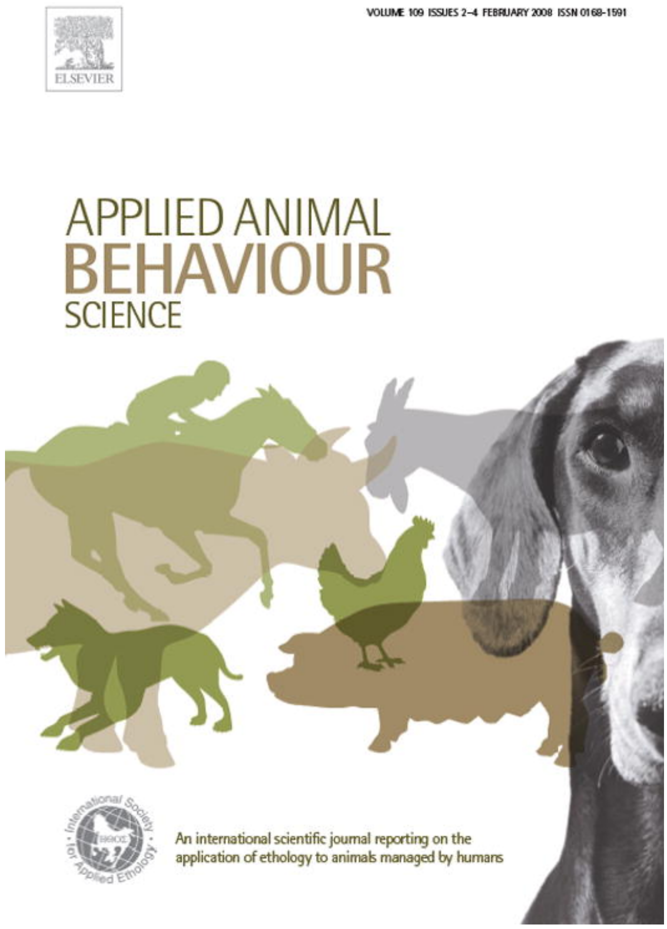
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Utility of social network analysis for primate behavioral management and well-being

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Abstract

New management strategies for detecting social instabilities and promoting social cohesion are needed to reduce aggression-based morbidity and mortality among captive groups of rhesus macaques. This study was conducted to determine the utility of social network analysis for deciphering patterns of aggression and wounding in rhesus macaques. Over 37,000 observations of affiliative, submissive and aggressive activities were collected over a 3-year period on ~1300 rhesus macaques housed in 13.2 ha enclosures. Data also were analyzed on management factors such as age/sex composition and matriline configuration that might promote or reduce aggression in rhesus macaques. Results suggest that social network measures such as subordination degree (social power), displacement fragmentation and groom reciprocity within social groups were not only significantly associated with rates of contact aggression and wounding but with the occurrence of severe aggressive outbreaks, known as cage wars. In addition, groups with a lower proportion of adult females and a more uniform distribution in the number of individuals across matrilines exhibited higher social power and lower fragmentation. These data indicate that by manipulating group composition and matriline configuration of social groups to promote social cohesion and stability, behavioral managers may be able to reduce the level of aggression and aggression-based morbidity and mortality. These data also show that social network measures are valuable predictors of deleterious aggression and even cage wars indicating that such measures could be used to longitudinally track changes in social dynamics to detect significant instabilities, allowing managers to prevent severe outbreaks before they occur in populations of rhesus macaques and perhaps other non-human primate species.

Keywords: Aggression; Social network analysis; Demographics; Macaque; Behavior management; Primate well-being

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1. Introduction

In the breeding programs of many primate centers and other facilities in the US, rhesus macaques (*Macaca mulatta*) are housed in multimale–multifemale social groups in large outdoor corrals, which simulates the natural social and environmental features characteristic of the species, enhancing their reproductive performance as well as their psychological well-being. Despite the importance of this naturalistic social housing, one of the most difficult problems in socially housed rhesus macaques is their propensity for spontaneous bouts of deleterious aggression (Thierry et al., 2004). Although aggression serves crucial functions in preserving social structure and order in rhesus groups (Bernstein and Ehardt, 1985; Flack and de Waal, 2004), in a captive setting aggression can become prolonged, escalated and intensified to the degree that it results in serious physical trauma and reduced psychological well-being.

In the wild, rhesus groups are characterized by female philopatry and male dispersal; females remain in their natal groups and form dominance hierarchies according to their matrilineal kinship (known as matrilines) while males emigrate from their natal groups at the beginning of the breeding season shortly before puberty, and may transfer groups throughout their lives in search of mating opportunities (Melnick et al., 1984). Female rhesus macaques very rarely leave their natal groups (Fooden, 2000).

Among females, rank remains relatively stable over a lifetime and is passed on to female offspring. Each female rises in rank above her older sister, and therefore when old, high-ranking females disappear or die, they are usually replaced by their youngest daughters, known as the youngest ascendancy rule. Dominance status and rank among males is not stable over a lifetime, compared to female rhesus macaques. Immature males inherit the rank of their mothers, but as they mature, their status changes based upon a combination of social and aggressive skills (Lindburg, 1971; Berard, 1999). Aggression is frequently used by both sexes to establish and reinforce social position, and aggressive behavior seen in macaques includes slapping, pushing, pulling fur, tail yanking, and biting as well as other non-contact behaviors such as displays and threats (Lindburg, 1971).

While social housing of rhesus as large multimale–multifemale breeding groups in outdoor corrals simulates the natural features of free-ranging rhesus macaques, because rhesus macaques rely so heavily on aggression to mediate their dominance relationships, there is enormous potential for aggression to escalate out of control when social groups become unstable (Bernstein and Ehardt, 1985), leading to severe wounding especially in the confines of a captive environment of densely housed groups. The dominance style of both captive and free-ranging rhesus macaques has been described as the most despotic of all macaque species by numerous experts on macaque behavior (de Waal and Luttrell, 1985). Both field and captive research have shown that 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). Conflict asymmetry in dominance relationships is high and aggression plays a particularly important role in maintaining dominance relationships (Bernstein and Ehardt, 1985). Lower level non-injurious aggression such as chasing and threatening serves to maintain social structure, order and stability within as well as between matrilines (Bernstein and Ehardt, 1985), but more severe aggression can result when dominance relationships between individuals become ambiguous or during conflicts over important resources (e.g., high quality food, reproductive opportunities). In captivity, such ambiguity can occur as a result of changes in management such as the removal of key individuals from an enclosure, but more frequently is a result of seemingly unpredictable changes in intra-group dynamics (Bernstein and Ehardt, 1985).

The frequency and intensity of aggression events and outbreaks varies significantly across different social groups demonstrating that certain groups may exhibit greater social stability than others. Such differences in cohesion across groups can be attributed to both endogenous and exogenous factors. Within-group social factors include differences in the expression of social relationships, partly due to variation in the personality and temperament (Capitanio, 1999; Capitanio and Widaman, 2005) as well as the dominance style of key animals within groups; while group-level management factors include group density, matriline/kinship structure and age/sex composition (Chapais and Berman, 2004; Aureli and de Waal, 2000; Thierry et al., 2004). Both factors are equally important and inextricably linked. For example, group-level management modifications such as animal relocations can affect group stability and further aggravate problematic aggression if key individuals are removed who serve as 'brokers' within social groups. Thus alternative management protocols based upon the factors known to promote social cohesiveness need to be developed to guide group formations and maintenance so as to preserve social stability and reduce deleterious aggression in rhesus macaque breeding groups. Key predictors of social instability in groups are also needed so as to prevent severe aggressive outbreaks before they occur.

This study was conducted to determine the utility of social network analysis (Carrington et al., 2005; Freeman et al., 1991; Gould and Fernandez, 1989; Sade, 1972; Sade et al., 1988; Scott, 2000; Wasserman and Faust, 1995) for deciphering patterns of aggression and wounding in rhesus macaques. Social network analysis is comprised of tools that provide a visual map of the connections among individuals and quantitative measures that substantiate the maps and the underlying patterns of relationships. The focus on patterns of relationships is what distinguishes social network analysis from other analytical techniques. This approach can analyze the structural properties of a network as a whole or from an individual's perspective; it is capable of identifying key individuals and examining how they fragment or integrate the overall structure of a social system. Therefore social network analysis could provide insight into the patterns of social relationships through quantitative measures such as "degree", "reciprocity", "betweenness", and "fragmentation" that are indicative of social instability that leads to higher rates of deleterious aggression and wounding.

The objective of this study was to evaluate dominance, affiliative and submission networks with respect to group-level management factors and patterns of aggression and wounding in group-housed rhesus macaques. This work was conducted to provide insight into designing beneficial management practices for group-housed macaques that minimize aggression-based morbidity and mortality and prevent severe outbreaks in rhesus breeding groups.

2. Methods

2.1. Subjects and behavioral observations

Data were collected using an event-sampling regime (Altmann, 1974) over 1 h sessions bimonthly across a 3-year period from each of 13.5 acre enclosures, each housing 70–150 rhesus macaques, at the California National Primate Research Center. Enclosures in which a cage war occurred were not observed after the cage war as the groups were fissioned or completely disbanded. Observers stood adjacent to or walked around the enclosure while collecting event-based data on subjects uniquely dye-marked for identification. Pedigrees and kinship for almost all animals in the enclosures are known. Observers were instructed to sample individuals evenly by equally scanning each quadrant in an enclosure to view different areas so as to minimize sampling bias of dominant and/or noticeable individuals. Interactions among infants and juveniles (less than 3 years of age) were excluded because the dominance relationships among juveniles are not well established. Adult and subadult subjects comprised 37–54% of the animals in groups. Data were collected on the affiliative, submissive and aggressive interactions among individuals within each group comprising a total of ~1000 h and 37,000 event samples in the data set. During observation sessions, one of four observers recorded the following information using a modified event-sampling design (Altmann, 1974) for each affiliative, submissive and aggressive interaction: (1) identification of the actor, (2) identification of the recipient, and (3) type of interaction for both actor and recipient (e.g., displacement, no contact aggression, contact aggression, conflict intervention, scream, silent-bared teeth display, other submissive behavior, groom, lipsmack, huddle, etc.). An interaction was defined as any act of affiliation, submission or aggression between two individuals including both the initial act and the recipient's response if any. Event-sampling was chosen over focal sampling to (1) maximize samples collected, thereby, improving statistical power and (2) because it allows for entire interactions involving multiple individuals to be followed. Inter-observer reliabilities were conducted and resulted in significant agreement ($\kappa = 0.65$, $p < 0.0001$), with a mean of 91% and a standard deviation of 3% (range: 86–94%) across the four observers.

2.2. Operational definitions of social behaviors

2.2.1. Displacement

One individual causes another individual to physically move away from the first individual.

2.2.2. Subordination

One individual produces a sign of submission such as the silent bared-teeth display to another individual that shows no noticeable signs of aggression or threat to the first individual. First individual also shows no sign of fear (e.g., fleeing, crouching, screaming, running away, etc.).

2.2.3. Groom

One individual moves hands through hair or over face (including eyes) of another individual.

2.2.4. Contact aggression

Contact during conflict with another individual such as pouncing, slapping, hitting, wrestling, grappling, and biting.

2.2.5. Wounds

Wounds severe enough to require that an individual be hospitalized for veterinary treatment.

2.2.6. Cage war

Severe and massive outbreak in aggression within or among matrilines, which leads to severe wounding and hospitalization (sometimes death) and results in the fission or complete disbanding the group.

2.3. Definitions of network measures

2.3.1. Displacement fragmentation

Fragmentation is defined as the proportion of mutually reachable nodes as each node is removed or unconnected from the network and calculated using the F measure as described in Borgatti (2003) and provided below as:

$$F = 1 - \frac{\sum_k s_k(s_k - 1)}{n(n - 1)}, \tag{1}$$

where s is the size of component k (groups of nodes remaining connected after removal of a node) and n is equal to the number of nodes (number of individuals in network). Values close to 1 indicate high fragmentation and values close to 0 indicate low fragmentation. As such, fragmentation is an inverse measure of the amount of connectedness or connection redundancy in a network. In the context of displacements, a higher degree of redundancy in dominance interactions among individuals (thus representing lower fragmentation) should result in less ambiguity over dominance relationships. Less ambiguity over dominance relationships should result in lower levels of aggression during displacement activities. Overall fragmentation for each group was calculated using the specified algorithm in the UCINet program (Borgatti et al., 2002).

2.3.2. Social power (subordination degree)

Degree was calculated in Netminer II (Cyram, 2005) as the number of subordination signals a given individual received multiplied by the number of individuals from whom subordination signals were given. Degree in this case represents both the number of individuals from which an individual receives subordination signals (diversity) as well as the number of subordination signals received from those individuals (rate). This measure is similar to the ‘‘social power’’ measure in (Flack and de Waal, 2004; Flack and Krakauer, 2005). These measures represent how others in the network perceive individuals by measuring the extent to which individuals agree over the status of dominant individuals in a group or the perceived capability of individuals to use force (Flack and de Waal, 2004; Flack and Krakauer, 2005). The greater the consensus the more ‘‘powerful’’ an individual is. The values from each analysis (representing rate and diversity) obtained for each individual were then used to calculate a mean to represent average social power or subordination degree and a standard deviation to represent variation among individuals in social power or subordination degree for each group. Social power or subordination degree was therefore considered as a measure of social cohesion because higher values of social power represent greater consensus by the social group over the status of the more dominant individuals within a group (Flack and de Waal, 2004; Flack and Krakauer, 2005). It is important to note that this measure is biased by the more dominant individuals in the group by default because these animals are more likely to receive signals of subordination than less dominant animals in the group.

2.3.3. Groom reciprocity

Reciprocity was calculated using data on grooming interactions as the ratio of the maximum number of reciprocated ties to the total number of ties for each group and was calculated using Netminer II (Cyram, 2005). Groom reciprocity represents the degree to which individuals in a group reciprocate the grooming of partners that had previously groomed them.

2.4. Group management data

Data were also collected on several group-level management factors including group size, proportion of different sex/age classes, number of matrilines, mean and standard deviation in the number of animals in each matriline, percentage of unrelated males, mean and standard deviation in kin coefficients representing the degree of relatedness among individuals within groups, as well as the number of wounds requiring hospitalization across the 1-year period for each group collected from CNPRC online veterinary records. These data were used as either outcomes or covariates in the statistical models (see below) to examine how group-level management factors influence levels of aggression and wounding across the 13 social groups.

2.5. Statistical analyses

All three network measures were then used to statistically examine, using normal, negative binomial or logistic regression in STATA 9.0 (Stata, 2005) with year as the clustering variable, the associations between the social network structures, rates of contact aggression, rates of wounding, and the occurrence of a cage war. Associations between the social network measures and group management factors were also examined. Group size was included as a covariate in each analysis to statistically adjust for differences in social network measures due to group size across enclosures.

3. Results

3.1. Associations with conflict, wounding and war

Fig. 1 presents the rates of wounding in relationship to social power, groom reciprocity and fragmentation across groups. Social power and groom reciprocity showed a significant negative relationship with wounding rate ($\beta = -0.12, p < 0.0001; \beta = -0.023, p < 0.02$; Fig. 1) while fragmentation showed a significant positive relationship with the rate of wounding ($\beta = 0.008, p < 0.02$; Fig. 1) as well as significant negative relationship with both social power ($\beta = -0.007$, $p < 0.0001$) and groom reciprocity ($\beta = -0.11$, $p = 0.059$; Fig. 1). These data indicate that groups with higher average social power (more consensus by others over the status of dominant individuals) and higher levels of groom reciprocity exhibit lower displacement fragmentation (less ambiguity over dominance relationships) and lower rates of wounding within their groups.

Social power showed a similar relationship with rate of contact aggression across social groups. Social power showed a significant negative relationship ($\beta = -1.69$, $p < 0.02$) (Fig. 2) with contact aggression, again indicating that higher social power is associated with a lower intensity of aggression within social groups. Social power did not show a negative relationship with rate of non-contact aggression ($p = 0.54$) across groups indicating that rate of overall aggression is not as important as the level at which it is expressed.

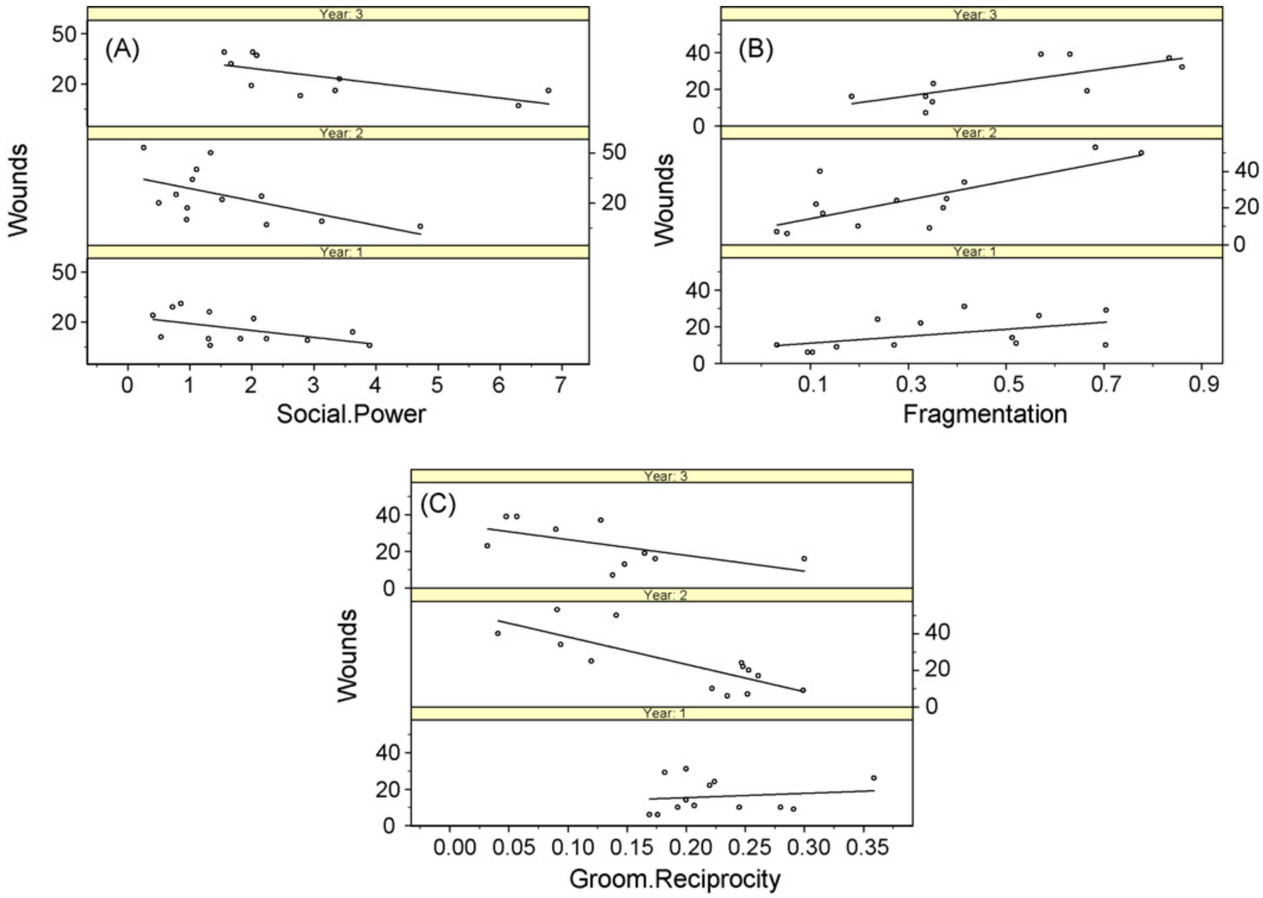

Fig. 1. Relationship between the rate of wounding requiring hospitalization and (A) social power, (B) displacement fragmentation and (C) groom reciprocity across groups for years 1–3 of the study.

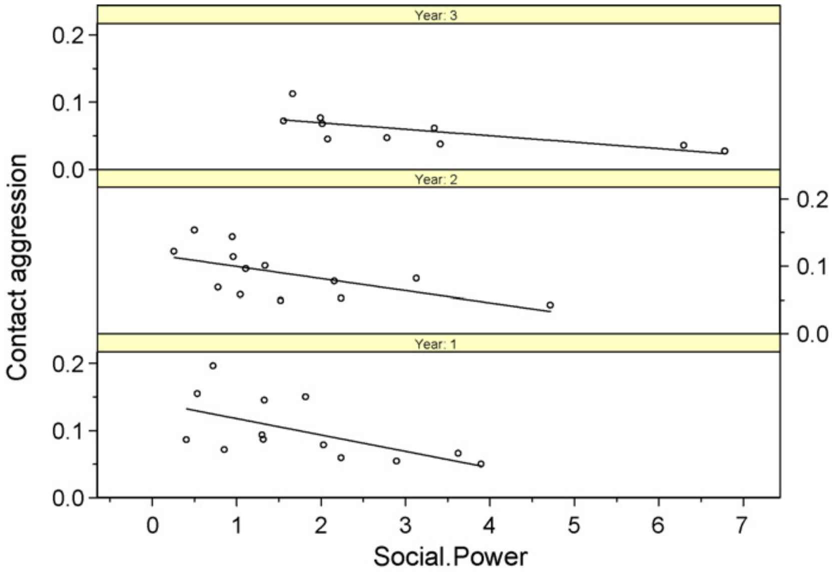

Fig. 2. Relationship between rates of contact aggression and social power across groups for years 1–3 of the study.

Finally, social network measures were used to forecast the occurrence of cage wars in rhesus groups ($N = 4$). The occurrence of a cage war in groups was associated with low social power ($\beta = -3.77$, $p < 0.009$), low groom reciprocity ($\beta = -0.59$, $p < 0.007$) and high fragmentation ($\beta = 0.11$, $p < 0.02$).

3.2. Associations with group management factors

We also examined whether group-level factors such as age/sex composition or matriline configuration might be used to explain the emergence of specific patterns in social relationships and thus deleterious aggression within groups. A higher proportion of adult females were associated with a lower average social power ($\beta = -0.03$, $p < 0.02$; Fig. 3). A more even distribution in the number of individuals across matrilines, as measured by the standard

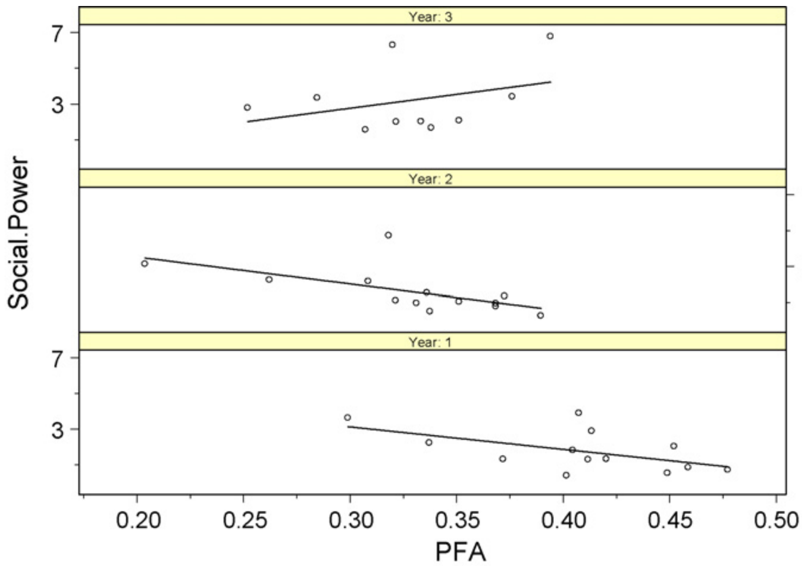

Fig. 3. Relationship between proportion of adult females in the group and social power across groups for years 1–3 of the study.

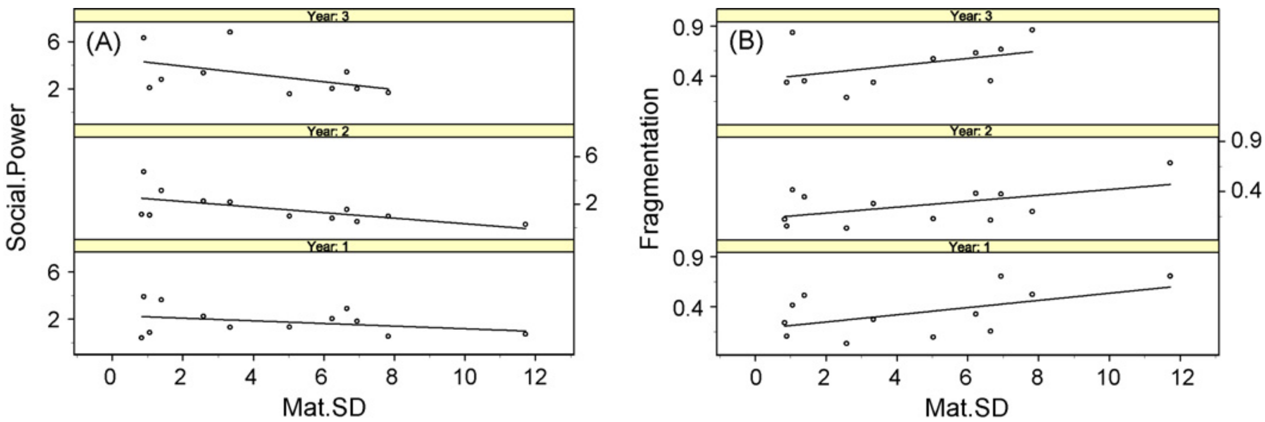

Fig. 4. Relationship between standard deviation in number of individuals per matriline and (A) social power and (B) displacement fragmentation across groups for years 1–3 of the study.

deviation, showed a significant negative relationship with social power ($\beta = -11$, $p < 0.0001$) and a significant positive relationship with displacement fragmentation ($\beta = -0.07$, $p < 0.0001$; Fig. 4). The alpha and beta males exhibited the most social power within groups with higher social power ($\beta = 0.22$, $p < 0.05$) and lower fragmentation ($\beta = -0.19$, $p = 0.05$). Furthermore, groups in which the alpha and beta males were unrelated males (unrelated to any of the animals in the group's matrilines) showed higher average social power and lower fragmentation than groups in which they were not ($\beta = 0.55$, $p < 0.004$; $\beta = -0.45$, $p < 0.004$).

4. Discussion

The results presented in this study quantitatively show that variations in management such as differences in group composition, matriline configuration and kinship patterns influence patterns of dominance and affiliation relationships which in turn may influence the integrity or cohesiveness of social groups resulting in variable rates of deleterious aggression and wounding within social groups. Groups with a lower proportion of adult females and a more even distribution in the number of individuals within matrilines exhibited higher average social power (higher consensus by others over the status of dominant individuals) and lower displacement fragmentation (less ambiguity over dominance relationships) as well as lower intensity of aggression and rates of wounding within their groups. We expected that groups with a higher proportion of adult females to show lower social power or higher fragmentation because adult females are known to be some of the worst instigators of deleterious aggression within social groups (Chapais and Berman, 2004; Bernstein and Ehardt, 1985).

Interestingly, the alpha and beta males were most powerful within groups with higher social power and lower fragmentation. In addition, groups in which the alpha and beta males were unrelated males (i.e., adult males who are unrelated to any of the matrilines in the social group) showed higher average social power than groups in which they were not. These results are also expected because alpha and beta males are commonly the individuals that intervene during third party conflicts (Flack et al., 2003) and may particularly be apt to do so when they have high social power within groups and thus a low cost of being injured during conflicts (Flack et al., 2003; Flack and de Waal, 2004).

Matriline configuration may also play a role in promoting social cohesion within groups. Our data indicate that a more even distribution in the number of individuals comprising each matriline may reduce the probability that a highly despotic social structure (with one or two large dominant matrilines and a number of smaller matrilines) could persist in a social group. Because kin recruitment and support is so critical during conflict resolution and in maintaining dominance status in rhesus societies (Aureli and de Waal, 2000), greater kin support across matrilines should keep dominant matrilines and individuals ‘‘in check’’ and thus reduce the despotic tendencies of more dominant individuals from being expressed.

Furthermore, results from the analysis of grooming networks indicate that more cohesive social networks, as measured by lower fragmentation in displacement networks, appear to be associated with higher rates of affiliative reciprocity among social group members.

Finally, the results on the occurrence of cage wars within groups indicate that social network measures such as displacement fragmentation, social power and groom reciprocity may be valuable predictors of severe aggressive outbreaks in rhesus groups and might be used to longitudinally monitor changes in social group dynamics indicative of instability in order to prevent severe outbreaks before they occur. However, it is important to note that the relationships observed between social network measures, wounding and war in this study are only associations. Current work is being focused on building longitudinal temporal models (that includes the amount of weekly monitoring time necessary for detection) so that we can design a practical monitoring regime that will allow the detection of problematic social patterns in groups and thus prevent social overthrows and cage wars before they occur.

Therefore, in combination, these data indicate that a continued effort in understanding how these and other group management factors (animal harvesting, husbandry procedures, etc.) impact social group stability through influences on the structure and patterns of social relationships on a longitudinal basis will us allow us to gain greater insight into why focal events and large outbreaks of severe aggression occur. Such insight will allow us to develop improved management practices for group-housed macaques that will minimize deleterious aggression, reduce its associated morbidity, mortality and animal welfare concerns and prevent severe aggressive outbreaks in rhesus groups and perhaps other non-human primate species.

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