tolerance is interpreted as reflecting aggression avoidance within the group. Since the MIMI was often followed by grooming (Ogawa, 1995a) the increased time males spent in close proximity after MIMIs might increase the likelihood to engage in other affiliative interactions, which in turn might shape affiliative relationships between males paralleling results of our study. Male Assamese macaques stayed on average up to 50% longer in close proximity to higher ranking males if they engaged in a MIMI upon their approach. Interestingly, this was irrespective of their affiliative relationship strength indicating that every subordinate male had the same beneficial outcome of MIMIs regardless of the relationship they shared with the higher ranking male.

As in other species (e.g. female baboons, Silk et al., 2006b), male chimpanzees (Langergraber et al., 2009; Mitani, 2009), strongly bonded male Assamese macaques spent significantly longer time in close proximity than non-bonded dyads (Kalbitz et al., 2016) and therefore should not need to engage in a MIMI simply to increase their time in close proximity with each other. Interestingly, male Assamese macaques sharing a stronger than average affiliative relationship ( $CSI \geq 1$ ) were about five times more often involved in MIMIs than male-male dyads with a weaker relationship ( $CSI < 1$ ) and relationship strength was positively associated with MIMI frequency even after controlling for the time they spent in 5m spatial proximity. These results, together with the finding that the dyadic frequency of MIMIs influences future cooperation in Barbary macaque males (Berghänel et al., 2011a) support the hypothesis that MIMIs function to form and reinforce male social bonds (Paul et al., 2000). In this sense MIMIs in macaque males may functionally parallel “greetings” exchanged between baboon males that are also proposed as a bonding mechanism enhancing a male’s willingness to cooperate (Smuts and Watanabe, 1990; Paul et al., 2000; Whitham and Maestriperri, 2003).

Our results do not provide direct support for the idea that MIMIs function also in bond formation. We found no evidence that current MIMIs predicted the time two males spend in close proximity in the future, which may have been caused by the long-term stability of male relationships in our dataset. Throughout the study period we did not observe adult males immigrating into our study groups. Thus the relationships among males may have had established before the onset of the study. Therefore, we cannot rule out a role of MIMIs in bond formation especially since we found an effect of MIMIs on immediate proximity time even for non-bonded individuals which would be the pre-condition for establishing new bonds.

Having a closely bonded male partner might be an important factor enhancing male Assamese macaques' fitness. Males of this species form coalitions with closely bonded partners to attain and maintain high social status which in turn regulates their paternity success (Schülke et al., 2010; Sukmak et al., 2014). Yet the opportunity to bond might be limited in Assamese macaques since a male approach any other male on average only 0.22 times per hour and only 10% of these approaches are followed by an affiliative social interaction. A male's time budget and its ability to devote time to establish and maintain affiliative relationships with other males is restricted by time devoted to other activities such as bonding with females (Goffe et al., 2016; Haunhorst et al., 2016) and infants (Palombit, 1999; Palombit et al., 2000; Minge et al., 2016; Kubenova et al., 2016), sexual consortships (Bercovitch, 1983; Weingrill et al., 2003; Ostner et al., 2011; Girard-Buttoz et al., 2014; Schülke et al., 2014) and foraging (Dunbar, 1992; Kurup & Kumar, 1993; Menon & Poirier, 1996). In light of these time constraints, males should optimize the little time they can afford to invest in bonding. In this respect, MIMIs might be more efficient than grooming. Grooming is an important affiliative bonding behaviour in primates (reviewed in Sussmann & Garber, 2004) and has been often used as the main measure of the strength and the quality of dyadic relationships (e.g. Silk et al., 2006b; Mitani, 2009; Surbeck & Hohmann, 2015; Kalbitz et al., 2016). Yet, quantitative data suggest that MIMIs might be as important as grooming in the bonding of male Assamese macaques since a similar percentage of approaches are followed by grooming (2.89%) or MIMIs (3.69%). Grooming is time consuming and is a directional behaviour. In contrast, MIMIs are brief contact behaviours with no specific directionality and might, therefore, serve as an appropriate additional

behaviour to maintain affiliative relationships by alleviating the constraints related to reciprocity needs.

Similar to grooming, the effect of MIMIs on bonding may be mediated by underlying neurochemical mediators like endorphins or oxytocin (Machin & Dunbar, 2011; Crockford et al., 2013; Crockford et al., 2015). The hormonal release of oxytocin alleviates stress but also increases prosocial behaviour and enhances trust between individuals, thereby enhancing the bonding process (Heinrichs et al., 2009; Olf et al., 2013). Similarly, affiliative physical contact such as grooming leads to an endorphin release followed by an activation of the neural reward system in association with a feeling of pleasure (Curley and Keverne, 2005; Machin & Dunbar, 2011). Due to rapid degradation of endorphins individuals are motivated to continue engaging in social contact leading to the maintenance and reinforcement of affiliative relationships (Machin & Dunbar, 2011).

Such a possible increase of partner-specific positive emotions might constitute a bookkeeping system which triggers future affiliative (e.g. MIMI, grooming) and cooperative interactions (e.g. coalitions) with specific partners (Uvnäs-Moberg, 1998; Aureli and Schino, 2004; Schino and Aureli, 2009; De Dreu, 2012), thereby maintaining and strengthening affiliative relationships over time.

To conclude, MIMIs so far were mainly linked to the agonistic buffering hypothesis stating that MIMIs enables subordinate males to approach males higher in rank. Paul et al. (2000) suggested the possible influence of MIMIs in male-male social bonding. In accordance with this notion, the results of our study show that MIMIs might be an important behavioural mechanism in male Assamese macaques that functions on a proximate level with an increase in proximity time as well as on an ultimate level to establish and maintain social bonds and thereby enhance immediate and future benefits.

### **Acknowledgements**

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## Chapter 4

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### General Discussion

The overall aim of this thesis was to investigate three characteristics of social bonds among dispersing males by studying adult males of two wild groups of Assamese macaques. As an important note beforehand, the use of a mixture of the terms social bond and affiliative relationship in the literature makes species comparison extremely difficult. In my thesis I apply to the term “social bond” if an affiliative relationship between two individuals fulfil the following three characteristics (suggested by Mitani, 2009; Ostner and Schülke, 2014; Silk et al., 2010a):

- relationships are differentiated among group members in a way that partner preferences arise and
- an increase in affiliative relationship strength leads to an increase in equability in the exchange of service and
- an increase in affiliative relationship strength leads to long-term partner stability.

I assessed whether these characteristics of social bonds apply to male Assamese macaques. First, I investigated whether male-male affiliative relationships are differentiated among male-male dyads (**Chapter 2**). I looked at the exchange of grooming within dyads and whether the short-term grooming equability was driven by the strength of male-male affiliative relationships (**Chapter 2**). Most importantly, in the same study, I shed light on the stability, the most crucial component (and so far the most understudied) of social bonds in the dispersing sex, by examining partner stability among males using a long-term data set (**Chapter 2**). In my third chapter, I investigated male-infant-male interactions (MIMIs), a specific behaviour which has been little studied in the context of social bonding but which may play an important role in the formation and maintenance of social bonds in male Assamese macaques (**Chapter 3**).

In the following general discussion, I will first give a summary of my main findings (section 4.1). I will then discuss more broadly the pattern of male-male relationships and compare them to variation in affiliative relationship strength found in the philopatric sex (section 4.2.1). Further, I will discuss the second characteristic of social bonds: the exchange of commodities between males depending on the affiliative relationship they share. Here I will compare my results to findings from studies on individuals from the philopatric but also from the dispersing sex and highlight some factors which might shape the differences (section 4.2.2). In section 4.2.3, I will place my finding in a general context by examining our

current knowledge about the stability of social relationships across mammals. In section 4.3, I will discuss the proximate mechanisms involved in bond formation and maintenance in male Assamese macaques and briefly their possible underlying physiological mechanism. After, I will present some benefits that individuals gain from having social bonds (section 4.4). In the last section (4.5), I will conclude my results and propose ideas of future research for our general understanding of male-male relationships. In particular, I would like to encourage studies on how an individuals' decision to interact with partners is affected by social relationship status and partner availability.

#### **4.1 Result summary**

In **chapter 2**, I assessed three characteristics of social bonds (Mitani, 2009; Silk et al., 2006a; Silk et al., 2006b; Silk et al., 2010a; Silk et al., 2013) and could show that male Assamese macaques form and maintain strong social bonds with specific male partners. First, I examined the pattern of male-male affiliative relationships by using the composite sociality index (CSI, Silk et al., 2006b). I found a highly skewed distribution of relationship strength among male dyads indicating a strong variation in the frequency and duration of close proximity, body contact and grooming across the different male dyads. The majority of male-male affiliative relationships were weak (i.e. they had below average rates and duration of affiliative interactions) and 34% of dyads shared an above average affiliative relationship (CSI  $\geq 1$ ). Weaker affiliative relationship had higher rank differences compared to stronger bonded male dyads.

Secondly, I investigated the symmetry of grooming exchanges and its link to male-male relationship strength. Over the whole study period, only 47% of all possible male-male dyads engaged in grooming interactions. This alone shows relatively strong grooming partner selectivity among male Assamese macaques. Partner identity did not only play a role in the decision to groom or not but also for short-term reciprocity of grooming since the likelihood that grooming was directly reciprocated within a dyad was higher the stronger the affiliative relationship was between two males. Further, I found that in all grooming bouts, in which grooming was reciprocated (i.e. individual A groomed individual B and then B groomed A within the same bout), the reciprocation of grooming time within a grooming

bout was more balanced the stronger a relationship was. I found, the same result regarding differences in dominance rank between the two grooming partners (i.e. the smaller the rank distance of the grooming partners was the more equitable was their immediate grooming exchange). In addition, close proximity was more equally initiated by each male within male-male dyads who shared a stronger affiliative relationship compared to dyads sharing a weaker affiliative relationship.

Finally, I assessed the third characteristic of social bonds by investigating the long-term stability of affiliative relationships. At the group level, the pattern of dyadic male-male relationships strength was stable over seven years. Due to emigration, death and maturation the residence time of adult males varied from one to seven years. Overall, the strength of male-male relationships influenced partner stability. Half of the males kept two of their three favoured partners (i.e. with whom they shared the strongest relationships) over the entire common residence time that they shared. The partner stability was less constant among dyads sharing weaker affiliative relationships, which indicates that males are less selective with males they affiliate less or at least are less consistent in this respect.

In **chapter 3** I investigated whether MIMIs promote social bonding. Here, I extracted all approaches initiated by subordinates and assessed whether MIMIs influence immediate proximity time between two males of a dyad. Subordinate males who did not engage in MIMIs after an approach could stay up to 50% longer in close proximity than without engaging in MIMIs. Interestingly, this was irrespective of their affiliative relationship strength indicating that every subordinate male had the same beneficial outcome of MIMIs regardless of the relationship they shared with higher ranking males.

Further, I investigated the influence of male-male relationship strength on MIMI frequency. Male Assamese macaques sharing a stronger than average affiliative relationship ( $CSI \geq 1$ ) were about five times more often involved in MIMIs than male-male dyads with a weaker relationship ( $CSI < 1$ ). Relationship strength was overall positively associated with MIMI frequency even after controlling for the time they spent in 5m spatial proximity. This results support the hypothesis that MIMIs function to maintain social bonds in male-male dyads. However, my results do not provide direct support for the idea that MIMIs are also involved in bond formation. In fact, there was no evidence that the frequency of current MIMIs predicted the time two males spend in close proximity in the future.

## 4.2 The characteristics of social bonds

In the following three subsections I will discuss three characteristics (i.e. variation in affiliative relationship strength, equitability and stability) of social bonds within the framework of social bond literature.

### 4.2.1 Variation in affiliative relationships strength

Among a wide range of mammalian species, evidence shows that individuals favour some conspecifics over others within a group leading to differentiated affiliative relationships (e.g. dolphins (Connor, 2000); elephants (Moss et al., 2010), giraffes (Carter et al., 2013); feral goats (Stanley and Dunbar, 2013), Eastern grey kangaroos (Carter et al., 2009); yellow and chacma baboons (Silk et al., 2012); spotted hyenas (Holekamp et al., 1997); sperm whales (Gero et al., 2008); chimpanzees (Gilby and Wrangham, 2008; Lehmann and Boesch, 2009; Mitani, 2009). Yet, most of the studies characterise preferences solely on association data and give little insight into dyadic affiliative relationships themselves (Barrett et al., 2012). Furthermore definition and assessment of proximity and association vary dramatically across studies which affect their interpretability and their biological relevance. For instance, female giraffes being several times observed together in the same transect were considered as being close (i.e. associated) even though a transect had a size that “could be fully explored by a vehicle in half a day” (Carter et al., 2009). In another study on giraffes, individuals were considered to be close if they were seen within 500m (Leuthold, 1979). In contrast, a study reporting association data in common marmosets (*Callithrix jacchus*), determines that individuals are close only within a meter (Koenig and Rothe, 1991). Even after accounting for the huge body size difference between marmosets and giraffes, marmosets are still proportionally much closer to each other at 1m distance and have much more opportunity to interact socially with each other (which is necessary to establish an affiliative relationship) than two giraffes 500m from each other (Hinde, 1983).

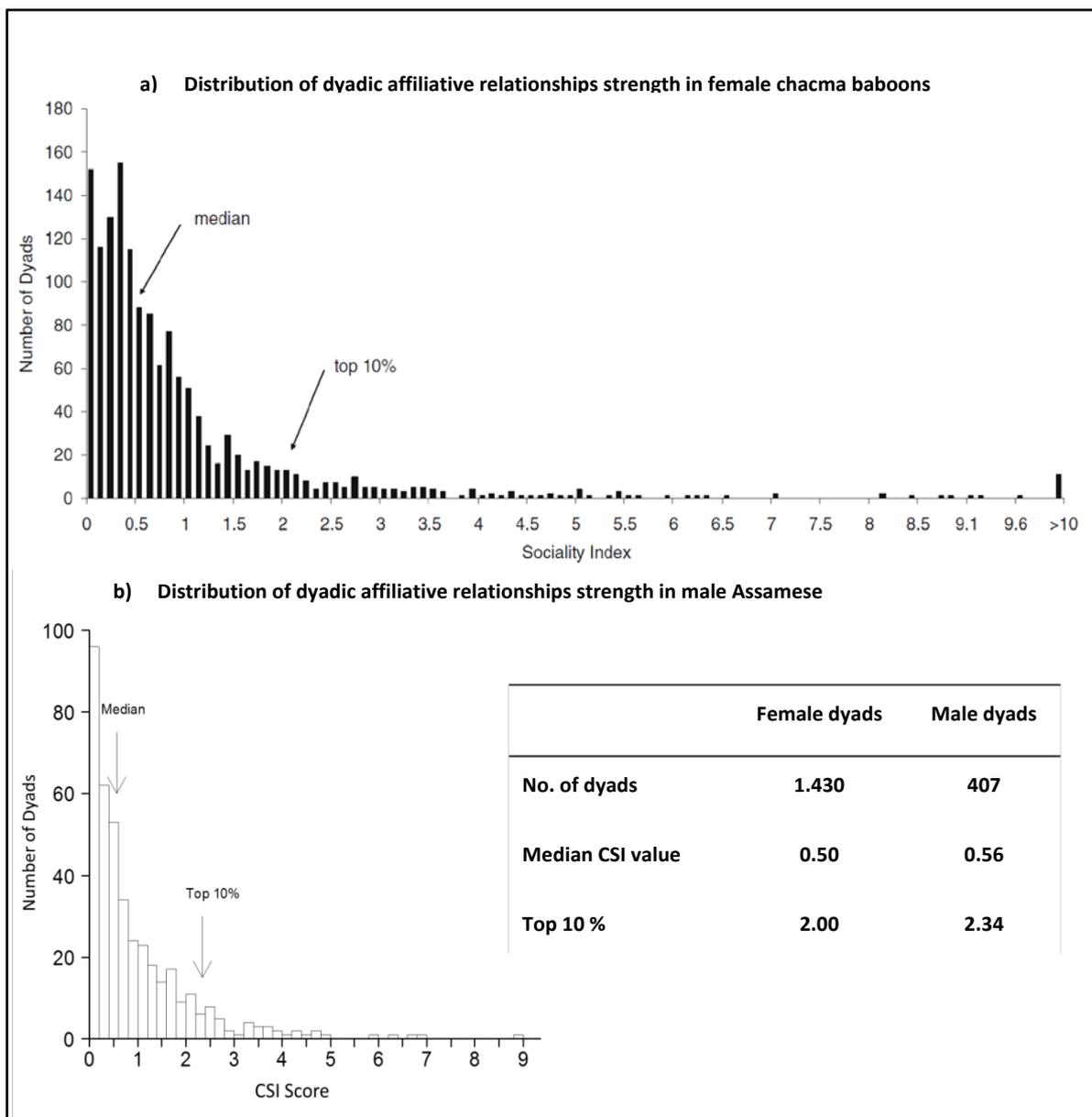
In contrast to using only one behaviour, variation in partner preferences reported in some primate groups is based on a combination of several behaviours suggested to be good indicator of relationship status between individuals (e.g. close proximity, body contact, grooming) (e.g. Tibetan macaques, Adishesan et al., 2011; chimpanzees, Lehmann and

Boesch, 2009; Mitani, 2009; female Assamese macaques, Macdonald et al., 2014; female baboons, Silk et al., 2006b; Silk et al., 2010a). By incorporating different species specific affiliative behaviours (e.g. proximity, huddling, grooming, and embrace) through which individuals are in physical contact and physically interact with each other, one can better pinpoint the behaviours which are essential to establish, maintain and strengthen social relationships. The variation in frequency and duration of those affiliative behaviours determines the strength of an affiliative relationship among individuals. Therefore, by definition, individuals who share a stronger affiliative relationship associate and interact more often with each other than individual who share weaker affiliative relationships (Hinde, 1976; Silk, 2002). To make my study as best as possible comparable to other studies, I used three different factors (i.e. proximity (<1.5m), body contact and grooming) to identify the strength of affiliative relationship among male Assamese macaques.

The majority of studies on social relationships are reported in the philopatric sex. The differentiation of affiliative relationships in male Assamese macaques (**Chapter 2**) closely resembles the distribution found in philopatric females. Both, female baboons and male Assamese macaques show a highly skewed distribution: most of the relationships are weak, a few are strong and only a very minor proportion of dyads have very strong affiliative relationships (Figure D1).

As mentioned in the introduction, in species with female philopatry, dominance rank relationship plays often an important role in female-female relationships due to its link to kinship. In most cercopithecine species the older females of each matriline hold the highest rank position and adult daughters acquire their rank positions right below their mothers (reviewed in Kapsalis, 2004). Thus, females often “inherit” their dominance rank position rather than achieve it through direct physical contest competition. It is therefore not surprising that, the strongest bonds in female baboons are formed between mothers and daughters and between maternal and paternal kin (but to a lesser extend) (Kapsalis, 2004). Those strongly related dyads form coalitions to support each other and strengthen their matrilineal rank positions leading to close affiliation partners being often similar in rank (Chapais, 1992; Kapsalis, 2004; Lea et al., 2014; Silk et al., 2004; Silk et al., 2006b). In philopatric cercopithecine females there is therefore a combined effect of rank inheritance and maternal kinship in explaining the strength of social relationship and it is hard to

disentangle this two factors. The role of kinship in male Assamese macaques is largely unknown but males sharing an mtDNA haplotypes form social bonds as often as males with different haplotypes (Schülke et al., 2010). Male Assamese macaques form stronger affiliative relationships with individuals closer in rank. Yet, the fact that rank is achieved and maintained through coalition formation with strongly bonded partners in male Assamese macaques (Schülke et al., 2010) may explain why strongly bonded individuals eventually end



**Figure D1:** Distribution of CSI values across female chacma baboons (a) and male Assamese macaques (b). CSI is plotted on the x-axis, and the number of dyads is plotted on the y-axis. Each bar indicates the number of dyads with a specific CSI score.

up being close in rank (Schülke et al., 2010). The rank similarity of closely bonded dyads in the philopatric but also in the dispersing sex might therefore be a consequence of the relationship strength itself in macaques (mediated by kinship in female baboons) rather than the cause of relationship formation.

The pattern of highly differentiated affiliative relationships strength that I found in male Assamese macaques was also reported among other males of the dispersing sex (e.g. Bonnet macaques, Adishesan et al., 2011; Silk, 1994; and Barbary macaques, Young et al., 2014b). In addition, even across philopatric male chimpanzees it appears that despite having possibly more kin in the group than male macaques, neither relationship structure nor coalition formation pattern was influenced by kinship (Goldberg and Wrangham, 1997; Mitani, 2009; Mitani et al., 2000). Thus, kinship is not the only driving factor for establishing differentiated affiliative relationship among individuals and the adaptability of affiliative relationships among non-related individuals is rather explained by reciprocal altruism (Trivers, 1971) and mutual benefits gained by both cooperative partners (West et al., 2007, see section 4.2.2).

### *4.2.2 Equitability of service exchanges*

The variation in frequency and duration of the behaviours across dyads lead to a differentiation in dyadic affiliative relationship strength (see above). In turn, the strength of each dyads affiliative relationship influences the reciprocal exchanges of grooming in that the stronger a dyadic affiliative relationship the greater the likelihood that a grooming interaction gets reciprocated (**Chapter 2**) and the stronger an affiliative relationship the more balanced is the exchange of grooming interactions (e.g. female baboons, Silk, 2002; Silk et al., 2010a; male chimpanzees, Mitani, 2009; male bonobos, Surbeck and Hohmann, 2015; male Assamese macaques, **Chapter 2**). Thus, the influence of relationship strength seems to be a good measure for relationship quality (Silk et al., 2013). In male Assamese macaques the stronger the affiliative relationship is the more balanced is the exchange of grooming within a bout, whereas in male bonobos the grooming exchange is the most balanced between males who associate with each other the least often (Surbeck and Hohmann, 2015). These contrasting results might emerge due to the differences in the time-

frame during which males have the opportunity to reciprocate in both species. Given the high degree of fission-fusion in bonobos, males who are associating rarely might need to reciprocate grooming within the same bout since they might end up being apart for periods up to a month (Surbeck, personal communication). In contrast, male Assamese macaques live in stable social group and males have in theory the opportunity to reciprocate any time.

In male Assamese macaques, dyads sharing a stronger than average affiliative relationship, both partners benefit from this immediate reciprocal exchanges (Trivers, 1971; West et al., 2007). The possible release of endorphins and oxytocin while grooming activates the neural reward system associated with a feeling of pleasure (Curley and Keverne, 2005; Machin and Dunbar, 2011). The level of released endorphin degrades fast which might motivate stronger bonded individuals to continue engaging in grooming. This in turn keeps up the level of pleasure (Machin and Dunbar, 2011) and might serve as an update for each partner on the quality of the relationship by demonstrating their commitment to the maintenance of this relationship (van Schaik and Aureli, 2000). It also provides information about the quality of a relationship two males share with other group members (Dunbar, 1993; Dunbar and Sharman, 1984). This balanced exchange in Assamese macaques might motivate and reinsure each partner's willingness to join future coalitions (see section 4.4) and thereby allow for the emergence of long lasting reliable social relationships. This motivation might be much less present in male bonobos who form coalition with each other extremely rarely (Surbeck and Hohmann, 2013).

Overall, grooming can be exchanged for grooming itself but also for other commodities (e.g. access to infants, support in coalitions, tolerance), and it can be exchanged on the short-term but also on the long-term (Schino, 2007; Schino and Aureli, 2008). To which extent the exchange of grooming is reciprocated between stronger or weaker bonded dyads might vary across species depending on the context, the level of grooming partner competition as well as ecological influences.

#### *4.2.3 Partner stability*

Among a wide range of mammalian species, evidence is showing that partner preferences remain stable over month up to several years (e.g. dolphins, Connor, 2000; elephants, Moss

et al., 2010; feral goats, Stanley and Dunbar, 2013; yellow and chacma baboons, Silk et al., 2012; spotted hyenas, Holekamp et al., 1997; sperm whales, Gero et al., 2008; chimpanzees, Gilby and Wrangham, 2008; Lehmann and Boesch, 2009; Mitani, 2009). The comparability across taxa remains limited since most of these studies are based on association data which provides little insight on the dyadic relationships themselves (Barrett et al., 2012). Yet, within primates and cetaceans a comparison can be achieved since partner stability was reported in some species based on spatial proximity and repetitive exchanges of goods and services (e.g. Connor, 2000; Langergraber et al., 2009; Silk et al., 2006a; Silk et al., 2012; Silk et al., 2010a). These repeated exchanges allow for the establishment (see above) but also for long-term maintenance of affiliative relationships (Mitani, 2009; Silk et al., 2006a; Silk et al., 2012). The environment of philopatric living females and males is relatively stable regarding their social partner availability and perhaps also regarding their social dominance rank relationships which facilitates the formation of long-lasting affiliative relationships. Females prefer to be close and to exchange services with kin rather than with non-related females since each investment in a partner has indirect fitness benefits on the female itself (Massen, 2010a; Silk et al., 2006a; Silk et al., 2010b). On the other hand, male chimpanzees favour specific partners over other males regardless of whether the partner is related or not (Mitani, 2009). One reason for forming strong long-lasting affiliative relationships between possibly non-related males as reported for instance in chimpanzees (Mitani, 2009), Barbary macaques (Young et al., 2014b) and Assamese macaques (**Chapter 2**), might be to facilitate the formation of coalitions with reliable partners (Ostner and Schülke, 2014; Silk, 2007b, see section 4.4). Studies on the stability of male-male social bonds in the dispersing sex are rare, possibly because, in the past, researches assumed that strong bonds were unlikely to arise between non-kin.

The existence of social bonds has been reported in a few mammalian species (see above) in the philopatric sex but also in the dispersing sex. In the following paragraph I will discuss some of the proximate mechanisms, which might lead to the formation and maintenance of those special affiliative relationships.

### **4.3 Formation and Maintenance of Social Bonds**

In primates, grooming is an important affiliative bonding behaviour (reviewed in Sussmann & Garber, 2005) and has been often used as the main measure of the strength and the quality of dyadic relationships (e.g. Silk et al., 2006b; Mitani, 2009; Surbeck and Hohmann, 2015; **Chapter 2**). As mentioned in section 4.2.2, the effect of grooming on social bonding may be mediated by underlying neurochemical mediators (e.g. endorphins or oxytocin, Crockford et al., 2015; Machin & Dunbar, 2011) in the sense of motivating each individual to continue engaging in social contact, which enhances trust formation between individuals (Heinrichs et al., 2009; Olf et al., 2013) and thereby enhances the maintenance and reinforcement of affiliative relationships, which in turn enables affiliative relationships to get stable over time (Machin & Dunbar, 2011).

A male's time budget and its ability to devote time to establish and maintain affiliative relationships with other males is restricted by the time devoted to other activities such as sexual consortships (Bercovitch, 1983; Weingrill et al., 2003; Girard-Buttoz et al., 2014; Schülke et al., 2014), foraging (Dunbar, 1992; Kurup & Kumar, 1993; Menon & Poirier, 1996), bonding with females (Goffe et al., 2016; Haunhorst et al., 2016) and infants (Palombit, 1999; Palombit et al., 2000; Kubenova et al., 2016; Minge et al., 2016). Thus, those time constraints might have pushed males to evolve alternative bonding behaviours in order to optimize the time invested in the bonding process.

In a broad range of baboon species (e.g. olive baboons, DeVore, 1962; Ransom, 1981; Smuts and Watanabe, 1990; yellow baboons, Altmann and Altmann, 1970; chacma baboon, Saayman, 1971; guinea baboons, Dal Pesco, 2013; Fischer et al., submitted; Whitham and Maestriperieri, 2003) for instance males exchange ritualized socio-positive behaviours, i.e. "greetings" (Kutsukake et al., 2006), which are proposed as a bonding mechanism enhancing a male's willingness to cooperate (Paul et al., 2000; Smuts and Watanabe, 1990; Whitham and Maestriperieri, 2003). Such "greetings" involve for instance posterior presenting, mounting, and genital touching or hip-touches (Kutsukake et al., 2006). Similar to those "greetings", MIMIs observed in male macaques decrease the likelihood of aggression and increase close spatial proximity (Ogawa, 1995; Paul, 1984; Silk and Samuels, 1984; Taub, 1980; **Chapter 3**) and hence probably also the likelihood to engage in other affiliative interactions (Paul et al., 2000). In Assamese macaques, the engagement in MIMIs was

strongly positively correlated with male-male affiliative relationship strength (**Chapter 3**). The increase in close proximity time for weaker and stronger male-male relationships as well as males' preference to engage in MIMIs with their stronger bonded partners, together with the finding that the dyadic frequency of MIMIs influences future cooperation in Barbary macaque males (Berghänel et al., 2011a) support the hypothesis that MIMIs serve to maintain male social bonds (Kuester and Paul, 2000; Paul et al., 2000). While grooming, greetings and MIMIs may reinforce bond maintenance, I found no evidence that MIMIs enhance bond formation among the male Assamese macaques of my study groups. This might be caused by the long-term stability of male-male affiliative relationships during the study period and by the lack of successful immigrated males in the study groups (**Chapter 3**). The balanced grooming exchange between male dyads sharing a weaker affiliative relationship in bonobos (see section 4.2.2) might indicate that the immediate benefits both partners gain helps to establish social bonds.

It is likely that MIMIs generate a physiological response similar to the one associated with grooming behaviour, which might lead to similar outcomes. Those physiological responses might be partner specific (Crockford et al., 2013) with regard to the male partner but also with regard to the infant. It has been shown that male macaques share close affiliative relationships with specific infants (Minge et al., 2016; Kubenova et al., 2016). Here, the infant might not only be the social tool to avoid aggression by the partner; but it might also trigger the hormonal release of oxytocin in non-bonded male dyads. This hormonal phenomenon might be responsible for the immediate increase of spatial tolerance and hence the increased likelihood to engage in other affiliative interactions. Such a possible increase of partner-specific positive emotions might constitute a bookkeeping system over time, which triggers future affiliative (e.g. MIMI, grooming) and cooperative interactions (e.g. coalitions) with specific partners (Aureli and Schino, 2004; De Dreu, 2012; Schino and Aureli, 2008; Uvnäs-Moberg, 1998), thereby maintaining and strengthening affiliative relationships over time.

Socio-positive behaviours such as grooming, "greetings" (e.g. hyenas, Smith et al., 2011; baboons, Smuts and Watanabe, 1990), MIMIs (e.g. macaques, Ogawa, 1995a; Paul et al., 2000, **Chapter 3**), head rubbing and licking (e.g. lions, Matoba et al., 2013) but also exchanges of different commodities like food sharing (Wittig et al., 2014) might functionally

be similar to grooming and all seem to be involved in the formation, maintenance and reinforcement of affiliative relationships in mammalian species. Socio-positive behaviours seem to have different values. For instance, food sharing in chimpanzees releases more peripheral oxytocin than grooming does (Wittig et al., 2014). Most importantly this release was not limited to exchanges of food between bonded individuals but extended to any type of dyad which leads the authors to conclude that food sharing, a relatively rare behaviour compared to grooming, might have an impact not only on bond maintenance but might also play a crucial role in bond formation (Wittig et al., 2014). To which extend affiliative behaviours are similar or different or might serve only to establish or maintain social bonds in one species, but not in the other, varies across species. Future research should also measure neurochemical mediators of affiliative behaviours to better understand the bonding mechanisms from a physiological perspective.

#### **4.4 Benefits of Social Bonds**

Social bonds might be a strategy to lower the costs and optimize the benefits of group living (Ostner and Schülke, 2014, see **Chapter 1**). Following the criteria I used in my thesis to define social bonds, evidence for these special affiliative relationships among males are found only in male Assamese macaques (**Chapter 2**), Barbary macaques (Berghänel et al., 2011a; Young et al., 2014b) and chimpanzees (Mitani, 2009). Here we have to keep in mind that strong affiliative relationships between related and non-related males occur in other species as well (e.g. Bonnet macaques, Adiseshan et al., 2011; white-faced capuchins, Schoof and Jack, 2014; guinea baboons, Patzelt et al., 2014; dolphins, Connor, 2000) but they do not qualify yet as social bonds according to the criteria I used, mainly because of missing evidence for one or the other characteristic of social bonds. The motivation to form social bonds, in the meaning of its stability, the differentiation of relationship strength across dyads and the equitability might vary across species and sex and so do the resulting benefits, but overall social bonds play an important role on individuals' fitness and well-being (Alberts, 2010).

The main benefits of group living, such as predator protection and territory defence (e.g. Garay, 2009; Mosser and Packer, 2009; Wrangham, 1980), do not require the establishment of social bonds (Alberts, 2010). Neither the dilution effect in large groups

reducing the likelihood for each individual to get caught by a predator, nor does group territory defense require differentiated affiliative relationships. For this group level benefits, being “nice to everyone” without being selective about specific partners might be sufficient to obtain communal coalitionary support. However other benefits can be derived from having social bonds as exemplified by few seminal studies on baboons showing that social bonds enhance for instance longevity and reproductive rate (Silk, 2003; Silk et al., 2010b; Silk et al., 2009).

Several mechanisms can explain those results. The quality of affiliative relationships a given individual has, influences its ability to cope with higher stress levels generated by environmental and social stressors (Crockford et al., 2008; Engh et al., 2006; McFarland and Majolo, 2013). Individuals sharing a closer bond have lower stress levels compared to those individuals who failed to establish a social bond (Crockford et al., 2008; McFarland and Majolo, 2013; Young et al., 2014a). Lower stress levels increase an individual’s well-being, which in turn might increase longevity. In Assamese macaques, high-ranking males (but not low ranking ones) consort females between days and weeks (Fürtbauer et al., 2011a; Ostner et al., 2011), thereby enhancing the likelihood of mating with the female in her fertile phase in this highly seasonal species with concealed ovulation (Fürtbauer et al., 2011a). These consorts appear to translate into higher reproductive success for high ranking males (Schülke et al., 2010). Thereby, achieving a high rank is a mandatory road towards fitness benefits for male Assamese macaques. In order to achieve higher rank positions, males form coalitions to outcompete other males, thereby rising in rank while limiting the fitness costs. Like in male chimpanzees (Foster et al., 2009), physically weaker male Assamese macaques might gain higher dominance rank position than physically stronger males through the formation of risky rank-changing coalitions (Schülke et al., 2014). To hold this higher rank position, further coalitions with the same specific and not a random partner might be needed in order to increase the insurance that the partner will be supportive in case of conflict (Ostner and Schülke, 2014; Young et al., 2014b). Individuals who reciprocate affiliative interactions regularly are more likely to form coalitions together (e.g. male chimpanzees, Gilby et al., 2013; Muller and Mitani, 2005; Seyfarth, 1977; Silk, 2003; male Barbary macaques, Berghänel et al., 2011a; Young et al., 2014b). Hence, the balanced grooming exchanges, the repetitive engagement in MIMIs as well as repetitive coalition formations of strong bonded

partners, might act as a feed-back loop on each other and ultimately built up and update the reliability of a coalitionary partner (van Schaik et al., 2006). The increase of reproductive success via coalition formation with specific bonded male partners has also been reported in non-primate species, for instance in dolphins (Connor, 2000; Connor et al., 1992).

In chimpanzees, females preferably disperse with closely bonded individuals (Lehmann and Boesch, 2009) and in white-faced capuchins dyads shared slightly stronger affiliative relationships in the group in which they immigrated if they previously engaged in parallel dispersal (Schoof and Jack, 2014). Both observations highlight the potential benefit of a previous relationship history prior to dispersal. So far little is known about the migration pattern of wild Assamese macaques. I can therefore only speculate about the benefits social bonds might have in male dispersal. After my study period, immigrations of young sub-adult male Assamese macaques were, so far, only successful if a team consisted of several sub-adult and juvenile males entering the group jointly. In cases where young males tried to immigrate on their own, they were badly injured by resident males and had to leave again. Here, a group of young males can support each other when entering a new group, which is not an option for a young male trying to enter a group on his own (primary dispersal). In lieu, old adult males did not have serious problems to immigrate into a new group (secondary dispersal) in that they hardly received physical aggressions. To me, this suggests the possibility that adult males who leave their current group might observe neighbouring groups for “familiar” males with whom they shared a strong affiliative relationship in earlier days in a common group. Males don’t have just one bonded partner but rather 2 or 3 (**Chapter 2**). A former history of two males might facilitate the immigration in a new group in terms of that the “newcomer” male who shares a previous history with a resident male of the new group, is more likely to be tolerated by the “known resident” male and hence might get closer to other resident males without receiving life threatening aggressions from residents compared to an immigration of a lonely sub-adult male who does not have such a common history. To better understand a possible link between social bonds and male dispersal, more demographic as well as genetic data on relatedness are needed.

Survival, enhanced reproductive success and longevity are some of the main forces which shaped the evolution of social bonds in primates. Whereas evidence is showing the importance of social bonds in some primate species, comparable data in other mammalian

species is mainly missing. In the latter taxa, the benefits reported are mainly related to group living as a whole (see **Chapter 1**). The social brain hypothesis posits that complex social structures require large and complex brains and due to our close relatedness to non-human primates we assume that they are more socially complex than other mammalian species. Several other species establish stable groups, show partner preferences, form coalitions, reconcile and recognize third party relationships and hence might be more complex than we think (reviewed in Silk, 2007a).

### 4.5 Conclusion and future research

The high level of competition over fertile females, the low level of co-residency of males and the common male dispersal in mammals, all hamper the likelihood of affiliative relationships among males (Greenwood, 1980; Isbell and van Vuren, 1996; Silk, 1994; van Hooff and van Schaik, 1992). In multi-male multi-female groups where the number of co-resident males is low, physical power asymmetry in males is large and/or high fluctuation of males in the group, the contest potential is high and fertile females are mainly monopolised by higher ranking males, which makes the investment to form social bonds among males unlikely (e.g. chacma baboons, Henzi and Barrett, 2003; mandrill, Setchell and Wickings, 2005). In species with a larger number of males within a group, less fluctuation of males and a lower contest potential, it can be beneficial for males to invest in social bond formation to increase their reproductive success (e.g. dolphins, Connor, 2000; Assamese macaques, Schülke et al., 2010; Barbary macaques, Young et al., 2014b). Building up a reliable long-term partner helps males to engage in repetitive coalitions to gain direct and future benefits (reviewed in Ostner and Schülke, 2014).

In this thesis I could provide empirical evidence that males of a female philopatric species form long-lasting social bonds equivalent to the bonds formed among philopatric individuals. It has been shown that social bonds are beneficial but the formation and maintenance takes time and might reduce feeding time or even mating opportunities (Dunbar, 1991). In my thesis I could show a proximate behaviour other than grooming that might have a similar influence on bond maintenance. This result adds to our understanding of the behavioural mechanisms involved in bond maintenance and possibly bond formation

in social mammalian groups and contributes to the general debate on which behaviours influence social dynamics in group living mammals.

However, to understand the value and importance of social bonds or how social bonds affect a male's life history, further research is needed. By applying the same criteria and using the same terminologies, species comparison would be facilitated. However, we have to keep in mind that the meaning of time for partner stability in terms of what is considered to be long-term (month, years) might strongly vary depending on species specific life-history traits. Similarly, behaviours might have different values across species which might lead to different outcomes in term of relationship strength calculation.

As a finale note, I will briefly outline some of the possible specific domains where future research could strongly enhance our current view.

*Intervention:* Since it is established that in certain species dispersing males do establish affiliative relationships, the next step is to investigate how males influence/manipulate the affiliative relationships of other males. Several studies on social knowledge in primates show that individuals are able to recognize their own relationship with other individuals but also relationships that exist among others (reviewed in Seyfarth and Cheney, 2012b). It would be interesting to know whether males interfere in socio-positive behaviours of other males based on their own relationship towards both partners. A similar study has been conducted in ravens. Individuals who already formed a tie intervened in affiliative interactions, and the interactions of those who had no ties were the ones which got interrupted and hence were prevented to form an affiliative relationship with a partner (Massen et al., 2014). If such interventions hamper strategically the establishment and maintenance of affiliative relationships in other male dyads or if the disruption results rather from a proximate arousal which is not directly related to a bonding strategy, would be very interesting to investigate.

*Audience effect:* The leverage of individuals can be measured relatively easily when animals form coalitions in agonistic context, since the power asymmetries between the aggressors and the target can be estimated (Berghänel et al., 2011b). It is however a much harder task to measure indirect leverage, whereby the simple presence of a potential supporter might prevent other individuals from aggressing a given target. This situation

might be common in bonobos where mothers support their sons in conflicts but in which the simple presence of the mother in the party might prevent other males from aggressing her son (Surbeck et al., 2011). In male Assamese macaques this could be investigated by monitoring whether grooming invitations or MIMI initiations of a signaller are rejected by the signal receiver when a closely bonded partner of the receiver or the initiator is present. Such audience effects might also influence the vocalizations used during MIMIs. Usually this behaviour is accompanied by appeasing vocalisations like “grunts” and “girneys” (Blount, 1985; Fischer and Hammerschmidt, 2002) but the fact that male Assamese macaques sometimes carry them out silently suggests that such an audience effect might take place in this species.

*Co-immigration:* In some species where males leave their natal groups, males manage long-term associations while migrating together (often called “parallel dispersal or transfer”) (e.g. lions, Packer and Pusey, 1982; squirrel monkey, *S. sciureus*, Mitchell, 1994). During my study the migration level of male Assamese macaques was low which limited our ability to assess the extent to which individuals disperse alone or together. However, since I completed my field work, other researchers have reported regular intergroup encounters, group fissions and migration in the study groups. Building up on my findings that males do form strong long-lasting affiliative relationships future research using direct observations of adult male dispersal could allow to assess whether adult males emigrate with close bonded partners or whether adult males preferably immigrate in groups where males reside with whom they share a common history. To clearly rule out kin among stronger bonded males, genetic analysis to assess relatedness (maternal and paternal) is needed.

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