SOCIAL NETWORKS DYNAMICS PRECEDE A MASS EVICTION IN GROUP-LIVING RHESUS MACAQUES

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ABSTRACT

Network dynamics have the ability to 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 examine the social networks of a group of rhesus macaques (*Macaca mulatta*) in the two years leading up to the eviction of 22% of adult females, who are the philopatric sex. We found that females engaged in the same amount of aggression and grooming in the two 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 discriminant 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 associate with the rest of the group as the eviction approached but were less likely to interact with them in an affiliative manner. These results have potential implications for understanding group cohesion and the balance between cooperation and competition that mediates social groups.

INTRODUCTION

Animals that live in groups are faced with the challenge of balancing the benefits of group living with the costs of conflicting interests between group mates (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 non-kin (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 intra-group 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, 2011; 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 intra-group 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 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 does not change in response to changes in climate, although the nature of social connections differs with fewer inter-sexual associations in drier years (Godfrey, Sih, & Bull, 2013). In contrast, the social networks of some populations do not appear to respond at all to changes in the physical environment; Although guppies (*Poecilia reticulata*) from areas with low levels of predation show more social mixing than their high-predation counterparts, no changes to social networks occur 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 group mates (Darden, James, Ramnarine, & Croft, 2009). Wild chacma baboon (*Papio ursinus*) females compensate for the death of close relative by broadening and strengthening their grooming networks (Engh et al., 2006), particularly by extending their social relationships to unrelated group mates. This apparent compensatory behaviour suggests that social relationships are valuable to female baboons, and also provides preliminary evidence regarding the differential value of social relationships with kin compared to non-kin. 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 who 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 can occur not only in response to changes to the environment but can also 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 intra-group aggression; and the dispersal, death (i.e. in cases where death is preceded by a gradual decline in condition) or permanent eviction of group mates. 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 often must rely on coincidental collection of behavioural data.

Here we evaluate 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 characterised 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 characterises 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: i) the rate at which individuals engaged in social interactions, ii) individuals' choice of social partners and the nature of their interactions with those partners, and iii) the clustering of local subgroups.

METHODS

Study Population and Eviction Event

Our subjects were rhesus macaques living in the semi-free-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-organise 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 matrilines, where all females in a given matriline are descendants of a single unique female, and where maternal relatedness between members of different matrilines is typically zero (Figure 1). The three matrilines were named after their founding females, 065, 004 and 073, who were first documented ranging together in group F over 50 years ago (unpublished, CPRC database), and varied in size (Mat_{065}, n = 32; Mat_{004}, n = 17; $Mat_{073,}$ n = 6). Due to the linear nature of dominance hierarchies and the maternal inheritance of dominance rank, rhesus macaque matrilines can also generally be categorised according to rank: Mat_{065} contained the highest-ranking females, females from Mat_{004} were the next highest in rank (apart from three members of Mat_{065} that were lower in rank than some members of Mat_{004} - two of these females did not to have many close relatives in the group and may have therefore lacked the social support needed to maintain high rank), and Mat_{073} contained the lowest ranking females (Figure 1).

[INSERT FIGURE 1 ABOUT HERE]

At the beginning of 2012, we observed a sudden outbreak of aggression which resulted in the death of the alpha female and the permanent eviction of 12 of group F's highest ranking females (22% of all adult females) (Figure 1). Although we could not collect systematic behavioural data during the aggressive outbreak, we opportunistically recorded cuts and wounds on the bodies of these members of $Mat_{065.}$ The injuries sustained by the alpha female were especially severe and she died two weeks later, presumably from sepsis. The remaining 12 females began to range independently from the group along with their offspring and a few males. First, they ranged separately in two daughter groups then, approximately eight months later, as one consolidated group.

Data Collection

As part of an unrelated study we collected behavioural data on the adult females in group F for two years prior to the eviction during two temporally similar periods: May-December 2010 and April-December 2011. These two periods were divided by a halt in behavioural data collection that takes place annually in the colony. All subjects were individually recognized and habituated to observer presence. We collected a total of 843.70 hours of continuous data using 10-min focal animal samples with means (SD) per individual of 4.07 (0.39) and 5.02 (0.11) hours in 2010 and 2011, respectively. We balanced observations of individuals across time to control for within-daily as well as monthly temporal variation. We recorded all instances of aggression, submissive gestures, and grooming. We used agonistic win/loss interactions to construct dominance hierarchies for the females independently in each year, although female ranks were stable across years. We limited our analyses to females that were present for the entirety of the two years, which excluded a small number of females that died (n = 2) as well as juvenile females that aged into our sample (n = 9).

Social Network Analysis

We used social network analysis to explore social dynamics. Social network analysis is comprised of a suite of statistics that describe various levels of a network: individualized scores that describe properties of a node (e.g. a node's centrality), metrics that describe dyadic interactions (e.g. the probability of an edge between two individuals), and metrics that describe global network properties (e.g. size, shape, connectedness), making it apt at addressing the variation between individuals within a network and between networks at a subgroup, group, population, or species level (Brent, 2015; Krause, James, Franks, & Croft, 2014; Wasserman & Faust, 1994).

To determine whether changes to networks occurred as the eviction approached, we compared the females' grooming and aggression networks from 2010 to those in 2011. We created one grooming and one aggression network for each year, resulting in four networks in total (Figure 2). Edges in these networks represented all observed grooming and aggressive interactions recorded within a given dyad. We treated networks as directed (i.e. the donor and recipients of an interaction are defined) and weighted (i.e. the rate at which a dyad interacted is represented rather than the simple presence/absence of an interaction). For grooming networks, edges were weighted by the seconds per hour of grooming that took place within each dyad; for aggression networks, edges were weighted by the frequency of aggressive interactions per hour per dyad. Within years, our grooming and aggression networks were not significantly related to one another (2010: correlation coefficient = -0.025, p = 0.052; 2011: correlation coefficient = 0.026, p = 0.086) and thus we treat them separately in analyses.

Changes in rates of social interaction. We first determined whether the general tendency for all females to engage in social interactions changed as the eviction event approached by comparing grooming network and aggression network densities across years. We performed this analysis using the paired nodes density function in UCINET v6.588 (Borgatti, Everett, & Freeman, 2002). Assessing changes to network density is an important first step before analysing differences in network structure because apparent structural changes can be brought about by changes to density alone (Brent, Maclarnon, et al., 2013) and so the impact of density on structural changes must be taken into account.

Changes in the identity of social partners and the nature of social relationships. We next explored whether the identity of social partners and/or the nature of social relationships changed in the year nearer to the eviction. Due to the maternal relatedness structure that underpins aggressive and affiliative interactions in this species (Brent, Heilbronner, et al., 2013; Missakian, 1972), we divided females according to their three ancestral matrilines in order to explore changes in social partnerships that occurred within and between related partitions of females. We further divided matriline 065 into two partitions, 'Evicted' and 'Resident' to reflect the fact that the eviction was localised within this matriline and to allow us to examine any social changes that occurred between/amongst these females.

We evaluated the extent to which social interactions were directed within and between partitions in each study period using a joint-count analysis. This procedure starts by calculating the ratio of the observed edge weights that occurred within or between a particular partition(s) and the expected edge weights, which are generated from networks of similar size, density, and for which the edge weights are the median of the observed values. The ratio of observed to expected edge weights therefore describes the extent to which observed edge weights differ from those that would be observed if individuals interacted at random (that is, a model in which our chosen partitions were not meaningful). We then simulated 5000 random graphs in which the edges were reshuffled randomly between nodes (Erdős–Rényi networks). For each permuted network we calculated the observed to expected edge weight ratio. We evaluated the statistical significance of our observed edge weights by determining the proportion of permuted values that met or exceeded the observed value, a technique that is akin to traditional p-values (Croft, Madden, Franks, & James, 2011). We also compared the ratio of observed to expected edge weights across study periods in order to assess how partner choice changed as the eviction approached.

We predicted that the nature of aggressive interactions would change the year nearer to the eviction in a manner that would indicate instability in the dominance hierarchy. We therefore determined if there was greater tendency for females from lower ranking partitions to direct aggression at higher ranking partitions in the year closer to the eviction. We additionally explored changes to aggression within partitions, as instability could also be localised to more closely related females. For affiliative interactions, we predicted that grooming would be more focused onto related partners (i.e. within partitions) in the year nearer the eviction, as an additional indicator of social instability (Beisner et al., 2011) and in accordance with previous findings in Old World monkeys that suggest that kin-based relationships are more valuable during times of hardship (e.g. Engh et al., 2006).

Changes to clustering of local networks. Finally, we determined whether there were changes to the nature of local grooming networks across years. To do this, we compared the mean clustering coefficient for each partition in each study period. Clustering coefficient measures the degree to which an individual's social partners are connected to each other (Newman, 2003). The mean of this measure is therefore an indicator of the degree to which a partition is structured into tightly-knit cliques or clusters. We explored clustering coefficients of the grooming networks only due to the linear, non-triadic, nature of aggressive interactions in this species (Datta, 1988). We calculated a weighted version of clustering coefficient of using the tnet package in R (Opsahl, 2009), which first necessitated converting our directed networks to undirected. We evaluated the statistical significance of observed clustering coefficients in two ways. First, we compared the clustering coefficient of a given partition within each study period to the clustering coefficient derived from a model of random association. To create random models, we generated 5000 (Erdős–Rényi graphs of similar size and density to the observed networks and calculated the mean weighted clustering coefficient in each partition for each permutation. We determined the proportion of these permuted values that met or exceeded observed values as a measure of statistical significance. In order to compare clustering coefficients across partitions, we performed a two-sample bootstrapping test. Here, we took the difference in mean clustering coefficients of the two partitions being compared (either the same partition across years, or different partitions within the same year). Then, we pooled together the clustering coefficients for each female in each partition. We resampled from this pool with replacement sets of equal size 5000 times, and calculated the difference in the clustering coefficients that were generated to create a null distribution. We calculated p-values as the proportion of differences in clustering coefficients between bootstrapped partitions that were more extreme than observed differences. To visualize differences in clustering across years, we generated 5000 random graphs in which the edge weights from a given partition were permuted but the positions of the edges held constant and created violin plots of the resulting values.

Ethical note. This research complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Puerto Rico (protocol #A6850108) and by the University of Exeter School of Psychology's Ethics Committee.

RESULTS

Rates of social interactions were static across years. We found no evidence for changes between 2010 and 2011 in the overall rate of aggression (2010: 0.02, 2011: 0.02; tstat=0.49; $p = 0.31$) or grooming (2010: 1.20; 2011: 1.17; t-stat=0.13; $p = 0.43$), as indicated by network densities. Any other structural differences in the observed networks (e.g. differences in clustering) cannot therefore be owed to differences in network density.

Aggression directed up the hierarchy was more likely in the year nearer the eviction. Aggressive interactions generally reflected the dominance hierarchy, with the majority of aggression emanating from higher ranking females and being directed at lower ranking females in both years (Table 1). However, changes from 2010 to 2011 in the extent to which aggression was directed up the hierarchy occurred and may suggest that there was instability in the dominance hierarchy that was largely localised to the 065 matriline. In particular, females from low-ranking matrilines 004 and 073 were more likely to give aggression to the Evicted females in 2011 compared to in 2010. Females from Mat_{004} were also more likely to give aggression to the Resident females in 2011 compared to 2010 (Table 1). Although these increases represent only a small absolute number of aggressive interactions, reflecting the smaller number of females that belonged to the lower ranking matrilines (Figure 2), they are notable due to the typically unidirectional nature of aggression in rhesus macaques. The probability of aggressive interactions also increased amongst Evicted females from 2010 to 2011. However, there were decreases in the probability of aggression being directed from the Evicted females to the Resident females, and from the Resident females to the Evicted females.

[INSERT FIGURE 2 ABOUT HERE]

Females changed grooming partners as the eviction approached. We found that, as expected, females were more likely to engage in grooming with members of their own partition. The Evicted, Resident, and Mat_{004} females were more likely to groom members of their own partition compared to members of other partitions in both 2010 and 2011 (Table 1). This pattern was not significant for females from the small 073 matriline Females also tended to groom females outside their own partition at rates either expected by chance or significantly lower than chance in both years. Yet there were notable differences in the identities of grooming partners both within and between partitions across years (Figure 2). For example, the tendency for females to groom members of their own partition increased from 2010 to 2011 for Evicted, Resident, and Mat_{004} females, with the Evicted females showing the largest increase in within-partition grooming (2010: 5.02 Obs/Exp, $p < 0.01$; 2011: 6.45, $p < 0.01$). In addition, the amount of grooming that occurred between Evicted and Resident females did not differ from chance levels in 2010 but was smaller than expected in 2011 (2010: 0.96, $p = 0.25$; 2011: 0.34, $p = 0.01$). In other words, in the year nearer to the eviction, Evicted females were more likely to groom one another and less likely to groom the Resident members of their matriline.

Evicted females formed tighter grooming clusters in the year before their eviction. The mean clustering coefficient of the grooming network of Evicted females was significantly greater than expected in 2011 but not in 2010 (Table 2). The mean clustering coefficient of no other partition differed from expected values in either year. In other words, the grooming relationships of Evicted females were more cliquish than expected based on random association in the year directly before their eviction, whereas no such differences were observed in the other partitions, including the Resident members of this matriline. The grooming relationships of the Evicted females were also significantly more clustered in 2011 than in 2010, and were significantly more clustered in 2011 than any other partition examined (Figure 3). Although there were small increases in clustering from 2010 to 2011 for the Resident and Mat_{004} females, this was only significant for the latter (Table 2). The clustering coefficient for Mat_{073} was zero because there were no closed triads within the network and thus no amount of edge-weight reshuffling could produce a result other than zero. We found relative similarities between our random graphs across years (Figure 3). Because changes in network densities were the central drivers of differences between the random graphs, which further suggests that differences across time in our observed clustering coefficients were not driven by differences in density alone.

[INSERT FIGURE 3 ABOUT HERE]

DISCUSSION

The study of dynamic social networks is an area of rapidly growing research interest (Bode, Wood, & Franks, 2011; Ilany, Booms, & Holekamp, 2015; Pinter-Wollman et al., 2014). Although social networks appear to be able to flexibly respond to changes in the social and physical environment, whether changes to social networks also precede major events is less clear. Here we report network dynamics in advance of the mass eviction of members of the philopatric sex. Prior to the eviction, researchers present in the group reported no conspicuous signs of social instability. Therefore the changes to the networks of these animals occurred in advance of a major event but were subtle and revealed only through subsequent analysis. Permanent evictions can have serious consequences for individuals; intragroup aggression prior to evictions can result in fatal injuries (Ehardt & Bernstein, 1986; Gygax, Harley, & Kummer, 1997; Samuels & Henrickson, 1983), decreased reproduction, (Dettmer, Woodward, & Suomi, 2015) and smaller post-eviction daughter groups can be subjected to higher risks of predation and reduced foraging efficiency (Krause & Ruxton, 2002). There is some evidence that reproductive competition is the trigger for evictions in cooperative breeding species (Thompson et al., 2016) but it is unclear whether similar factors would be at play in a primate such as the rhesus macaque that has highly polygynous mating and only moderate levels of reproductive skew (Dubuc, Ruiz-Lambides, & Widdig, 2014). Although we do not know whether there are causal links between changes to the social networks in this study and the eviction, a consistent patterning of network dynamics prior to evictions would nevertheless allow evictions to be predicted in future, which could have implications for the management of captive groups (Beisner et al., 2011) and the design of naturalistic experimental studies.

A number of theories have been put forward regarding the maintenance of group cohesion and the balance of competition and cooperation between unrelated group mates. For instance, group cohesion may be limited by the amount of time individuals have available to spend engaged in social interactions. This 'time-constraints' model predicts that groups break apart once individuals can no longer maintain or keep track of relationships with all other groups members (Dunbar, 1991, 1992). Prior to the mass eviction in this study, we did not detect any changes in the amount of time individuals dedicated to grooming or aggressive interactions. Although these animals are provisioned and may not easily suffer from restrictions in their daily time budgets, our results nonetheless suggest that the break down in group cohesion did not follow from reductions in social effort.

Group cohesion may depend not only on the amount of time individuals engage in social interactions but also on with whom they interact. For example, pay-to-stay mechanisms, whereby individuals 'pay' their group mates with affiliative interactions, have been proposed as a means to maintain groups of cooperative breeders with highly skewed reproductive success (Bergmüller & Taborsky, 2005; Gaston, 1978; Johnstone & Cant, 1999), as well as groups of unrelated animals faced with intense between-group competition (Radford, 2008; van Schaik, 1989; Wrangham, 1980). In the latter instance, dominant animals are proposed to use social interactions, e.g. grooming, to establish alliances with their lower-ranking group mates in order to ensure they will help in contests with other groups (Cheney, 1992; van Schaik, 1989). A meta-analysis of data from cercopithecine primates suggests the link between grooming relationships, intra-group contest, and the maintenance of group cohesion is weak if non-existent (Cheney, 1992) (although see: Majolo, de Bortoli Vizioli, & Lehmann, 2016). In the present study, an increase in cliquishness in the local grooming networks of evicted females suggests that grooming relationships amongst kin and non-kin of divergent social status may indeed play a role in the cohesion of rhesus macaque groups. However, cause and consequence cannot be disentangled here and just as the reduced diversity of grooming relationships may have caused the eviction, the pending eviction may have resulted in the reduction of diversity in grooming relationships.

Changes to affiliative relationships leading up to a mass eviction also reveal more direct information about the patterns and processes that underpin social relationships in these animals. Biologists' understanding of the evolution of social bonds in animals has grown rapidly in recent years (Archie, Tung, Clark, Altmann, & Alberts, 2014; Brent, Heilbronner, et al., 2013; Chang et al., 2013; Seyfarth & Cheney, 2012; Silk et al., 2009). Affiliative tendencies have been shown to be heritable (Brent, Heilbronner, et al., 2013; Brent, Semple, et al., 2014; Lea, Blumstein, Wey, & Martin, 2010), and a positive association between affiliative relationships and proxies of fitness have been found in a small range of species, including baboons (Archie et al., 2014; Silk et al., 2009; Cheney et al. 2016) and rhesus macaques (Brent, Heilbronner, et al., 2013; Brent et al. 2017). Yet despite these advances, the adaptive functions of social bonds remains unclear (Brent, Chang, et al., 2014). A growing number of studies that have shown that affiliative social relationships between members of the philopatric sex are more flexible in nonhuman primates than traditionally believed (e.g. (Barrett, Gaynor, & Henzi, 2002; Barrett & Henzi, 2002; Engh et al., 2006; Wittig et al., 2008). In accordance with this work, we found evidence for dynamic shifts in affiliative relationships in this study. Together, these findings may reflect the use of social relationships to cope with the vicissitudes of life such as death, disease, and shifts in social status, as well as other short-term social, environmental, and demographic events.

Our results may also hint that some social bonds are more valuable than others. Previous work has shown that instability in primate groups can be followed by shifts in social partners. Following the death of the alpha male in wild chimpanzees, individuals became more socially discriminant of grooming partners that failed to reciprocate (Kaburu & Newton-Fisher, 2013). In cercopithecines, social relationships are most common amongst related females (Cheney, 1992). Relatedness may be a useful shorthand for reliable cooperative partners because of the ability to gain inclusive fitness benefits via these relationships. Female baboons focused their grooming networks onto close kin following instability in the male hierarchy (Wittig et al., 2008). In the current study, grooming relationships largely collapsed along kin-lines prior to the mass eviction, with the females that would be evicted focusing their relationships onto their closest kin; in times of social instability, affiliative relationships with non-relatives may become too risky for rhesus macaque females.

The adaptive role of social relationships in variable contexts begs an understanding of how individuals of variable phenotypes integrate to form particular group dynamics. Here, we focused on rates of interactions and the formation of clusters as indicators of changes in network structure and partner choice. Other network metrics with alternative properties might differently elucidate social dynamics (Brent 2015). For example, eigenvector centrality, which uses direct and indirect connections to parse socially integrated from marginal individuals, was found to positively correlate with proxies of fitness in wild baboons (Cheney et al. 2016) and in the Cayo Santiago rhesus macaques (Brent et al. 2013). As our current analyses indicated the emergence of distinct subgroupings over time without any changes in the overall rates of interactions, we felt eigenvector centrality would be of limited analytical power (although will nevertheless continue to be important to consider in future studies focused on revealing information about differences in social connectedness between individuals) and we instead performed a joint count analysis to explore not just how involved the different subgroups were in social life, but with whom.

The stability of a group is not attributable to the phenotype of any one particular individual but it is nevertheless likely to impact upon individual fitness. Research in group-living species suggests that the interplay between group stability and individual fitness is complex (Muir, 2005; Saltz, 2013; Wolf, Brodie, & Cheverud, 1998). A more thorough understanding of how the metagenome (i.e. the influence of one individual's genotype and phenotype on another's) influences network dynamics will also be useful for behavioural ecologists approaching these questions.

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FIGURE LEGENDS

Figure 1. Maternal relatedness structure for the adult females in group F. Female names are listed along the top and right-hand edge and are coloured by matriline membership. Matriline 065 has been partitioned into females that were evicted and those that remained in the parent group ('resident') Females are ordered by descending dominance rank. Cells represent the maternal relatedness coefficient for each pair of individuals.

Figure 2. Grooming and Aggression Networks. The grooming (A,B) and aggression (C, D) networks for 2010 (A,C) and 2011 (B,D). Node colour represents partition membership where Evicted females are red, Resident females purple, Mat_{004} females green and Mat_{073} females blue. Colour intensity of the edge arrows indicates the relative weight of the interaction, with darker edges indicating greater intensity. Each network is force-directed using the Fruchterman-Reingold algorithm. Inset chord diagrams: width of chords represents that summation of interactions emanating from a given partition to other partitions. Chords take the colour of the partition from which interactions emanate.

Figure 3. Mean Clustering Coefficients by Partition. Violin Plots showing estimates of the mean clustering coefficient for each partition in each study period. Grey plots show estimates for the given partition and year based on Erdős–Rényi random graphs. Coloured densities represent mean clustering coefficients from 5000 permuted graphs in which we shuffled weights across edges while holding the positions of edges constant.

Table 1. Observed and expected rates of grooming and aggression within and between females

Donor	Recipient	Exp	Obs	Obs / Exp (Pval)	Exp	Obs	Obs / Exp (Pval)
		Grooming Networks					
		2010			2011		
Evicted	themselves	142	712	**5.02 (0.001)**	140	904	**6.45 (<0.001)**
	Resident	207	201	0.96 (0.25)	205	69	**0.34 (0.01)**
	Mat$_{004}$	185	3	**0.02 (<0.001)**	183	19	**0.10 (0.001)**
	Mat$_{073}$	65	0	**0.00 (0.05)**	65	0	**0.00 (0.03)**
Resident	Evicted	207	290	1.40 (0.48)	205	176	0.86 (0.17)
	themselves	303	825	**2.73 (0.01)**	299	983	**3.29 (0.001)**
	Mat$_{004}$	271	147	**0.54 (0.03)**	268	168	**0.63 (0.04)**
	Mat$_{073}$	96	0	**0.00 (0.02)**	95	25	**0.27 (0.05)**
Mat $_{004}$	Evicted	185	48	**0.26 (0.01)**	183	177	0.97 (0.24)
	Resident	271	244	0.90 (0.17)	268	245	0.91 (0.15)
	themselves	242	890	**3.67 (<0.001)**	240	666	**2.78 (0.01)**
	Mat$_{073}$	86	72	0.84 (0.32)	85	14	**0.17 (0.04)**
Mat$_{073}$	Evicted	65	32	0.49 (0.22)	65	5	**0.08 (0.04)**
	Resident	96	0	**0.00 (0.01)**	95	21	**0.22 (0.04)**
	Mat$_{004}$	86	68	0.79 (0.29)	85	7	**0.08 (0.02)**
	themselves	30	45	1.49 (0.30)	30	104	3.49 (0.08)
		Aggression Networks					
		Exp	Obs	Obs / Exp (Pval)	Exp	Obs	Obs / Exp (Pval)
Evicted	themselves	2.43	8.00	**3.30 (<0.001)**	2.18	8.37	**3.84 (<0.001)**
	Resident	3.56	11.73	**3.29 (<0.001)**	3.18	8.98	**2.82 (<0.001)**
	Mat$_{004}$	3.18	7.94	**2.50 (<0.001)**	2.85	9.56	**3.35 (<0.001)**
	Mat$_{073}$	1.12	2.50	**2.23 (0.04)**	1.01	2.93	**2.92 (0.004)**
Resident	Evicted	3.56	0.59	**0.17 (<0.001)**	3.18	0.40	**0.13 (<0.001)**
	themselves	5.20	6.21	1.19 (0.38)	4.65	5.26	1.13 (0.19)
	Mat$_{004}$	4.65	7.77	1.67 (0.08)	4.16	5.76	1.38 (0.48)
	Mat$_{073}$	1.64	2.56	1.56 (0.27)	1.47	1.48	1.01 (0.15)
Mat $_{004}$	Evicted	3.18	0.25	**0.08 (<0.001)**	2.85	0.49	**0.17 (<0.001)**
	Resident	4.65	1.13	**0.24 (<0.001)**	4.16	1.20	**0.29 (<0.001)**
	themselves	4.16	4.35	1.05 (0.19)	3.72	5.16	1.38 (0.37)
	Mat$_{073}$	1.47	2.80	1.92 (0.09)	1.32	2.75	2.09 (0.08)
Mat$_{073}$	Evicted	1.12	0.00	**0.00 (<0.001)**	1.01	0.10	**0.10 (<0.001)**
	Resident	1.64	0.12	**0.07 (<0.001)**	1.47	0.10	**0.07 (<0.001)**
	Mat$_{004}$	1.47	0.12	**0.08 (<0.001)**	1.32	0.10	**0.07 (<0.001)**
	themselves	0.51	0.95	1.82 (0.14)	0.46	1.17	**2.52 (0.04)**

The observed (Obs) and expected rates (Exp) of interaction, and the ratio of observed to expected for each network within and between the 4 partitions (Evicted, Resident, Mat$_{004}$, and Mat$_{073}$). Interactions emanate from "donors" and are received by "recipients." Pval is calculated as the proportion of simulated networks in which the Obs/Exp value exceeded or met the observed Obs/Exp value. Values in bold differed significantly from chance.

Table 2. Clustering of grooming relationships: Observed compared to randomised networks, comparisons between partitions of females, and comparisons within partitions of females across years.

	Year	Observed Clustering Coefficient	Randomised Networks	Evicted 2010	Evicted 2011	Resident 2010	Resident 2011	Mat_{004} 2010	Mat_{004} 2011	Mat_{073} 2010	Mat_{073} 2011
Evicted	2010	0.04	0.01 (0.49)		**0.23 (<0.01)**	-0.01 (0.31)	-0.02 (0.23)	0.03 (0.08)	**0.05 (0.05)**	0.05 (0.09)	0.05 (0.09)
	2011	0.28	**0.21 (<0.01)**			**0.24 (<0.01)**	**0.21 (<0.01)**	**0.26 (<0.01)**	**0.18 (<0.01)**	**0.28 (<0.01)**	**0.28 (<0.01)**
Resident	2010	0.02	0.02 (0.35)				0.03 (0.13)	0.02 (0.15)	**0.06 (0.03)**	0.04 (0.17)	0.04 (0.17)
	2011	0.07	0.001 (0.43)					**0.04 (0.01)**	0.03 (0.15)	**0.06 (0.02)**	**0.06 (0.02)**
Mat_{004}	2010	0.02	0.03 (0.22)						**0.08 (<0.01)**	0.02 (0.14)	0.02 (0.14)
	2011	0.08	0.02 (0.24)							**0.09 (0.01)**	**0.09 (0.01)**
Mat_{073}	2010	0.00	0.04 (0.69)								0.00 (1.00)
	2011	0.00	0.06 (0.29)								

P-values for the difference in observed and random networks are calculated as the proportion of random networks that produced values as extreme the observed value. P-values for the difference of observed values across partitions and study periods are based on a bootstrap two-sample permutation tests. Values in bold differ significantly from chance.