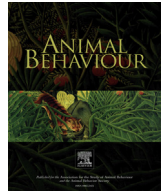




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Social network dynamics precede a mass eviction in group-living rhesus macaques

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Network dynamics can reveal information about the adaptive function of social behaviour and the extent to which social relationships can flexibly respond to extrinsic pressures. Changes in social networks occur following changes to the social and physical environment. By contrast, we have limited understanding of whether changes in social networks precede major group events. Permanent evictions can be important determinants of gene flow and population structure and are a clear example of an event that might be preceded by social network dynamics. Here we examined the social networks of a group of rhesus macaques, *Macaca mulatta*, in the 2 years leading up to the eviction of 22% of adult females, which are the philopatric sex. We found that females engaged in the same amount of aggression and grooming in the 2 years leading up to the eviction but that there were clear changes in their choice of social partners. Females that would eventually be evicted received more aggression from lower-ranking females as the eviction approached. Evicted females also became more discriminating in their grooming relationships in the year nearer the split, showing a greater preference for one another and becoming more cliquish. Put simply, the females that would later be evicted continued to travel with the rest of the group as the eviction approached but were less likely to interact with other group members in an affiliative manner. These results have potential implications for understanding group cohesion and the balance between cooperation and competition that mediates social groups.

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Animals that live in groups are faced with the challenge of balancing the benefits of group living with the costs of conflicting interests between groupmates (Krause & Ruxton, 2002; Silk, 2007). Balancing these costs and benefits may be especially difficult for individuals that live in groups composed of both kin and nonkin (Seyfarth & Cheney, 2012). Much theoretical and empirical research has focused on how individuals may use aggression, social status, cooperation and social bonds to cope with intragroup conflict. Yet a great deal about the origins and maintenance of group living remains unclear (Brent, Chang, Gariépy, & Platt, 2014; Krause & Ruxton, 2002; Nowak, Tarnita, & Wilson, 2010; Shultz, Opie, & Atkinson, 2011). Network dynamics within groups can reveal the processes that underpin the structuring of animal societies and can

uncover information about the adaptive functions of social behaviours and relationships (Berger-Wolf & Saia, 2006; Bode, Wood, & Franks, 2011a, b; Pinter-Wollman et al., 2014). Describing dynamic shifts in social networks and determining when and why these shifts occur is therefore an important route to understanding the maintenance of social groups, and hence the evolution of sociality.

A growing number of studies have documented network dynamics within groups that have followed changes to the physical environment. For example, association networks become more tightly connected when resources are scarce in killer whales, *Orcinus orca* (Foster et al., 2012). This finding is in accordance with the hypothesis that prosocial relationships are more valuable during times of hardship because they help individuals to cope with intragroup competition (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; van Schaik, 1989). In contrast, a negative relationship between network connectedness and the level of resource competition, as measured by

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group size, suggests competition rather than cooperation shapes sociality in wild chimpanzees, *Pan troglodytes* (Lehmann & Boesch, 2009). In sleepy lizards, *Tiliqua rugosa*, the number and strength of network connections do not change in response to changes in climate, although the nature of social connections differs with fewer intersexual associations in drier years (Godfrey, Sih, & Bull, 2013). In contrast, the social networks of some populations do not appear to respond to changes in the physical environment; although guppies, *Poecilia reticulata*, from areas with low levels of predation showed more social mixing than their high-predation counterparts, no changes to social networks occurred within populations following experimental manipulation of habitat complexity or predation risk (Edenbrow et al., 2011).

In addition to changes in the physical environment, network dynamics following changes in social factors, such as reproductive seasonality (Brent, MacLarnon, Platt, & Semple, 2013; Hamede, Bashford, McCallum, & Jones, 2009) and group composition, have revealed important information about social processes. For instance, network dynamics following the simulated, experimental or natural loss of individuals from groups suggests that some individuals are more important to group cohesion than others (Kanngiesser, Sueur, Riedl, Grossmann, & Call, 2010; Lehmann, Andrews, & Dunbar, 2010; Manno, 2008) and can occupy specific social roles (Flack, Girvan, de Waal, & Krakauer, 2006). Following experimental manipulation of the sex ratio of guppy groups, a breakdown in female–female associations in populations with a greater number of males, and hence a greater level of sexual harassment, suggests that repeated social interactions are needed to establish individual recognition between groupmates (Darden, James, Ramnarine, & Croft, 2009). Wild chacma baboon, *Papio ursinus*, females compensate for the death of a close relative by broadening and strengthening their grooming networks (Engh et al., 2006), particularly by extending their social relationships to unrelated groupmates. This apparent compensatory behaviour suggests that social relationships are valuable to female baboons, and provides preliminary evidence regarding the differential value of social relationships with kin compared to nonkin. Finally, changes to social networks have been observed in response to changes in the social hierarchy. The grooming networks of female chacma baboons were less diverse in the weeks following a period of instability in the alpha male position in their group (Wittig et al., 2008). Females that contracted their grooming networks the most showed a less dramatic rise in faecal glucocorticoid metabolite levels and returned to baseline levels more quickly (Wittig et al., 2008). Taken together, these findings suggest that affiliative bonds with a small number of preferred partners help these animals to cope with social instability.

Network dynamics not only occur in response to changes to the environment but also may precede or even provoke such changes. Understanding the links between network dynamics that occur in advance of shifts in the physical or social environment can therefore also have important implications for our understanding of social processes and relationships, and may even allow scientists to predict the occurrence of major events. Instances where we might expect network dynamics to occur in advance of social or physical perturbations include: seasonally predictable changes in climate or resource abundance; the joining/splitting of subgroups in species with high levels of fission–fusion sociality (Sueur & Maire, 2014); large outbreaks of intragroup aggression; and the dispersal, death (i.e. in cases where death is preceded by a gradual decline in condition) or permanent eviction of groupmates. However, few studies have documented network dynamics prior to major events because the occurrence of these events can be difficult to anticipate and studies of this nature must often rely on coincidental collection of behavioural data.

Here we evaluated network dynamics preceding the permanent mass eviction of many females from a group of rhesus macaques, *Macaca mulatta*. Rhesus macaques, like many primates, live in social groups composed of multiple adult males and females (Thierry, 2007). Females are the philopatric sex and membership of females in rhesus macaque groups is ‘closed’ (i.e. females do not disperse in/out of groups; they must be born into them). Nevertheless, rhesus macaque groups are characterized by a mixed relatedness structure, containing both related and unrelated females (Brent, MacLarnon, et al., 2013; Missakian, 1972). Affiliative relationships are often the strongest and most stable between kin, but social bonds between unrelated females are also common (Beisner, Jackson, Cameron, & McCowan, 2011; Cheney, 1992). In addition to high rates of affiliative interactions, social life in female rhesus macaques is characterized by high rates of aggression that is unidirectional (i.e. aggression is typically directed from high- to low-ranking animals) and that occurs within strict, linear and relatively stable dominance hierarchies (Datta, 1988). Females inherit the rank immediately beneath their mother and thus closely related females tend to be of similar dominance rank (Brent, Heilbronner, et al., 2013; Missakian, 1972). Permanent evictions of females have been documented in this species but are rare (Chepko-Sade & Sade, 1979; Ehardt & Bernstein, 1986; Widdig et al., 2006). Because of the relatively stable social structure that characterizes female rhesus macaque life, it is reasonable to assume that social markers of instability would be detectable prior to a mass eviction, but this has not yet been described.

The eviction that is the focus of this study occurred in a group of 55 adult females from three separate ancestral lines and resulted in the removal of the 13 highest-ranking females. We examined the aggression and grooming networks of all adult females during two periods preceding the eviction, the year immediately before the eviction (2011) and the year before that (2010). We determined whether network dynamics occurred in advance of the eviction by examining three aspects of social networks: (1) the rate at which individuals engaged in social interactions; (2) individuals’ choice of social partners and the nature of their interactions with those partners; and (3) the clustering of local subgroups.

METHODS

Study Population and Eviction Event

Our subjects were rhesus macaques living in the semifree-ranging colony on Cayo Santiago Island, Puerto Rico (18°09’N, 65°44’W; Rawlings & Kessler, 1986). Monkeys are provisioned daily at this site with commercial feed and with water supplied ad libitum. There are no predators present. Population control takes the form of annual removal of mostly juveniles. Beyond these measures, the monkeys are free to roam and to self-organize into groups and there is no medical intervention or contraceptive use.

We studied animals in a single social group (‘F’), which at the time of study was the largest of the six groups on the island ($N = 55$ adult females). Group F was made up of three separate female ancestral lines, or matriline, where all females in a matriline are descendants of a single unique female, and where maternal relatedness between members of different matriline is typically zero (Fig. 1). The three matriline were named after their founding females, 065, 004 and 073, which were first documented ranging together in group F over 50 years ago (Caribbean Primate Research Center, n.d.) and varied in size (065: $N = 32$; 004: $N = 17$; 073: $N = 6$). Owing to the linear nature of dominance hierarchies and the maternal inheritance of dominance rank, rhesus macaque matriline can also generally be categorized according to rank: matriline 065 contained the highest-ranking females, females from matriline

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