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Social management of laboratory rhesus macaques housed in large groups using a network approach: A review

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Abstract

Biomedical facilities across the nation and worldwide aim to develop cost-effective methods for the reproductive management of macaque breeding groups, typically by housing macaques in large, multi-male multi-female social groups that provide monkey subjects for research as well as appropriate socialization for their psychological well-being. One of the most difficult problems in managing socially housed macaques is their propensity for deleterious aggression. From a management perspective, deleterious aggression (as opposed to less intense aggression that serves to regulate social relationships) is undoubtedly the most problematic behavior observed in group-housed macaques, which can readily escalate to the degree that it causes social instability, increases serious physical trauma leading to group dissolution, and reduces psychological well-being. Thus for both welfare and other management reasons, aggression among rhesus macaques at primate centers and facilities needs to be addressed with a more proactive approach. Management strategies need to be instituted that maximize social housing while also reducing problematic social aggression due to instability using efficacious methods for detection and prevention in the most cost effective manner. Herein we review a new proactive approach using social network analysis to assess and predict deleterious aggression in macaque groups. We discovered three major pathways leading to instability, such as unusually high rates and severity of trauma and social relocations. These pathways are linked either directly or indirectly to network structure in rhesus macaque societies. We define these pathways according to the key intrinsic and extrinsic variables (e.g., demographic, genetic or social factors) that influence network and behavioral measures of stability (see Fig. 1). They are: (1) presence of natal males, (2) matrilineal genetic fragmentation, and (3) the power structure and conflict policing behavior supported by this power structure. We discuss how these three major pathways leading to greater understanding and predictability of deleterious aggression in macaque social groups.

Keywords

Aggression; Macaques; Social network analysis; Social stability; Social collapse

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1. Introduction

Biomedical facilities across the nation and worldwide aim to develop cost-effective methods for the reproductive management of macaque breeding groups, typically by housing macaques in large, multi-male multi-female matrilineal social groups that provide monkey subjects for research as well as appropriate socialization for their psychological well-being. Although these large outdoor social groups approximately simulate natural social and environmental features, one of the most difficult problems in managing socially housed macaques is their propensity for deleterious aggression. From a management perspective, deleterious aggression, such as severe biting and chasing, is undoubtedly the most problematic behavior observed in group-housed macaques. It can readily escalate to the degree that it causes social instability, increases serious physical trauma leading to group dissolution, and reduces psychological well-being (McCowan et al., 2008; Beisner et al., 2011; Beisner et al., 2015). Severe wounding can be frequent; up to 60% of an entire breeding population requiring hospitalization due to trauma resulting from wounding each year has been reported by some facilities resulting in a serious welfare concern for these populations (McCowan, unpublished data). Further, at recent professional meetings (e.g., Symposium on Social Housing of Laboratory Animals and American Association of Laboratory Animal Sciences), USDA representatives stated that providing social housing and limiting the trauma resulting from social housing at primate facilities will receive greater scrutiny. Thus for both welfare and other management reasons, aggression among rhesus macaques at primate facilities needs to be addressed with a more *proactive approach.* Such an approach involves the use of evidence-based, cost-effective management strategies to maximize social housing, employing methods for the detection and prevention of problematic social aggression, which can de-stabilize social groups.

The dominance style of both captive and free-ranging rhesus macaques has been described as the most despotic of all macaque species (Thierry, 2004). This despotic dominance style is characterized by unidirectional aggression directed at subordinate individuals, frequent severe aggression, strong emphasis on kinship, and infrequent post-conflict affiliation (Flack and de Waal, 2004). The hierarchy of rhesus macaques is very steep and aggression plays a particularly important role in maintaining dominance relationships (Bernstein and Ehardt, 1985). Lower level aggression, such as threats and lunges, serves to maintain social structure and stability within as well as between matrilines (Bernstein and Ehardt, 1985). More severe aggression, however, can occur during conflicts over important resources (e.g., high quality food, mates) or when dominance relationships between individuals become ambiguous. In captivity, removal of key individuals for management purposes can produce such ambiguity, but more frequently it is a result of seemingly unpredictable changes in intra-group dynamics.

Even among stable groups of rhesus macaques, aggression and trauma commonly vary both within and between groups. Seasonal changes in competition dynamics as well as differences in demographic structure lead to differential rates of aggression in these managed groups. Some level of aggression in rhesus groups is not only expected but desired because competitive interactions maintain social order. Conversely, unstable social groups typically exhibit evidence of disruption in social order such as higher incidence than expected by chance of pairs with bidirectional aggression in the absence of formal subordination signaling in the form of silent bared teeth displays (Beisner et al., 2015) (see below). The culmination of instability is characterized by sudden outbreaks of severe aggression involving a large proportion of group members – also known as overthrows or social collapse. Yet there is preliminary evidence that in the days leading up to an overthrow or collapse, levels of agonistic interaction decrease and the group appears quiet and unwilling to risk interaction (personal observation). Thus the very nature of this variation in aggression spanning from mild to severe provides the clear impetus for us to take a deeper look at how social groups maintain themselves (or not), focusing on both the risk factors and processes that contribute to such variation beyond simple rates of aggression. For example, why do some groups have greater or lower rates and severity of aggression than others and during different seasons? Indeed, why do some groups actually fail to thrive resulting in complete corral disbandment (due to social overthrow or collapse), even when severe aggression is not present?

The striking problem that we have revealed in our research program is that *simple* answers do not fix complex problems. Social stability is an emergent property of a complex system requiring a deeper understanding of the processes that lead to instability. Rates of aggressive behaviors or general trauma have given us little insight into how and why social groups become unstable to the point of requiring human intervention to restore order. To date, there has been almost no predictive power or early warning system in place to detect when social group instability will occur. Here we review a systems science network approach that has allowed us to model these emergent complex systems and (a) unravel the risks factors and processes leading to instability in these social groups and (b) detect and arrest these instabilities (Barrett et al., 2012; Beisner and Isbell, 2011; Beisner et al., 2011a,b, 2012; Beisner and McCowan, 2013; Beisner and McCowan, 2014a,b,c; Beisner et al., 2015; Beisner et al., 2016; Chan et al., 2013; Chen and Fushing, 2012; Flack and de Waal, 2004; Flack et al., 2006; Flack and Krakauer, 2006; Fujii et al., 2014; Fushing et al., 2014; McCowan et al., 2008; McCowan et al., 2011; Wasserman and Faust, 1994).

For more than 10 years, we have been conducting a long-term study using social network analysis to examine the internal (e.g., group composition, personality and temperament) and external (e.g., management factors) that influence rates of deleterious aggression and wounding in group-housed rhesus macaques (McCowan et al., 2008; Oates-O'Brien et al., 2010; Beisner et al., 2011a,b; McCowan et al., 2011; Beisner et al., 2012; Beisner and McCowan, 2013). Below we provide a review of this body of work to be used as a guide for managing large social groups of rhesus macaques and other macaque species in captivity. A review of network analysis is not within the scope of this paper, so we point to several review articles that have been published on the utility of and approach underlying social network analysis (Krause et al., 2007; Croft et al., 2008; Wey et al., 2008; Krause et al., 2009; Sih et al., 2009; Makagon et al., 2012; Krause et al., 2015).

2. Network structure influences stability along three major pathways

We were able to identify three major pathways leading to instability, such as unusually high rates and severity of trauma and social relocations (relocations of animals due to concern over their or others well-being due to aggression). These pathways are linked to network structure, that is how individuals in groups are directly and indirectly linked in their social relationships, in rhesus macaque societies. We define these pathways according to the key intrinsic and extrinsic variables (e.g., demographic, genetic or social factors) that influence network and behavioral measures of stability (see Fig. 1). They are: (1) presence of natal males, (2) matrilineal genetic fragmentation, and (3) the power structure and conflict policing behavior supported by this power structure. We discuss these three major pathways below.

To summarize the data used in these sets of studies, data were collected on 20 groups over a 9 year period using a combination of event and scan sampling for 6 h per a day on four days per week for various periods (six weeks to 12 months depending on the study) (McCowan et al., 2008; Beisner et al., 2011a,b; Beisner and Isbell, 2011; McCowan et al., 2011; Beisner et al., 2012; Beisner and McCowan, 2013; Beisner and McCowan, 2014a,b,c; Beisner et al., 2015; Beisner et al., 2016). Groups were comprised of 80–150 animals consisting of both male and female adults, subadults, juveniles and infants. Two observers focused on collecting event conflict behavior (e.g. aggression) and one observer focused scanned affiliation data (e.g. grooming). In total 4950 h were collected as part of this series of studies.

2.1. Natal male presence

The presence of natal males in the group is relatively unique to captive social groups, because colony management protocols of captive groups sometimes retain natal males in their large social groups, hence circumventing the male dispersal pattern typical of wild, free-ranging groups (but also see (Kaufman, 1976; Koford, 1963; Tilford, 1982) for examples of wild, free-ranging of males remaining in their natal groups). This presence of natal males influences male individual rank, aggressive behavior, as well as social position within the male displacement (i.e., approach-avoid) network through their alliances with others, and this is particularly true of maternal kin (Beisner et al., 2011a,b). Natal males vary in their frequency of kin alliances, forming kin alliances with higher frequency when their female relatives are high-ranking. Natal males that frequently cooperate with their maternal kin attain higher individual rank, use intense aggression more frequently, and also more central and influential (i.e., have higher Bona-cich power) in the male displacement network (see Fig. 2). Bonacich power is a network measure of power or influence where centrality in the network (Bonacich 1987) is measured not only by the diversity and frequency of a male's own connections but also those of his neighbors. Topological knockout (in which selected data are removed from a network) of these high-ranking, natal juvenile males revealed that group-level rates of intense aggression decreased in all groups upon removal of these males from the data (range: 4–14% decrease). Preliminary analysis of our experimental knockouts, in which we permanently removed 1–2 high-ranking natal males (2–6 years old) from the alpha matrilines of five social groups, showed similar trends (Beisner and McCowan, 2014a,b,c). Upcoming analyses of these experimental removals will more thoroughly examine the impact of removal on metrics of aggression and stability such as transitivity of aggression networks.

Our work suggests that the strategic, proactive removal of high-ranking natal males (see Fig. 3; (McCowan et al., 2008) are likely to improve stability in social groups, at least in rhesus, and likely in other macaque species as well.

2.2. Matriline genetic fragmentation

The importance of matrilines and their structure is a hallmark feature of macaque societies (Bernstein and Ehardt, 1985). Adult females and their female offspring provide the backbone of macaque society because females from the same kin group support one another in agonistic interactions, resulting in a dominance hierarchy with a clear matrilineal structure (Kawamura, 1958; Sade, 1969; Kurland, 1977; Datta, 1983). The necessity of cohesion within these social entities would therefore seem paramount to stability of social groups, and our research has indicated that this is indeed the case (Beisner et al., 2011a,b). Matrilines within groups that had lower genetic fragmentation, as measured by a greater average matrilineal degree of relatedness, had more cohesive grooming relationships (fewer grooming communities representing clusters of individuals that groom each other), less intense aggression among kin, and received less wounding than matrilines that had higher genetic fragmentation (see Fig. 4) (Beisner et al., 2011a,b). Also, matrilines received less wounding when their matriarch was present in the group (the matriarch being the common ancestor of all matriline descendants currently in the group). Topological knockouts in the groom networks of each matriline (removal of an individual's data from the dataset) showed that removal of matriline fragments decreased the number of grooming communities. Preliminary analysis of experimental knockouts (again physical permanent removals) of individuals to reduce matriline genetic fragmentation suggest a reduction of wounding approximately 12 weeks post-removal (McCowan, unpublished data). Upcoming analyses will examine whether (a) permanent removal of family fragments results in greater social cohesion (e.g., less sub-grouping in groom networks) and (b) any observed improvements in social cohesion are associated with reduced trauma or severe aggression at either the matriline or group level.

Again, our work suggests that selective proactive removal of individuals from matrilines to increase intra-matriline genetic relatedness has the potential to reduce aggression via cohesion in grooming relationships.

2.3. Power structure and conflict policing

Finally, we review below perhaps the most important feature of social stability in rhesus macaques: social power and conflict policing. While policing in macaque species was recognized early in the field of primatology (Bernstein and Sharpe, 1966; Bernstein and Ehardt, 1985), the potential importance of social power and conflict policing to social stability in macaque societies, more broadly, came to light in an experimental study of a captive group of pigtailed macaques. Flack and colleagues formally developed and described a measure of social power based upon formal signals of subordination (silent bared teeth signals) given in non-aggressive contexts and linked the emergent skewed distribution of social power to conflict policing by the most powerful individuals (Flack et al., 2005; Flack et al., 2006). Yet Flack and colleagues suspected that conflict policing may not be possible in more despotic species of macaques because social power was hypothesized to be more uniform in distribution (Flack and de Waal, 2004). In a series of linked and embedded analyses, we have shown that social power is critical to social stability in rhesus macaques for several reasons: (a) silent-bared-teeth signals given in peaceful contexts are formal subordination signals that communicate acceptance of one's subordinate role, and giving subordination signals is associated with lower rates of aggression (presumably because there is less need to aggressively reinforce the relationship; (Beisner and McCowan, 2014a,b,c); (b) the network of subordination signals (i.e. silent-bared-teeth signals given in peaceful contexts) illustrates how subordination signals (and pathways of signals) converge on a small number of individuals (i.e. the individuals with greatest social power), thereby generating a skewed distribution of social power (Beisner et al., 2016); and (c) individuals that receive frequent subordination signals from many different subordinates (including transitive network pathways of signals) are better able to police others' conflicts, because there is greater group consensus that they are powerful (McCowan et al., 2011; Beisner et al., 2016). Adult males, particularly males unrelated to the group, have the highest social power, and are the most frequent and successful policers (Table 1: McCowan, unpublished data). Due to the policing role that adult males play in the group, high unrelated adult male: female sex ratio is associated with high social power, high intervention success and less trauma (see Fig. 5). (Beisner et al., 2012).

Furthermore, social groups in which policing is more frequent and/or average social power is higher, show signs of greater social stability, including (a) lower rates of trauma and social relocations (McCowan et al., 2008; McCowan et al., 2011; Beisner and McCowan, 2013); (b) greater cohesion in their status/displacement networks (McCowan et al., 2011); and (c) less frequent escalation of conflict (i.e., shorter average conflict length: (McCowan et al., 2011).

2.4. Social instability: identifying the critical tipping point

The final piece to the puzzle of social stability lies in being able to accurately assess a specific social group for its current level of stability. Detecting the point at which a social group becomes unstable and is at risk of social collapse is challenging because stability is an emergent property of a complex social system. For example, outbreaks of unusually severe aggression can accompany social overthrow or social collapse but do not necessarily precede it (McCowan et al., 2008; Oates-O'Brien et al., 2010). Indeed, general rates of aggression show no predictable relationship with group stability. Until now, one could only be certain of the lack of stability when a group had fissioned or experienced a social overthrow or collapse. Joint network modeling (JNM) is a new tool that allow us to examine the interdependence between two different networks. It has proven to be extremely useful in detecting social instability prior to collapse, as it readily reveals aberrant patterns of social dynamics. Using JNM, we found that the interdependence between aggression and status signaling networks was consistent among stable groups, but different among unstable groups during the period leading up to their collapse (Beisner et al., 2015) (see Fig. 6). The most prominent feature of aggression-status network interdependence in stable social groups was the presence of more pairs than expected that displayed opposite direction status-aggression (i.e., A threatens B and B signals acceptance of subordinate status). On the other hand, unstable groups showed a relatively smaller magnitude of these opposite direction aggression-status pairs (but still higher than expected under the null hypothesis), as well as a greater than expected number of pairs with bidirectional aggression. JNM also confirms the importance of the power structure to group stability, because deterioration of the joint relationship between aggression and status networks is linked to, and likely driven by, significant loss of subordination signaling interactions (Chan et al., 2013; Fushing et al., 2014; Beisner et al., 2015).

The selection of which networks to include in joint network modeling is an important decision. The networks most relevant to social stability will depend upon the system in question but analyses should likely include a keystone network as opposed to more subsidiary networks. Keystone networks represent the most fundamental relationships in the system, because they govern or influence the manner in which other networks in the system interact (Fushing et al., 2014). As such, the presence and direction of links in these networks are less likely to be influenced by situational variables than other networks, which tends to generate a more rigid structure.

3. Practical application of findings

These findings suggest a number of improvements that can be made to current behavioral/colony management practices at facilities housing rhesus macaques in large matrilineal social groups. First, removal of natal males, particularly those from high-ranking families (that cooperate with their maternal kin to attain high rank) and/or those that occupy a similar network position as the alpha male, can prevent these males from becoming a source of social agitation and instability. In our experience, high-ranking natal males that become problematic do so around puberty (~3–5 years old), further suggesting that such males be monitored more closely behaviorally using focal sampling on a systematic basis (several times per week). Second, improvement and maintenance of matrilineal cohesion can be achieved by establishing a long-term plan for gradual removal of females to prune the growth of genetic lineages that would otherwise contribute to a social disconnect within the family. For example, if matriarch A1 has four daughters (A2, A3, A4, and A5), a long-term plan for maintenance of genetic cohesion might include consistent removal of A2 and A3's female offspring to allow only a few of the daughters' lineages to grow. Finally, behavioral managers should regularly monitor the subordination signaling network (i.e., the power structure), sex ratio, and conflict policing behavior present in their social groups to determine whether each group has the appropriate group composition to promote their own natural conflict management mechanisms. The amount of monitoring will depend on the choice of monitoring (focal, event, scan sampling) and group size, but we recommend that groups be monitored at least weekly, Sex ratios that differ dramatically from those of wild, free-ranging groups are less able to manage their own internal social conflicts and are therefore at greater risk of becoming unstable (Beisner et al., 2012). Managing social groups for appropriate sex ratios (especially unrelated males to females) by either reducing the number of females or introducing novel unrelated males would allow robust policing mechanisms to be firmly in place, and this could go a long way toward improving stability in social groups.

4. Evaluating the utility of network approaches to captive primate management

While the approach described in this review clearly demonstrates the utility of network analysis for improving management of captive animal populations, gathering network data clearly is time-consuming and requires well-trained observational staff, experienced data analysts, and a scientific approach. However, now that we understand key behaviors and mechanisms to monitor, the methods our team uses for research can be applied on a more limited and focused scale for monitoring laboratory populations of rhesus macaque social groups. There are still some additional costs of hiring and training appropriate staff, but these are likely to be offset by both the improvements in animal welfare (by maintaining individuals in naturalistic social groups for longer periods of time than previously possible), as well as cost savings in veterinary care related to treatment of social upheavals including high rates of severe physical trauma. Further, longer-term maintenance of social group housing also benefits research centers in particular, by fostering the conduct of high-quality science without concern about the confounding influences of less natural social environments. In sum, the potential benefits of implementing a network-based behavioral management program are sufficiently high to offset the costs of implementation.

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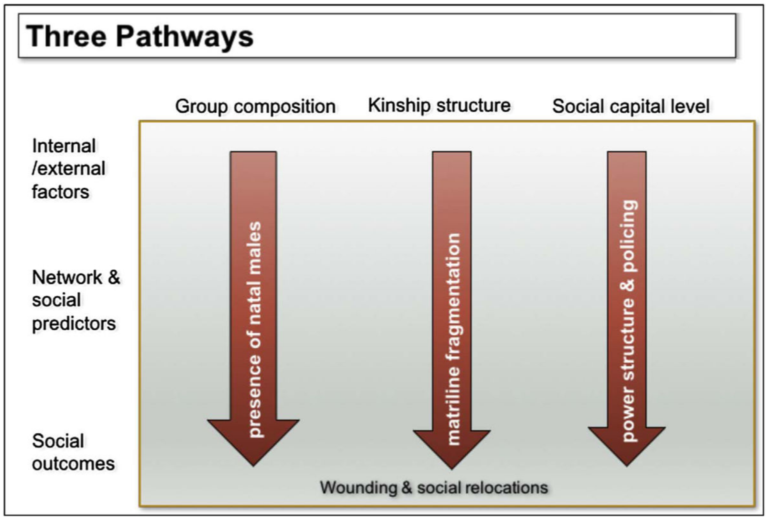

Fig. 1.

Three major pathways leading to instability in captive rhesus groups.

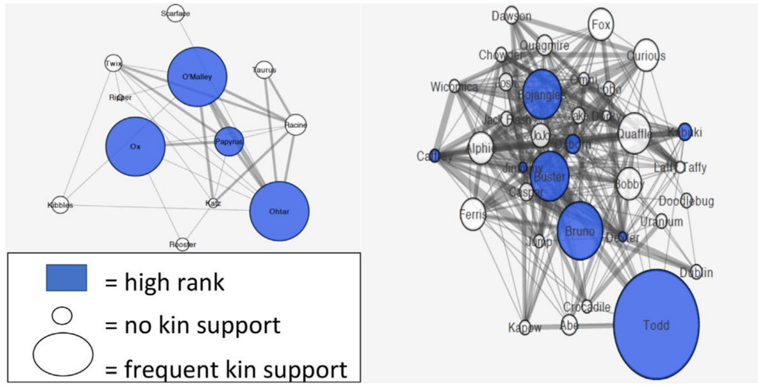

Fig. 2.

Network of natal males illustrating that high ranking natal males have high Bonacich power and frequent kin support.

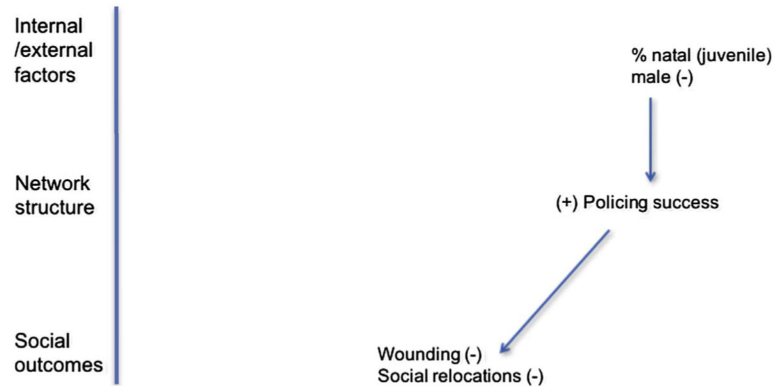

Fig. 3.
Effects of natal males on wounding and social relocations.

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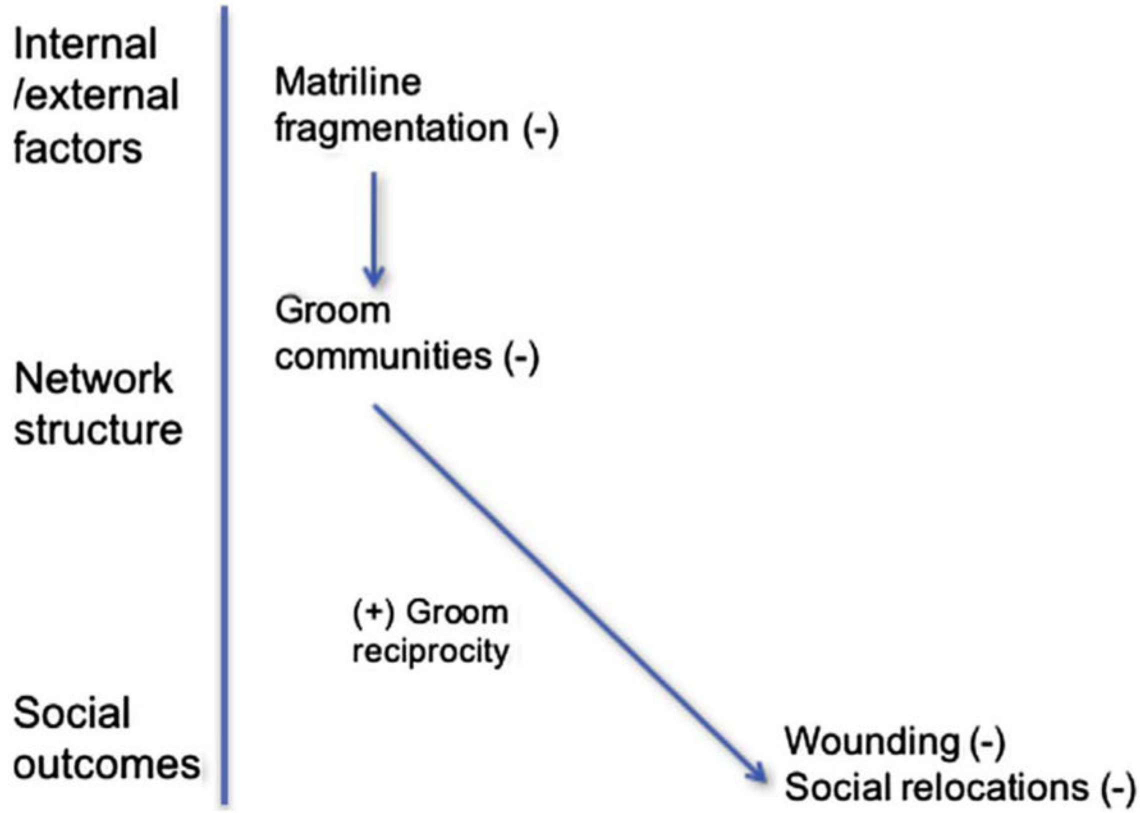

Fig. 4.
Effects of matriline fragmentation on wounding and social relocations.

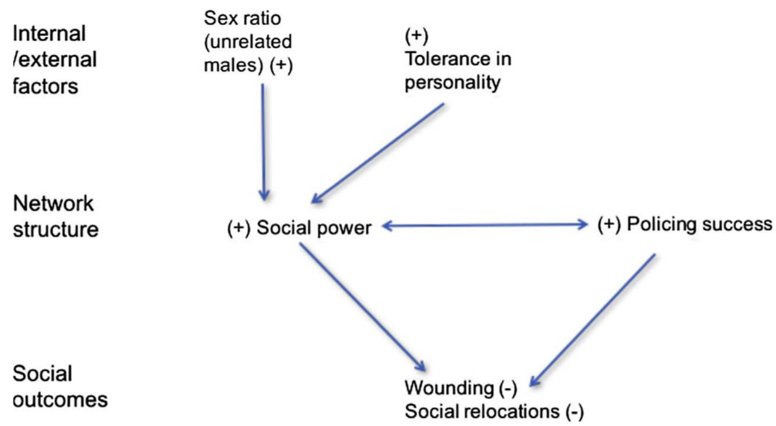

Fig. 5.
Effects of unrelated male: female sex ratio on wounding and social relocations.

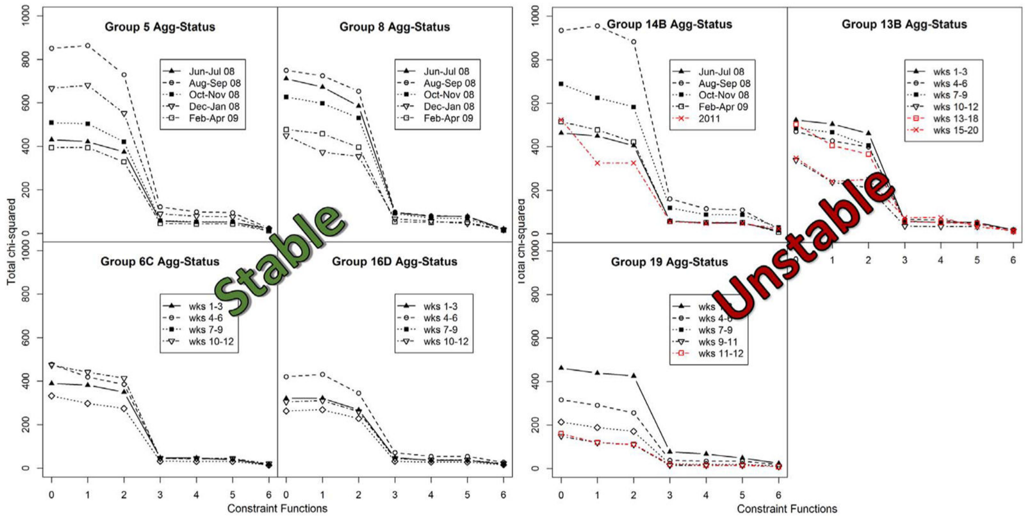

Fig. 6.

Joint modeling of aggression and status signaling networks during stable and unstable periods for stable and unstable groups of rhesus macaques. Note that the most common feature underlying unstable groups during unstable periods is a loss of linkage between aggression and SBT networks (constraint #3 in the figure) Reprinted from Beisner et al. (2015a,b).

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Table 1

Conflict policing behavior by male rhesus macaques.

Type of male	Mean impartial intervention freq.	[a] Mean support policing freq.	Mean male rank
Unrelated males	5 events/male	9.5 events/male	16.8
Natal males – alpha family	2.3 events/male	4.6 events/male	9.4
Natal males – other	0.7 events per male	1.4 events/male	51.2

[a]Support policing defined as a third party supporting an unrelated subordinate animal in a fight by directing aggression at the dominant animal in the fight, as in Beisner and McCowan (2013a,b).