



Degrees of freedom in social bonds of crested macaque females



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Social bonds between group members affect individual fitness and wellbeing. While the impact of bond strength is well studied, the consequences of bond predictability and equitability are often overlooked. Similarly, whether bonds reflect short-term contingencies and/or long-term social strategies remains understudied. We investigated these questions in female crested macaques, *Macaca nigra*, which display a tolerant social style within a nepotistic hierarchical social structure. We analysed the structure of social bonds by testing whether similarity within dyads (in kinship, dominance and age) predicted the strength, predictability and equitability of bonds. We then tested the value of social bonds by analysing the effect of their characteristics on three fitness-related behaviours: coalitionary support, feeding-in-proximity and aggression. We found that the bond characteristics of females differed substantially from those of other species with comparable data: bonds were of average strength, of moderate endurance and relatively balanced. Stronger bonds were more equitable but less predictable than weaker bonds. Closely ranked females, but not kin or age peers, had stronger, more predictable and more equitable bonds than others. Coalitionary support was not related to any of the bond characteristics, feeding-in-proximity was positively associated with strength and predictability and aggression was positively linked to strength and negatively to equitability. These results highlight the complex picture of the benefits of social bonds in this species. They reflect the degrees of freedom tolerant macaque females can express in their social relationships within their stable social structure, a pattern that may not be given enough consideration in stable nepotistic hierarchical societies. Comparative research is necessary to establish whether these patterns are more general than previously thought or a specific feature of tolerant macaques. Investigating various characteristics of bonds together is paramount to appreciate the dynamics of social relationships and to better understand the social components of fitness.

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Social bonds are positive social relationships among pairs of individuals of the same group (Silk, 2007a; Silk, Cheney, & Seyfarth, 2013). They are defined in a multidimensional space of relationship

qualities such as relative strength, predictability (or magnitude of change over time) and equitability (the balance of social exchanges within a dyad) (Silk et al., 2013; Whitehead, 2008). Variation in these components can affect individual fitness inasmuch as individuals with more numerous, stable or stronger bonds experience enhanced survival, greater reproductive success or improved general wellbeing compared to others (Cameron, Setsaas, & Linklater, 2009; Frère et al., 2010; McFarland & Majolo, 2013; Silk et al., 2010, 2009; Uchino, 2006; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). For individuals, the value of social bonds is also related to the direct or indirect benefits they may

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obtain from daily social exchanges, e.g. in reconciliation after conflicts (e.g. Fraser & Bugnyar, 2011), or for better access to food resources (e.g. Smith, Memenis, & Holekamp, 2007), which ultimately may impact their fitness and wellbeing (Ostner & Schülke, 2014; Silk, 2007a).

To understand the function and value of social bonds, i.e. which benefits can be obtained by forming and maintaining them, it is also crucial to investigate their underlying structure, i.e. the characteristics of the dyads forming certain bonds. In many animal societies, individuals that are similar in terms of genetic relatedness, dominance status, personality, reproductive state or energetic needs are more likely to form strong and enduring social bonds than others (Armitage & Schwartz, 2000; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Godde, Côté, & Réale, 2015; Hirsch, Stanton, & Maldonado, 2012; Seyfarth et al., 2014). Each of these characteristics can be uniquely important in influencing the formation and maintenance of a bond. For instance, although close kin are obvious coalition partners, kin-based coalitionary support may not be advantageous if such kin are low-ranking (Chapais, 2006), in which case establishing a bond with a higher-ranking nonrelative may be more valuable (Schino, 2007; Smith et al., 2010). Similarly, pregnant or early lactating female chacma baboons, *Papio ursinus*, were less likely to become involved in coalitions and, thus, were not reliable cooperation partners for both kin and nonkin (Barrett & Henzi, 2001).

Research on the benefits of social bonds among same-sex adult group members has so far mostly considered how bond characteristics at the extreme positive end of the spectrum, e.g. preferred associates (Frère et al., 2010) or top three partners (Silk, Altmann, & Alberts, 2006a), affect measures of fitness, health or wellbeing. However, animals may have a variety of options for regulating the consequences of bonds. First, establishing and maintaining predictable and/or equitable bonds may bring as many, if not more, benefits as having strong bonds (e.g. the sheer amount of research on cooperation and reciprocity: Nowak, 2006; Trivers, 1971, 2006). In addition, 'weak' bonds within a social network may be as important as 'strong' bonds, inasmuch as weak bonds contribute to stabilizing the overall network or to enhancing the propagation of information or innovation (Bakshy, Rosenn, Marlow, & Adamic, 2012; Granovetter, 1973). Finally, it has been shown that variance in bond strength rather than absolute strength itself predicts fitness (e.g. Barocas, Ilany, Koren, Kam, & Geffen, 2011; Wey, Burger, Ebersperger, & Hayes, 2013). Studies integrating the different dimensions of social bonds simultaneously and on a continuous scale are therefore indispensable for deepening our understanding of the link between sociality and fitness.

Individuals may thus use various social strategies, reflecting certain degrees of social freedom, depending on the social context, the spatial or temporal availability of partners or environmental conditions, even when living in stable organized societies. Consequently, it has been argued that social bonds are likely to be formed and maintained based on contingencies (short-term, opportunistic tactics) rather than, or in addition to, long-term, fixed strategies (Barrett & Henzi, 2006). For instance, female chacma baboons did not sustain constant differentiated relationships with other females over time but changed cyclically between 'brief associations', 'casual acquaintances' and 'constant companionships' in line with food availability in the environment (Barrett & Henzi, 2006). Although this seems rather straightforward in animal societies with a flexible social structure, such as in fission–fusion societies, variation in social strategies has only recently begun to be considered in species with a stable, nepotistic, hierarchical social structure such as those of many primates, hyaenas or elephants (Barrett & Henzi, 2001, 2006; Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009; Ilany, Booms, & Holekamp, 2015; Sick et al., 2014).

Macaques (genus *Macaca*) are an ideal candidate for the investigation of such variation in social strategies. Although they share the same social organization (philopatric females organized in stable, matrilineal dominance hierarchies), the different macaque species are described as more or less socially tolerant depending on the degree of nepotism, power asymmetries, conciliatory tendencies and counter-aggression in social relationships (Thierry, 2007, 2013). Regardless of how such patterns emerged (see van Schaik, 1989; Thierry, 2004), this social variation can be expected to influence the structure and function of social bonds (Butovskaya, 2004; Thierry, 1990). Specifically, when power asymmetries are moderate and the degree of nepotism is weak, as in more tolerant macaques, individuals can interact with diverse partners and develop a great diversity and number of social bonds (Butovskaya, 2004; Cooper & Bernstein, 2008; Duboscq et al., 2013; Thierry, 1990). In contrast, less tolerant macaques are more constrained in their behavioural options and may rely on relatively few strong, predictable and equitable partnerships instead. Thus, the degrees of freedom that individuals have in their relationships within their group could be assessed through the size and diversity of their social network in relation to the influence of dominance and kinship on an individual's social options, or lack thereof (Butovskaya, 2004; Thierry, 1990).

In this study, we aimed to investigate these degrees of freedom and the interplay between the structure and the value of social bonds in wild female crested macaques, *Macaca nigra*, which express a tolerant social style (Duboscq et al., 2013; Petit, Abegg, & Thierry, 1997). Crested macaques live in a relatively predictable and safe ecological environment (low predation risk and abundant food year-round; O'Brien & Kinnaird, 1997) while facing dynamic social conditions, e.g. male migration and hierarchical changes, which are a potential source of social instability in the group (Marty, Hodges, Agil, & Engelhardt, 2015; Neumann, 2013). Females reproduce year-round (Kerhoas et al., 2014), which is another potential source of fluctuation in the amount of time and attention females can devote to their female social partners (Barrett & Henzi, 2001; Bardi, Shimizu, Fujita, Borgognini Tarli, & Huffman, 2001; Brent, MacLarnon, Platt, & Semple, 2013; D'Amato, Troisi, Scucchi, & Fuccillo, 1982). Previous studies on the same population showed that female crested macaques form highly diverse affiliative social networks (Duboscq et al., 2013). In one study, the strength of female–female social bonds was positively linked to predator deterrence, suggesting that strong bonds play a role in enhancing survival (Micheletta et al., 2012). In another, bond strength did not affect the occurrence and frequency of reconciliation, an important conflict management strategy (Duboscq, Agil, Engelhardt, & Thierry, 2014). Nevertheless, other relationship qualities, such as equitability and predictability, increased the likelihood of reconciliation (Duboscq et al., 2014). As such, it seems that social bond characteristics have different values depending on the context of the social benefits to be gained in this species and we would expect females to express many degrees of social freedom in their choice of social partners and the patterning of their social bonds.

Specifically, since macaques form stable, matrilineal, hierarchical societies, kin and adjacently ranked dyads are expected to form the strongest, most predictable and most equitable bonds (Silk, 2007b). However, given the tolerant social style of crested macaques and their expected great degrees of social freedom, we hypothesized that these dyad characteristics would not predict social bond characteristics. To test this hypothesis and to quantify the structure of bonds, we analysed the relationship between three measures of dyadic similarities (relatedness, similarity in age and dominance rank) and three social bond characteristics, namely strength, predictability and equitability. Furthermore, under the

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