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Sex Ratio, Conflict Dynamics, and Wounding in Rhesus Macaques (*Macaca mulatta*)

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Abstract

Rhesus macaques, like many other primates, live in stable, multi-male multi-female groups in which adult females typically outnumber adult males. The number of males in multi-male/multi-female groups is most commonly discussed in terms of mate competition, where the sex ratio is a function of an adult male's ability to monopolize a group of females. However, the relationship between sex ratio and group stability is unclear because the presence of many males may either reduce stability by increasing mate competition or may improve stability if adult males are key conflict managers. We investigated the relationship between sex ratio, male intervention behavior, and trauma in seven groups of captive rhesus macaques. Our results show that high-ranking adult males intervene twice as frequently as adult females ($P < 0.0001$) and are about twice as successful ($P < 0.0001$). Furthermore, the type of adult males present in the group affects the relationship between intervention behavior and rate of traumas: males must be unrelated to the highest-ranking matriline. Groups with a lower ratio of females per male unrelated to the alpha and beta matriline had better intervention success ($P < 0.04$) and fewer traumas requiring veterinary care ($P = 0.003$). We conclude that conflict management behavior by adult males, particularly those unrelated to the highest-ranking matriline, is the mechanism by which sex ratio influences the frequency of traumas, and thus group stability. We therefore suggest that monitoring and managing the sex ratio of captive primate groups is one of many measurements to predict group stability.

Keywords

intervention; conflict management; group stability; captivity; aggression; males

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1. Introduction

1.1 Sex Ratio

Rhesus macaques, like many other cercopithecine primates, live in stable, multi-male multi-female groups in which adult females typically outnumber adult males (Lindburg, 1971). The presence of multiple males per group typically arises when a single adult male cannot monopolize a group of females from other adult males (Andelman, 1986; Clutton-Brock, 1989). While a small group of females may be defensible by one male, a large group of females is not only less defensible, but attracts more potential male competitors (Andelman, 1986). Indeed, smaller wild groups of rhesus macaques may have a single adult male, whereas larger groups typically have multiple adult males (Lindburg, 1969; Neville, 1968). Therefore, according to socio-ecological theory, group sex ratio is a function of the number of females a male is able to successfully defend, and its evolution is the product of selective pressures such as mate competition. However, there may be other factors that contribute to the maintenance of group sex ratio.

In a recent study, Flack and colleagues investigated conflict management behavior as a potential robustness mechanism, which serves to prevent the outbreak of very severe or uncontrolled aggression, within a captive group of pigtailed macaques (*Macaca nemestrina*) (Flack et al., 2005b). In this study, three adult males were the primary conflict managers in the group, suggesting that adult males play a role in the maintenance of group stability. If this is generally true for other multi-male/multi-female species, then the relative number of males has the potential to influence group aggression and stability, particularly in captive groups where the sex ratio cannot be adjusted by the group members themselves via immigration and emigration. As a result, the successful management of captive groups of primates may involve active management of group composition to achieve an optimal sex ratio.

1.2 Group stability

Stable social groups are those that persist through time in spite of competition that regularly arises among group members. However, incipient instability is difficult to measure because typically an unstable social group may only be identified as being unstable after it has fallen apart. Among wild primate groups, a reduction in group stability may lead to group fission (Dittus, 1988) whereas among captive primate groups, fission is not possible because emigration is constrained by the confines of the enclosures. Rather, in captivity, increased rates of aggression and wounding appear to be indicators of group instability as these are associated with decreased network cohesion and incidence of social overthrow (Flack et al., 2006; Flack et al., 2005b; McCowan et al., 2008; Oates-O'Brien et al., 2010). This is perhaps because as conflict among group members increases within a captive group, targeted individuals cannot escape their attackers, resulting in higher rates of injury.

1.3 Sexual dimorphism and the role of adult males

The mechanism by which sex ratio may influence group-level aggression and stability may be through the role that males play in the group, which in part is associated with their physical size. In general, sexual dimorphism is thought to result from sexual selection favoring large body size, large canine size, and aggressiveness in males. While sexual dimorphism is most pronounced in single-male/multi-female groups, males of species living in multi-male/multi-female groups exhibit a more intermediate degree of sexual dimorphism (Harvey and Harcourt, 1984). For example, among macaques, adult males are larger than adult females, and the degree of body size sexual dimorphism (natural log of male body weight minus female body weight) ranges from a high of 0.59 in *Macaca nigra*, in which males are close to twice the size of females, to a low of 0.2 in *M. cyclopis* and *M. mulatta*.

(Thierry, 2007). Certainly, sexually dimorphic males have a competitive advantage over females due to their physical size and strength. So if males use their competitive advantage to intervene in others' conflicts and diffuse aggression, then groups with lower ratio of females to males will have lower rates of aggression, less trauma and better stability.

1.4 Males as conflict managers

Agonistic interactions among macaques frequently involve three (or more) participants because third-parties often intervene in others' conflicts to influence the outcome (Boehm, 1981; Datta, 1986; Kaplan, 1978). Interventions that result in the termination of the original conflict are successful interventions, and the frequency of such interventions may impact group stability by diffusing aggression and preventing aggression from spiraling out of control. Indeed, Flack and colleagues identified third-party impartial intervention (also referred to as policing) as a robustness mechanism that promotes group stability in a captive group of pigtailed macaques (*Macaca nemestrina*) (Flack et al., 2005b). In this group of pigtailed macaques, a few very powerful group members successfully, and impartially, intervene in the conflicts of others by approaching, but not threatening or attacking, the participants of the conflict. The function of impartial policing in promoting group stability was supported by a knockout experiment: when the three most frequent and successful interveners were temporarily removed, rates of aggression increased and social cohesion decreased, suggesting that group dynamics were temporarily destabilized (Flack et al., 2005a; Flack et al., 2006).

1.4.1 Must the conflict managers be males?—High-ranking adult males were the most frequent and successful policers in Flack and colleagues' captive group of pigtailed macaques, but the alpha female was also a key policer (Flack et al., 2005a). Thus, it is unknown whether adult males are typically the primary conflict managers, or whether females, or even lower-ranking individuals, might be key interveners in some groups. Flack and colleagues (2005a; 2005b) argue that these policers have high social power (defined as a high degree of group consensus that the individual is capable of successfully challenging others) and low intervention cost because there is a low risk of retaliation. Group members may regard adult males as having high social power because sexually dimorphic adult males are physically larger and stronger than females, which gives males a competitive advantage and a lower risk of retaliation from other group members, particularly against females and juveniles. We predict that, in sexually dimorphic species, adult males intervene more frequently and are more often successful than adult females. We further predict that groups with a lower ratio of adult females to adult males will have (1) a higher proportion of successful interventions, (2) shorter average conflict event lengths, and (3) fewer traumas per year.

1.4.2 Intervention behavior as conflict management?—Intervention behavior does not necessarily have a positive influence on group stability. Interventions that result in the continuation of the original conflict may contribute to instability, particularly if the intervention triggers a cascade of aggression. Indeed, outbreaks of severe aggression have been associated with social overthrow in captive rhesus groups (McCowan et al., 2008; Oates-O'Brien et al., 2010). We predict that groups with more frequent successful interventions have shorter conflict events and lower rates of trauma.

1.5 Rhesus macaques and the captive environment

If adult males are indeed important conflict managers for rhesus groups, two questions remain (1) how many adult males are needed to maintain group stability and (2) in captivity, where male dispersal is not possible, do unrelated males have different rates of success compared to natal/related males. First, if larger groups exhibit greater stability when more

conflict managers are present, then group stability might be maximized at an optimal ratio of females per male such that there is a sufficient number of conflict managers per group member but not so many males that intrasexual competition increases. Furthermore, wild groups are more likely to possess this optimal sex ratio due to group members' ability to adjust group membership via male dispersal/immigration, whereas captive groups likely have a higher ratio of females to males. Second, high-ranking juvenile natal males have been found to act in opposition to group stability in rhesus macaques (Beisner et al., 2010) while alpha and beta males that are unrelated to the groups' matriline are associated with improved group stability (McCowan et al., 2008). This suggests that unrelated males may be more effective interveners, and that groups with a lower ratio of adult females per unrelated adult male will have better intervention success, lower rates of trauma and shorter conflict events.

2. Methods

2.1 Study site and subjects

The study was conducted at the California National Primate Research Center (CNPRC) in Davis, CA, USA from June 2008 through early December 2009. This research was approved by the University of California, Davis Institutional Animal Care and Use Committee, protocol #11843. The subjects of this study were seven groups of rhesus macaques housed in 0.2 ha enclosures. Although the degree of group stability is difficult to ascertain prior to its dissolution, we attempted to select study groups of varying degrees of stability as variation is necessary to detect relationships among variables. All enclosures were similar in having ten A-frame houses, multiple suspended barrels, swings and several perches. Groups were fed a standard monkey chow diet twice per day at approximately 07:00 h and again between 14:30 and 15:30 h. Fresh fruit or vegetables were provided twice per week.

2.2 Sampling methods

Two observers (primary observers: BAB, MEJ) recorded aggressive interactions among juvenile, subadult, and adult males and females. Inter-observer reliability tests were conducted every few months in which all observers would watch the same group for 30 minutes and score the same conflicts. Inter-observer reliabilities had a mean of 91% agreement and a standard deviation of 3%; range: 86–94%; kappa = 0.65, $p < 0.0001$ across three observers. Each group was observed from 09:00 – 12:00 h and 13:00 – 16:00 h, four days per week, on a 4-week rotating schedule. Groups 5, 8, and 14 were observed June 2008 - April 2009, and Groups 1, 10, and 18 were observed May - December 2009, which yielded 8–11 weeks of observation (192–264 h) per group. Group 16 was observed only June - November 2008 due to a social overthrow that occurred December 3, 2008.

An event sampling design was used to collect data on agonistic events which were recorded as an ordered series of dyadic interactions. Observers made an effort to record all occurrences of agonistic interactions, but if multiple events occurred simultaneously, each observer followed only one event (the event that started first). Both aggressive and submissive behaviors were recorded for all individuals participating in each agonistic event; aggression and submission were categorized in increasing levels of severity (Table 1). Intense aggressive interactions included aggression levels 6 – 8 (see Table 1): bite < 5 s, chase and bite < 5 s, and bite > 5 s.

We collected a total of 76,168 aggressive dyadic interactions (from 18,920 conflict events) and a total of 6,924 conflict interventions in the seven study groups. Conflict intervention is the involvement of a third-party in a conflict between others that is already occurring. From these data, we calculated several individual- and group-level variables (defined below), including intervention success and conflict event length. Successful intervention was defined

as cessation of aggression between the targeted dyad. We measured intervention success at the level of the individual as the proportion of conflict interventions that are successful multiplied by the number of successful interventions for each individual. This measure takes into account how successful an individual is in stopping conflict but also the rate at which they do so. Individuals with higher intervention success are those that intervene successfully and do so regularly. We also calculated intervention success at the group level as an averaged measure of the proportion of successful interventions multiplied by the number of successful interventions, weighted by individual. Conflict event length, a measure of conflict severity, is the total number of aggressive dyadic interactions per conflict event (it was not possible to record total duration of these complex conflicts). We also calculated the average conflict event length as an additional measure of intervention success – groups with more successful interveners should also have shorter conflict event lengths.

The adult sex ratios reported for wild and free-ranging groups typically define female rhesus macaques to be sexually mature at 3.5 – 4 years old based upon first pregnancy (Bercovitch and Harvey, 2004; Drickamer, 1974). However, we defined females as being sexually mature at 2.5 – 3 years of age since 11–16% of 3-year-old females give birth each year, and most 2–3 year old female rhesus macaques at the CNPRC have begun cycling, which is likely due to better nutrition and higher body fat percentage (Small, 1981). The age of sexual maturity among male rhesus macaques is less obvious, and is reported to be between 4.5 – 6 years of age (Melnick, 1981; Napier and Napier, 1967). However, whether better nutrition in captivity reduces the age at sexual maturity for male rhesus macaques is unclear because viable sperm production is not easily observed. Males in our captive groups regularly participate in consortships with adult females beginning around 4 years old, and so we defined males as being sexually mature at 4 – 4.5 years old. The adult sex ratio of each group was calculated as the number of adult females per adult male, and was based upon the median group membership for each year.

Sex ratio was also calculated with regard to unrelated adult males: first as adult females per adult male not related to the alpha or beta matriline and second as adult females per adult male unrelated to any other group member. We investigate these additional measures of sex ratio for two reasons. (1) Males in captive groups cannot disperse and these natal males, particularly those from high-ranking families, may have a negative impact on group stability (Beisner et al., 2010), and (2) the presence of unrelated alpha and beta males is associated with decreased incidence of contact aggression, wounding, and risk of social overthrow in captive rhesus groups (McCowan et al., 2008; Oates-O'Brien et al., 2010).

We counted the total number of traumas (injuries requiring veterinary care) for each of 13 groups for two years (2008 and 2009). Data on traumas were obtained from CNPRC veterinary hospital records. Information on age and sex composition and group size of each group was obtained from CNPRC behavioral management records.

2.3 Statistical analyses

We analysed the data using linear and generalized linear mixed-effects regression models with either Poisson or Gaussian distributions depending on the outcome measure (McCullagh and Nelder, 1989). Models were fit to the data for five dependent variables (two dependent variables at the individual level, $N=323$ individuals; three at the group level, $N=7$ groups and 13 groups, see below): (1) count of interventions per individual, (2) intervention success per individual, (3) the average conflict event length per group, (4) the averaged weighted intervention success per group, and (5) the count of annual traumas per group. There were two datasets for the dependent variable annual traumas per group. The first dataset included the seven groups for which behavioral observations were conducted between June 2008 and December 2009 to perform regression analyses using the fixed

effects of average conflict event length per group and the averaged intervention success per group. The second dataset included 13 groups (the seven study groups plus six additional groups that had not been observed, but for which sex ratio, group size, and trauma data were available) over two years ($N = 26$ group years) to perform a regression analysis using the fixed effect of sex ratio. To assess whether one measure of sex ratio is a better predictor of group stability than the other, we used Akaike's Information Criterion (AIC) scores to select the best fit model, i.e., the model with the lowest AIC score. Models having a difference in AIC less than or equal to two were considered equivalent (Burnham and Anderson, 2002). For individual-level analyses, fixed effects included sex, rank, the interaction term sex $\times$ rank, and male's relatedness to the alpha and beta matriline. For group-level analyses, fixed-effects included the number of adult females per adult male, the number of females per adult male unrelated to the alpha and beta matriline, average group size, the proportion of successful interventions per group, and the average conflict event length per group. Most group-level analyses were univariate due to lack of power with a sample of $N=7$ groups.

To assess whether the sex ratio differs significantly between wild, free-ranging rhesus groups and captive rhesus groups at the CNPRC, we performed a Mann-Whitney U-test on the number of adult females per male. Sex ratios for wild, free-ranging groups were obtained from the literature (Makwana, 1978; Sahi and Sharma, 2004; Southwick et al., 1965; Southwick et al., 1961; Teas et al., 1980). All analyses were performed using Stata (Stata Corporation, College Station, Texas) and the R statistical computing program (R Development Core Team, 2008).

3. Results

3.1 Individual-level

3.1.1 Intervention frequency—We fit a multi-level Poisson regression model to counts of interventions per adult for each group, and fixed-effects included sex, rank, and the interaction term sex $\times$ rank. Adult males intervened in others' conflicts more often than adult females ($\beta = 0.67$ $P < 0.0001$; Fig. 1), and high-ranking individuals intervened more often than lower-ranking individuals ($\beta = -0.02$, $P < 0.0001$). The interaction term indicated that high-ranking adult males in particular intervene most frequently ($\beta = -0.02$, $P < 0.0001$).

3.1.2 Intervention success—We fit a negative binomial regression model to intervention success (the number of successes multiplied by the proportion of successful interventions per individual; $N=323$), and fixed-effects included sex, rank and the interaction term sex $\times$ rank. Adult males were more often successful in stopping the conflict than adult females ($\beta = 0.81$ $P < 0.0001$), and high-ranking individuals were more successful than lower-ranking individuals in stopping others' conflicts ($\beta = -0.01$, $P < 0.0001$). The interaction term indicated that high-ranking adult males in particular were the most successful interveners ($\beta = -0.02$, $P < 0.0001$; Fig. 2).

We fit a Poisson regression model to intervention success among males only ($N = 88$) with fixed-effects for male's relatedness to other group members and rank. Adult males that were unrelated to any other group member were more often successful in stopping conflicts than related males ($\beta = -0.27$, $P = 0.01$; Fig. 3).

3.2 Group-level

3.2.1 Conflict event length—We fit a linear model to the average length of conflict events per group ($N = 7$ groups) with fixed effects for the average group size and average group-level proportion of successful interventions. Groups with a higher proportion of successful interventions also had shorter conflict events, on average ($\beta = -0.77$, $P = 0.002$),

and larger groups had shorter conflict events, on average, than smaller groups ($\beta = -0.003$, $P = 0.04$).

3.2.2 Intervention success—We fit three linear models to the average intervention success per group (averaged weighted measure by individual of the proportion of successful interventions multiplied by the number of successful interventions), with a fixed-effect for the three different measures of sex ratio. The best fit model had a fixed-effect for sex ratio measured as the ratio of adult females per adult males unrelated to the alpha and beta matrilines. A high ratio of adult females per adult male unrelated to the alpha and beta matrilines was associated with lower intervention success ($\beta = -0.079$, $P < 0.04$). However, all three models had very similar AIC scores (AIC = 3.51, 3.94, 3.99). In the second and third best fit models, the ratio of adult females per adult male ($\beta = -0.18$, $P = 0.53$) and the ratio of adult females per adult male unrelated to any group member ($\beta = -0.26$, $P = 0.93$) were not significant.

3.2.3 Traumas per group—We fit two separate Poisson regression models to the count of annual traumas per group, one with a fixed-effect for proportion of successful interventions per group and the second with a fixed effect for average conflict event length per group ($N = 7$ groups). Groups with a higher proportion of successful interventions had fewer traumas per year ($\beta = -49.4$, $P < 0.0001$), and those with shorter conflict events had fewer traumas per year ($\beta = 103.9$, $P < 0.0001$).

We fit three negative binomial regression models to the count of annual traumas per group with fixed-effects for the three different measures of sex ratio and for group size ($N = 26$ group years). The best fit model had fixed-effects for group size and sex ratio measured using adult males unrelated to the alpha and beta matrilines. Groups with more adult females per adult male unrelated to the alpha and beta matrilines had significantly more traumas per year ($\beta = 0.10$, $P = 0.003$). However, all three models had very similar AIC scores (AIC = 242.0, 242.9, 244.0). In the second and third best fit models, groups with more adult females per adult male ($\beta = 0.11$, $P = 0.006$; $N = 26$; Fig. 3) and those with more adult females per adult male unrelated to any group member ($\beta = 0.01$, $P = 0.013$) had significantly more traumas per year. However, there was no effect of group size on the frequency of traumas ($\beta = 0.003$, $P = 0.5$; $N = 26$).

3.3 Adult sex ratio in wild versus captive groups

On average, the number of adult females per adult male was significantly higher for CNPRC groups than among wild rhesus groups (Mann-Whitney U-test: $U = 291$, $P = 0.03$) Wild groups ranged from 1.2 – 5.7 adult females per adult male (median = 2.4, $N = 16$ groups), and CNPRC groups ranged from 0.6 – 10.7 adult females per adult male (median = 5.3, $N = 26$ group years; Fig. 4).

4. Discussion

The number of males in multi-male/multi-female groups is most commonly discussed in terms of mate competition, where the sex ratio (the number of females per male) is a function of an adult male's ability to monopolize a group of females. Larger groups of females are less defensible, which allows additional males to join the group. However, the relationship between sex ratio and group stability is unclear. One might expect that multi-male/multi-female groups with many male competitors would be unstable because of the potential for increased intrasexual competition for females. However, previous research on a captive group of pigtailed macaques suggests that adult males may play a crucial role in conflict management and preventing outbreaks of severe aggression (Flack et al., 2005b), thereby indicating that groups with a lower ratio of adult females to adult males have greater

stability. We investigated the relationship between sex ratio, male intervention behavior, and trauma in seven groups of captive rhesus macaques. Our results indicate that conflict management behavior by adult males is the mechanism by which sex ratio can influence group stability.

4.1 Individual-level results

Adult males, rather than adult females, appear to be the key conflict managers in rhesus groups, which is consistent with patterns of intervention behavior noted in other macaque species (Flack et al., 2005a; Petit and Thierry, 1994). Males intervened more frequently than females and were more successful than females in stopping the targeted conflict. There are several possible reasons for this sex difference in intervention behavior. First, male rhesus macaques are sexually dimorphic, having larger body size and canine size than females (Thierry, 2007), suggesting that males' greater physical strength and competitive ability allows them to intervene with less risk of retaliation or injury, which may in turn result in a higher probability of stopping the conflict. Second, females outnumber males in multi-male/multi-female groups, meaning that most conflicts are between females. Since sexually dimorphic adult males have a competitive advantage over females, there are fewer conflicts in which a female can successfully intervene without significant risk to herself. Finally, females' ranks are established and maintained through alliances with both kin and nonkin, whereas males' ranks are more often based upon age, body size, or group tenure (Sprague, 1998). Therefore, any conflict involving females is likely to have an impact, either directly or indirectly, on females' individual or matriline rank and is less likely to influence males' rank. As a result, females may often intervene to exacerbate a conflict, whereas male interventions should less often result in the exacerbation of a conflict. Females do, however, perform interventions, frequently supporting kin during fights, particularly their own offspring (Cheney, 1977; Horrockes and Hunte, 1983; Kaplan, 1978). But females may be less successful interveners than males.

Furthermore, high-ranking adult males intervened most frequently and had the greatest success in stopping conflicts. This is not surprising because high-ranking adult males most likely attained their high rank as a result of their competitive ability, which is linked to body size, and canine size (Sprague, 1998). However, high-ranking individuals in general intervened more often and had a higher proportion of successful interventions than low-ranking individuals regardless of sex, which suggests that an individual's ability to manage the conflicts of others is not entirely explained by sexual dimorphism. These results support the finding that the alpha female in a captive group of pigtailed macaques was one of the four most successful conflict managers (Flack et al., 2005a; Flack et al., 2005b). Thus, adult females may also be key conflict managers, but are perhaps less successful and less influential than adult males.

4.2 Group-level results

Conflict intervention behavior by adult males appears to be the mechanism by which sex ratio is associated with group-level stability and it matters what type of males are present. At the group-level, a high ratio of adult females per adult male unrelated to the alpha and beta matrilines is associated with lower intervention success and higher rates of wounding across groups. Given the individual-level result that high-ranking adult males are the most frequent and successful interveners, it seems that these high-ranking males are responsible for the group-level intervention success rate and average conflict event length, and therefore contribute to group-level stability. Thus, calculating the group sex ratio may be a simple way of predicting the group's overall health and stability, particularly in captive settings where behavioral managers need to determine the likelihood of severe aggression and social overthrow.

4.2.1 Sex ratio as a measure of group stability—The utility of sex ratio as a tool to predict the stability of primate groups depends upon the definition of sex ratio. The best fit models indicate that sex ratio, as measured by the number of adult females per adult male unrelated to the alpha and beta matriline, is associated with both the frequency of wounding per group and intervention success. However, the second and third best fit models suggest that calculating sex ratio using all adult males is also pertinent to understanding the frequency of traumas, but is not relevant to intervention success. Therefore, while calculating the ratio of adult females per adult male may provide an approximation of the likelihood of trauma and instability, it is not sufficient for primate groups to meet a criterion for a particular number of adult males. Those adult males must be unrelated to the females of the alpha and beta matriline to have more successful interventions and maximally contribute to group stability. These results support our previous findings that unrelated alpha and beta males contribute to group stability while natal juvenile males may act in opposition to group stability (Beisner et al., 2010). At the CNPRC, groups with unrelated alpha and beta males have lower rates of contact aggression, trauma, and lower probability of social overthrow (McCowan et al., 2008), whereas groups with more high-ranking natal juvenile males have higher rates of trauma because these juvenile males started more fights and used intense aggression more frequently than other males (Beisner et al., 2010). We suggest that calculating group sex ratio, particularly the ratio of adult females to adult males unrelated to the highest-ranking matriline, is a simple, preliminary method of estimating the degree of group stability, which may inform behavioral managers which captive groups merit further investigation and attention.

4.2.2 Optimal sex ratio—Among the 13 captive rhesus groups measured at the CNPRC, the ratio of adult females per adult male ranged from 0.6 to 10.7 (mean = 4.9) which is significantly higher than wild rhesus groups (range: 1.2 – 5.7; mean = 2.6) (Makwana, 1978; Sahi and Sharma, 2004; Southwick et al., 1965; Southwick et al., 1961; Teas et al., 1980). Wild rhesus groups are more likely to be at their optimal sex ratio than captive groups because adult males in wild groups are free to disperse and to compete with other males and change the sex ratio whereas male dispersal is not possible in captivity, and group members cannot adjust their group membership. This suggests that a sex ratio of approximately two or three adult females per adult male is the optimal sex ratio for rhesus macaques, and behavioral managers should aim for this sex ratio in their efforts to improve group stability. However, the need for maintenance of stability may be greater in captive groups, where the rate of conflicts is typically higher (Rowell, 1967; Southwick, 1969), which might suggest that an even lower sex ratio is ideal for captive groups relative to wild groups. Alternatively, animals in captive groups are in closer proximity, and it may be possible for a few males to do the job of many when in such close quarters, whereas males in wild groups may be more spread out and less able to intervene frequently enough to have an effect on group stability.

4.2.3 Managing rhesus in captivity—Rhesus macaques are classified as the most despotic of the macaques (Thierry, 2004), meaning they are characterized by frequent, severe aggression and highly asymmetrical dominance interactions compared to other species of macaques. Additionally, rates of aggression are higher in captive than in wild, free-ranging groups (Southwick, 1969). For these reasons, aggression may be more likely to spiral out of control in captive groups of rhesus macaques, and it may be relatively easy for one aggressive transaction to trigger a cascade of aggression. Captive rhesus group stability might, therefore, be more dependent upon third-party interventions to maintain group stability. Alternatively, with such frequent and severe aggression, and a high probability of triggering a cascade of aggression or a high probability of retaliation, as evidenced by low rates of reconciliation, (De Waal and Ren, 1988), it might be too risky for third-parties to get involved in others' conflicts, particularly if the intervener's goal is to stop the aggression.

rather than join the winning side. In our study groups, intervention behavior by adult males is associated with rates of trauma and conflict event length, indicating that third-party intervention is indeed important to group stability but may be too risky for all but the largest, most powerful males in the group.

An association between adult male conflict intervention behavior, sex ratio, and group stability has implications for the successful management of captive groups of primates. First, management of captive groups of primates is challenging, and sufficient behavioral observation to diagnose group instability is time consuming. Therefore, sex ratio may be a simple first step in predicting whether or not the captive group is stable and healthy, or whether the group is in need of further management attention. Second, rhesus macaques are the most commonly used primate species in captive research facilities, and are also highly aggressive and prone to severe outbreaks of aggression (McCowan et al., 2008; Oates-O'Brien et al., 2010), which results in injury to the animals and compromises their welfare. Therefore, conflict management by adult males may be particularly crucial to the effective management of rhesus groups, and our results will be applicable to a large number of research facilities.

5. Conclusion

Third-party interventions by high-ranking adult males unrelated to the highest-ranking matriline appears to be the mechanism by which sex ratio influences group stability, as measured by intervention success, average conflict length, and frequency of traumas. Behavioral managers may calculate the group sex ratio, particularly with respect to males unrelated to the alpha and beta matrilines, as a quick estimate of the current stability and social health of captive groups of primates.

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Fig. 1. Intervention frequency by sex

The expected frequency of interventions per individual ($N = 323$) for male and female interveners, calculated from model coefficients from the multi-level Poisson model of intervention frequency. Intervention frequency was measured as the total count of interventions per individual over the study period.

Fig. 2. Intervention success by sex and rank

The expected intervention success per individual ($N = 323$) for male and female interveners across all ranks, calculated from model coefficients from the negative binomial regression model of intervention success. Intervention success was calculated as the number of successful interventions multiplied by the proportion of interventions that were successful, which accounts for both rate and extent of success.

Fig. 3. Intervention success for adult males based upon relatedness to alpha and beta matriline
 The expected intervention success per adult male ($N = 88$) across all ranks for males unrelated to the alpha and beta matriline and those related to them, calculated from model coefficients from the Poisson model of male intervention success. Intervention success was calculated as the number of successful interventions multiplied by the proportion of interventions that were successful, which accounts for both rate and extent of success.

Fig. 4. Annual trauma rate by sex ratio

The annual rate of traumas per group is plotted by group sex ratio for 13 captive rhesus groups at the CNPRC across two years ($N = 26$ group years). Sex ratio was calculated as the number of adult females per adult male, and annual trauma rate was calculated as the total frequency of injuries per group per year (for both 2008 and 2009) divided by the mean group size for that year. The least-squares regression line is included.

Fig. 5. Sex ratio in wild versus captive rhesus groups

The ratio of adult females per adult males for 13 captive rhesus groups at the CNPRC (N = 26 group years) and 16 wild rhesus groups (Makwana, 1978; Sahi and Sharma, 2004; Southwick et al., 1965; Southwick et al., 1961; Teas et al., 1980). Boxes represent the inter-quartile range, and the black bar is the median sex ratio. The upper (and lower) whiskers are drawn to the largest (or smallest) data point not lying above the 75th percentile (or below the 25th percentile) + 1.5*IQR.

Table 1

Aggression and submission behaviors categorized by increasing levels of severity

Level	Aggression	Submission
1	threat	SBT ^a
2	vocal threat or threat and follow	turn away
3	lunge or mild slap	turn away + SBT
4	chase < 3 m	move out of arms' reach
5	chase > 3 m or grapple	move out of arms' reach + SBT
6	bite < 5 s	run away < 3 m
7	chase and bite < 5 s	run away < 3 m + SBT
8	bite > 5 s	run away > 3 m
9	N/A	run away > 3 m + SBT
10	N/A	prolonged scream
11	N/A	crouch ^b
12	N/A	crouch ^b + SBT

^aSilent bared-teeth display^bAnimal stops resisting aggression and gives up, e.g. during mobbing events