Social status drives social relationships in groups of unrelated female rhesus macaques

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Strong social relationships confer health and fitness benefits in a number of species, motivating the need to understand the processes through which they arise. In female cercopithecine primates, both kinship and dominance rank are thought to influence rates of affiliative behaviour and social partner preference. Teasing apart the relative importance of these factors has been challenging, however, as female kin often occupy similar positions in the dominance hierarchy. Here, we isolated the specific effects of rank on social relationships in female rhesus macaques by analysing grooming patterns in 18 social groups that did not contain close relatives, and in which dominance ranks were experimentally randomized. We found that grooming was asymmetrically directed towards higher-ranking females and that grooming bouts temporarily decreased the likelihood of aggression between grooming partners, supporting the idea that grooming is associated with social tolerance. Even in the absence of kin, females formed the strongest grooming relationships with females adjacent to them in rank, a pattern that was strongest for the highest-ranking females. Using simulations, we show that three rules for allocating grooming based on dominance rank recapitulated most of the relationships we observed. Finally, we evaluated whether a female's tendency to engage in grooming behaviour was stable across time and social setting. We found that one measure, the rate of grooming females provided to others (but not the rate of grooming females received), exhibited modest stability after accounting for the primary effect of dominance rank. Together, our findings indicate that dominance rank has strong effects on social relationships in the absence of kin, suggesting the importance of considering social status and social connectedness jointly when investigating their health and fitness consequences.

Strong affiliative relationships can confer important health and fitness-related benefits, including increased reproductive success and longer life spans (reviewed in Silk, 2014). For example, wild female baboons that form strong affiliative relationships (often termed 'social bonds') have been shown to live longer and experience higher offspring survival than females that are more socially isolated (Archie, Tung, Clark, Altmann, & Alberts, 2014; Silk,

Alberts, & Altmann, 2003; Silk et al., 2009, 2010). Similar benefits of affiliative social relationships have been found in rats (*Rattus norvegicus*; Yee, Cavigelli, Delgado, & McClintock, 2008), guinea pigs, *Cavia porcellus* (Hennessy, Zate, & Maken, 2008), rock hyraxes, *Procavia capensis* (Barocas, Ilany, Koren, Kam, & Geffen, 2011), horses (*Equus caballus*; Cameron, Setsaas, & Linklater, 2009), dolphins (*Tursiops* sp.; Stanton & Mann, 2012), and, most robustly, in humans. Indeed, a recent meta-analysis of 148 studies in humans estimated a 50% decreased mortality risk for socially integrated individuals of both sexes, across all adult ages (Holt-Lunstad, Smith, & Layton, 2010). Understanding these substantial effects on fitness requires understanding how affiliative relationships arise. In

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addition, because patterns of social relationships help determine overall group structure (Hinde, 1976; Seyfarth, 1977), such analyses are important for understanding the evolution of group living.

Among species that exhibit female philopatry, in which females remain in their natal social groups after maturity, the most consistent predictors of social bond formation are kinship and dominance rank (Langergraber, 2012; Range & Noë, 2002; Seyfarth, 1980; Seyfarth, Silk, & Cheney, 2014; Silk, 2007, 2009; Smith, Memenis, & Holekamp, 2006; Tiddi, Aureli, & Schino, 2012; Tinsley Johnson, Snyder-Mackler, Beehner, & Bergman, 2014; de Waal, 1991). Preferential bond formation with close kin, when available, probably arises because it maximizes the indirect genetic benefits of affiliative relationships (i.e. opportunity for kin selection: Hamilton, 1964; West-Eberhard, 1975). In turn, preferential bond formation with higher-ranking individuals could be favoured if investing in these females increases levels of social tolerance or rates of social support. In support of this idea, a meta-analysis of 14 different nonhuman primate species found a significant positive relationship between grooming and social support (Schino, 2007; but see Molesti & Majolo, 2015; Schino & Alessandrini, 2015; Silk, Alberts, & Altmann, 2004), although the directionality of this relationship (i.e. grooming leading to social support or social support driving increased grooming) is often unclear (but see Hemelrijk, 1994; Koyama, Caws, & Aureli, 2006).

Understanding the relative impact of dominance rank and kinship in social bond formation is important for two reasons. First, such an understanding would help to disentangle the degree to which the effects of rank and social bonds on health and fitness outcomes are independent. Studies of the effects of social status in female primates have tended to produce mixed results (Abbott et al., 2003; Pusey, 2012), with the strongest relationships often identified in captive settings in which females are not housed with kin (Abbott et al., 2003; Gust, Gordon, Hambright, & Wilson, 1993; Michopoulos, Higgins, Toufexis, & Wilson, 2012; Michopoulos, Reding, Wilson, & Toufexis, 2012; Muller & Wrangham, 2004; Scott, 2001; Shen & Kern Reeve, 2010). These observations suggest that the absence of kin could exacerbate rank effects in these settings, especially if dominance rank becomes the primary determinant of social relationships. Second, rank effects on social bond formation may account for several emergent features of hierarchical societies. For example, Seyfarth (1977) suggested a simple but highly influential model that showed how preference for higher-ranking individuals, combined with limited resources to invest in social relationships, could explain two common properties of social bonds in female philopatric primates: a correlation between high rank and increased affiliative behaviour, and the existence of strong bonds between adjacently ranked females. Seyfarth's model assumed that all females have the same objective: to invest their limited time budget in giving and receiving grooming by partnering with high-ranking females. However, because grooming is dyadic, and a female's rank may constrain her ability to express her preference, the grooming availability of the highest-ranking females is quickly exhausted. As a result, middle- and low-ranking individuals can only satisfy their preference for grooming higher-ranking individuals by targeting the remaining 'available' females, which will tend to be close to them in the hierarchy (Seyfarth, 1977).

Empirical tests of rank effects on grooming relationships in female philopatric mammals are generally consistent with these arguments (Schino, 2001; Silk, Altmann, & Alberts, 2006; Smith et al., 2006; Tiddi et al., 2012; Tinsley Johnson et al., 2014; de Waal, 1991). However, data interpretation is complicated by the tight correlation between dominance rank and relatedness in female philopatric species. In all species investigated thus far, closely ranked females have also tended to be close relatives, making it difficult to untangle the relative impact of dominance rank versus kinship on social bond formation. Indeed, a 2001 meta-analysis found no significant signature of rank adjacency when kin were excluded from the sample (Schino, 2001), an observation that is interesting but challenging to interpret, given that kin were still available in these groups as potential social partners.

Here, we aimed to investigate the effects of dominance rank on social partner choice in the absence of kin networks. To do so, we focused on behavioural data collected on 45 female rhesus macaques, housed in nine experimentally manipulated social groups (five females per group) that were rearranged in a mid-study intervention to form nine new social groups. None of these groups, either pre- or post-intervention, contained close maternal or paternal relatives, and, prior to group formation, no members of the same group shared any prior social history. We were thus able to observe the emergence of completely novel social bonds in the context of stringently enforced dominance rank hierarchies, which are typical for this species and arise rapidly in newly formed groups (Bernstein, 1976; Bernstein & Gordon, 1974; Bernstein, Gordon, & Rose, 1974). We used this paradigm to investigate four questions: (1) whether grooming was associated with social tolerance, suggesting that high-ranking females are more valuable social partners; (2) whether dominance rank therefore structured the establishment and maintenance of grooming relationships in the absence of kin networks; (3) what rules, including those suggested by Seyfarth (1977), best predicted observed rank-structured grooming patterns; (4) whether an individual's tendency to engage in affiliative social behaviours was primarily determined by rank or by individual characteristics that remained stable across the mid-study intervention.

METHODS

Study Subjects

Study subjects were 45 adult female rhesus macaques (median age at the start of the study = 7.2 years, range 3–20 years) housed in nine social groups of five females each at the Yerkes National Primate Research Center (YNPRC). Groups were initially formed in January–June 2013 using an established protocol (Jarrell et al., 2008; Tung et al., 2012). Briefly, females at the YNPRC Field Station with no shared social history were sequentially introduced to indoor–outdoor run housing (25×25 m for each area) over the course of 2–15 weeks, until all groups included five unrelated adult females (see Supplementary Table S1 for information about individual study subjects). In this paradigm, females introduced earlier tend to occupy higher subsequent dominance ranks (Jarrell et al., 2008; Tung et al., 2012).

The current study was divided into two phases: phase 1 (February 2013–March 2014) and phase 2 (April–December 2014). Starting dates for each group and phase were defined by the date of completion of group formation (after addition of the fifth female into each group: see Supplementary Table S1). Phase 1 groups were formed as described above. Phase 2 groups consisted of the same 45 females included in phase 1, but with females reorganized into new groups. Specifically, groups in phase 2 consisted of females that all shared the same or similar dominance ranks in phase 1 (maximum difference of 1 ordinal rank value; Supplementary Table S1), a strategy that altered the dominance ranks of the majority of the females across the phases (Supplementary Fig. S1). As in phase 1, the phase 2 groups contained unrelated females with no prior social history. In both phases, order of introduction was strongly correlated with dominance rank (Pearson correlation: phase 1: $r_{43} = -0.54$, $P = 1.1 \times 10^{-4}$; phase 2: $r_{43} = -0.68$, $P = 3.4 \times 10^{-7}$).