Reproductive males are effective at managing conflict in captive Sulawesi crested macaques (*Macaca nigra*)

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Abstract
Group size, density, and composition significantly influence the expression of agonism and, as demography is frequently manipulated in captivity, natural mechanisms of conflict management may be disrupted. Here, we examine how changes to the social and physical environment of a captive group of Sulawesi crested macaques, *Macaca nigra*, influenced mechanisms of conflict management. The initial group was comprised of females, juveniles, and castrated males; under a series of management interventions, the group was moved to a new enclosure, 75% of the castrated adult males were removed, 67% of the females were contracepted, a novel, intact male was introduced, and the group was allowed access to an outdoor enclosure. Despite a decreasing trend in aggression following the changes to the social group, we found no significant differences in aggression or intervention behavior in the 5-week periods immediately following changes to the social group, apart from a significant decrease in aggression following the introduction of the novel male. This decrease in the frequency of aggression was still evident 10 weeks after the interventions occurred, and was coupled with a decrease in the intensity of aggression. Moreover, the intensity of aggression as well as the frequency of aggression and intervention were significantly lower under low-density conditions.

Our results highlight how management changes to the social and physical environment can influence aggressive behavior, albeit following a period of acclimation. We discuss the relative impacts of social group composition, social density, and individual reproductive status on the management of conflict behavior in a captive setting.

KEYWORDS
aggression, castration, group composition, sexual status, social density, Sulawesi crested macaques

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1 | INTRODUCTION

Competition for resources is a major cost of living in social groups, which can lead to within-group conflict (Hand, 1986; Majolo et al., 2008; Swedell, 2012). Often, direct competition is manifested through aggressive interactions which are costly, both directly, due to the risk of injury (Aureli & de Waal, 2000), but also indirectly by potentially disrupting group cohesion and stability (Flack et al., 2006). In a captive setting, aggression is reported to escalate as animals are less easily able to escape conflict (Hoese, 2005; McCowan et al., 2008), social interactions occur more frequently, and resources are more easily defended by dominant individuals (Stevens et al., 2008). Given the increased risk of trauma and stress, excessive aggression has significant impacts on animal health and welfare (Broom & Kirkden, 2004; McCowan et al., 2008; Ross et al., 2009), therefore, managing conflict-related behavior is a primary focus for many ex situ institutions (Beisner & Isbell, 2011).

In a captive setting, group size and composition are actively managed and are two aspects of sociality that significantly influence competition (Majolo et al., 2008; Weir et al., 2011). Under natural conditions, social groups are shaped by predation pressure and resource availability (Hill & Lee, 1998; Janson, 2000; Sterck et al., 1997), and group size associates positively with competitive behavior as more individuals attempt to access finite resources (Majolo et al., 2008; Wheeler et al., 2013). In captivity, however, associations between group size and aggression are less uniform (Judge, 2000). Short-term increases in social density result in both immediate increases in low to medium intensity aggression, as well as significant decreases in all levels of social behavior (Aureli et al., 1995; Crast et al., 2015; de Waal, 1989; Erwin & Erwin, 1976; Sannen et al., 2004). Under long-term crowding, however, these effects become less pronounced as the novelty of high-density social conditions abates (Crast et al., 2015). If competition does occur, more subtle forms of agonism such as submission are observed more frequently than overt aggression, although this can vary between species, contexts, and sexes (de Waal, 1989; Judge & de Waal, 1997; Judge, 2000). Moreover, affiliative behaviors occur more frequently in long-term, high-density conditions, presumably in an attempt to offset the effects of increased social tension (Crast et al., 2015; de Waal, 1989; Nieuwenhuijsen & de Waal, 1982).

Key members within a social group may also have a disproportionate influence on the associations of others (Flack et al., 2006; Lusseau & Newman, 2004), through their role in coordinating group behavior (King et al., 2009; Sueur et al., 2013), transferring social information (Sueur et al., 2011), regulating group conflict (Flack et al., 2006), or in maintaining social homeostasis (Bernstein, 1974). In captive primates, for example, high-ranking males frequently intervene in conflict, preventing the escalation of aggression by physically separating or calming combatants (Flack, Krakauer, et al., 2005; Beisner & McCowan, 2013; von Rohr et al., 2012). This behavior prevents the escalation, if not the initiation of conflict; ultimately promoting social cohesion and affiliation (Flack et al., 2006). Empirical studies in captive primates demonstrate that the temporary removal of conflict “policers” increases the rate and intensity of aggression in the remaining group, while also decreasing levels of affiliative behavior (Flack et al., 2006; Oswald & Erwin, 1976). The permanent removal of these individuals meanwhile remains relatively understudied. In captivity, permanent changes to the group composition occur frequently as animals are transferred between institutions to maximize the genetic diversity of the captive population (Frankham, 2007; Leus et al., 2011; WAZA, 2015). Individuals are primarily identified for transfer based on their genetic, rather than social attributes, and the impacts on behavioral mechanisms of conflict management and social integration are currently unknown and understudied.

Social group demography significantly influences the degree to which aggression is expressed (Beisner et al., 2012; Majolo et al., 2008; Weir et al., 2011; Wheeler et al., 2013). On one hand, male-population biases may, for example, mitigate conflict behavior as the number of individuals capable of effectively terminating conflict are increased (Beisner et al., 2012), but may also increase intrasexual competition for access to females (Kvarnemo & Ahnesjö, 1966; Smuts & Smuts, 1993; Weir et al., 2011). Female competition, on the other hand, is strongly associated with the availability of resources required for reproduction (Sterck et al., 1997), and unsurprisingly, female competition for mates increases in female-biased populations (Cheney et al., 2012). Birth-sex ratios in captivity are predominantly male-skewed (Faust & Thompson, 2000) and managing a surplus number of males is a primary challenge for many breeding program coordinators (Faust & Thompson, 2000; Margulis et al., 2011; Vermeer & Devreeze, 2015). In an attempt to artificially mitigate sexually driven aggression, animal managers increasingly use surgical and hormonal contraception to suppress the production of testosterone (Asa & Porter, 2005; de Nys et al., 2010; Muller, 2017; Penfold et al., 2005). Results have, however, been mixed (Carbajal et al., 2018; Fernández-Bellon et al., 2013; May; Takeshita et al., 2017), particularly as the interaction between hormones and behavior is complex (Anestis, 2010). This is further complicated as contraceptive effects will also vary depending on the product, sex and age of the individual, learnt behaviors, as well as existing social dynamics (Asa & Porter, 2005; Cowl et al., 2018; Kleiman et al., 2010).

In this opportunistic study, we investigate the impact of changes to the social group composition and social density on conflict management. We collected data from one group of captive Sulawesi crested macaques (Macaca nigra) at Chester Zoo while the group was subjected to a series of zoo-led management perturbations. Changes to the social group composition included the removal of 75% of the castrated males, contraception of 67% of females, and the introduction of a new, intact male 5 weeks later, whereas changes to social density occurred when the group was given access to an outdoor enclosure. Sulawesi crested macaques live in large multimale, multifemale groups, with group sizes ranging between 50 and 97 individuals (O’Brien & Kinnaird, 1997; Thierry et al., 2004). Sulawesi crested macaques are classified as “tolerant” on Thierry’s four-grade scale of macaque social organization (Thierry, 2000), indicating that they have symmetrical agonistic interactions and a high
tendency to reconcile (Petit et al., 1997). There is little seasonal variation in the activity budgets of Sulawesi crested macaques (O’Brien & Kinnaird, 1997). Sulawesi crested macaques are the most sexually dimorphic species of macaque, and males are, approximately, twice the size of females (Thierry, 2007). Given their physical dominance, we expect that males play a disproportionate role in mitigating group levels of conflict (Beisner et al., 2012). Indeed, Sulawesi crested macaques have been reported to intervene in conflict by appeasing opponents (Aureli & de Waal, 2000), as well as through “loud calls” produced by males (Kinnaird & O’Brien, 1999). The removal of the majority of males from the group should, therefore, result in significantly more frequent and more intense group levels of conflict. Following the introduction of the new male, the frequency of aggression should remain high as the new male attempts to integrate himself into the social hierarchy. The increase in aggression should, however, decrease once the macaques are given access to an outdoor enclosure.

2 | METHODS

2.1 | Ethics statement

The interventions described in this study were part of scheduled management interventions for the Sulawesi crested macaques at Chester Zoo. This study was approved by the Chester Zoo Science Committee. This study complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and the legal requirements of the United Kingdom.

2.2 | Study site

Data were collected from a captive group of Sulawesi crested macaques housed at Chester Zoo. At the beginning of the study, the macaques were kept in an indoor enclosure of 191.5 m², with a height of 5.7 m. The initial enclosure featured a pond, heater, two large trees, three small caves in a wall, six wooden uprights, as well as three large fallen logs. Multiple ropes, logs, and hammocks were suspended from a mesh ceiling. Following the enclosure move, the macaques were initially kept in an indoor enclosure of 186.5 m², with a height ranging between 6.3 and 8.5 m. The multilevel enclosure featured large trees and ropes hanging from a mesh ceiling. All indoor enclosures had wood chip substrate. In mid-October, the macaques were also given access to an outdoor enclosure of 1900 m². In their initial enclosure, individuals were always observable. However, in their new enclosure, the macaques had access to a large “off-show” area, as well as tunnels leading to their outdoor enclosure. All group members were, therefore, not always visible following the enclosure move. The macaques were fed with fruits, vegetables, and monkey pellet twice a day; feeding times were randomized throughout the study.

2.3 | Study subjects

Veronica B. Cowl (VBC) collected data on a total of 21 Sulawesi crested macaques. All macaques at the start of the study were natal to Chester Zoo (Table 1). All castrated male macaques were castrated before reaching sexual maturity (Melfi & Marples, 2000; Napier & Napier, 1985), at a mean age of 5.25 years (range = 4.39–5.89 years).

Prior to this study, the most recent change to the social group, excluding natural births and deaths, was the introduction of three males in September 2009. These animals were deceased at the time of the study. The macaque group had been housed in their original enclosure since 2001.

2.4 | Observation conditions

Data were collected from January to December 2015 between the hours of 09:00 and 15:00. During the observation period, the groups were subject to a series of management perturbations, including changes to group size, composition, and their enclosure (Table 1). The observation period was separated into five 5-week periods determined by group membership or social density. In chronological order, observation conditions included (Table 1):

- The original observation period (O), management interventions.
- The period of male removal (MR), in which the group moved enclosures and the six oldest adult males (age range: 8- to 12-years old) and one adult female (age: 10-years old) were removed from the group for management reasons, and six of the remaining nine females were placed on hormonal contraception.

| Condition       | Dates       | Group composition (age range at start of study) | Reproductive status | Density (individual/m²) |
|-----------------|-------------|-----------------------------------------------|---------------------|-------------------------|
| Original        | Jul-Aug 2015| M: 8 (6–12), F: 12 (1–15)                     | M: Castrated, F: Reproductive | 0.10                    |
| Male removal    | Aug-Sep 2015| M: 2 (6), F: 11 (1–15)                        | M: Castrated, F: 6 contracepted | 0.07                    |
| Male introduction| Sep–Oct 2015| M: 3 (6–7), F: 11 (1–15)                     | M: 2 castrated, F: 6 contracepted | 0.08                    |
| Outdoor         | Oct–Nov 2015| M: 3 (6–7), F: 11 (1–15)                     | M: 2 castrated, F: 6 contracepted | 0.006                   |
| Post-acclimation| Nov–Dec 2015| M: 3 (6–7), F: 11 (1–15)                     | M: 2 castrated, F: 6 contracepted | 0.006                   |

Note: The duration of each observation condition was 5 weeks. Abbreviations: F, females; M, males.
• The period of male introduction (MI), during which a novel, reproductive male (age: 7-years old) was introduced to the group.
• An outdoor period, where the macaques were given access to an outdoor enclosure, 5 weeks after the new male was introduced.
• The post-acclimation (PA) period, which included data collected 10 weeks after the interventions occurred to determine whether there was a period of acclimation for the management changes to have an effect on behavior. During this time, there were no changes to the social group composition and the macaques were able to access both indoor and outdoor enclosures.

Before the outdoor period, the macaques only had access to an indoor enclosure.

2.5 | Data collection
VBC collected all data on dyadic contact aggression by all-occurrence sampling to maximize the number of conflict events we were able to record (Altman, 1974; Flack, Krakauer, et al. 2005). In total, VBC observed the macaques for 40.00 h in the original condition, 43.00 h during MR, 32.00 h following the introduction of the new male, for 43.40 h while the macaques were given outdoor access, and for 45.90 h during the PA period. VBC recorded all information relating to dyadic, contact aggressive events, including the intensity of aggression, and whether any attempts to intervene occurred (Table S1). Aggressive events included slaps, pushes, pulls, grabs, and biting (Table S1).

2.6 | Statistical analyses
We analyzed all data as group-level data. We examined differences in group aggression and intervention behavior in each observation condition as counts, using generalized linear models (GLMs) with a Poisson or quasipoisson distribution in which social composition or social density were independent factors. Observation conditions for social composition analyses included the original condition (O), period following MR, the introduction of the novel male (MI; before being allowed outdoor access), and the PA period. Social density conditions were high (comprising data collected in O, MR, and MI conditions) and low (comprising data collected during the outdoor and PA periods). These models included an offset term to account for differences between the observation periods and the frequency of conflict or intervention behavior. Offset terms included hours observed per day for the frequency of aggression, the total number of daily conflict events for the frequency of intervention behavior, and the total number of daily interventions when analyzing each type of intervention behavior separately. To improve model fit, all offset terms were log-transformed.

We assessed the mean intensity of aggression within each observation period using linear models (LMs), with social composition or social density as the independent variable. To calculate the mean intensity of aggression, we gave low, medium, and high-intensity conflict scores of 1, 2, and 3, respectively (Table S1). Total daily scores were then divided by the daily number of aggressive events. To improve model fit, the mean intensity of aggression was log-transformed.

We carried out Tukey post hoc contrasts on estimated marginal means for all LMs and GLMs in which condition was significant following ANOVA or analysis of deviance tests, respectively. We assessed model fit for LMs by examining the $R^2$, residual plots, Q–Q plots, and the distribution of residuals. We assessed the suitability of Poisson models by comparing the mean and variance of the input data, which are assumed to be equal under a Poisson distribution. If the data were overdispersed (mean < variance), we used a quasi-poisson distribution to account for this (Ver Hoef & Boveng, 2007). Model fit for GLMs was determined by examining the residual deviance ($D^2$) (Cameron & Windmeijer, 1996; Pierce & Schafer, 1986), residual plots, and Q–Q plots. No aggressive interventions occurred during the original condition, and no interpositions occurred following the removal or introduction of the males, nor during the PA period. Moreover, no passive interventions occurred in the PA period. As such, complete separation occurred in Poisson models that included these variables. To address this, we calculated adjusted coefficients and confidence intervals using a penalized maximum likelihood estimation (Firth, 1993; Greenland & Mansournia, 2015). We determined whether there was a significant effect of condition on aggression and intervention behavior using $p$ values with a significance of 0.05.

To determine whether certain types of intervention behavior occurred more frequently than expected, or whether individuals of a certain sex or reproductive status intervened more frequently than expected, we carried out $\chi^2$ tests of independence on the counts of each behavior.

2.7 | Software
We carried out all analyses using R (R Development Core Team, 2013). We used the rsquared function in the piecwiseSEM package to extract $R^2$ values for LMs (Lefcheck, 2016), and the dsquared function in the modEvA package to extract $D^2$ values for GLMs (Barbosa et al., 2013). We calculated adjusted coefficients and confidence intervals for Poisson models in which complete separation occurred by fitting GLMs with the “brglmFit” method, using the package brglm2 (Kosmidis et al., 2020). We assessed analysis of deviance using the Anova function in the “car” package (Fox & Weisberg, 2019). We calculated estimated marginal means and carried out post hoc tests using the emmeans and pairs functions in the package “emmeans” (Lenth et al., 2018). Lastly, we calculated $\chi^2$ tests using the chisq.test function.

3 | RESULTS
3.1 | Conflict behavior
In total, we observed 55 dyadic and physically aggressive events across the study period (Table S2). The intensity of aggression was consistently low across observation conditions and was significantly
lower following the introduction of the novel male and the PA period than during the original condition (Figure 1 and Table 2). There was a general decreasing trend in the frequency of aggression following each intervention event, with significantly lower frequencies of aggression following the male introduction and during the PA period than following the removal of the males (Figure 1 and Table 3). Moreover, the frequency of aggression remained lower during the PA period than during the original condition, before any interventions (Figure 1 and Table 3).

Similarly, both the intensity of aggression and the frequency of aggression were significantly lower under low-density social conditions than high-density conditions (Figure 2 and Table 2 and 4).

### 3.2 | Intervention behavior
Conflict intervention occurred in 47.27% of the dyadic conflicts during the study period. Multiple group members intervened in nine of the 26 conflicts that were intervened in. We included each of
these interventions in the data separately and analyzed a total of 39 interventions (Table S3). Despite an overall significant effect of social composition on intervention behavior in the ANOVA analysis, significant effects did not remain in post hoc analyses (Figure 1 and Table 3). We did, however, find a significant effect of social density on intervention behavior, with a significantly higher number of interventions occurring when the macaques did not have access to their outdoor enclosure (Figure 2 and Table 4). In each observation condition, individuals of a particular sex and reproductive status did not intervene more frequently than expected (O: $\chi^2_{1,8} = 0.00$, $p = 1.00$; MR: $\chi^2_{2,16} = 2.20$, $p = .33$; MI: $\chi^2_{3,6} = 0.67$, $p = .88$; O: $\chi^2_{3,6} = 7.33$, $p = .06$; PA: $\chi^2_{3,2} = 2.00$, $p = .57$).

3.3 | Types of Intervention Behavior

Overall, there were significant differences in the types of intervention that occurred, with aggressive and passive interventions occurring more frequently than expected ($\chi^2_{3,39} = 12.59$, $p < .01$). However, the number of aggressive or affiliative interventions did not differ significantly in relation to social group composition or social density (Figures 1 and 2; Tables 3 and 4). Significantly fewer interpositions occurred immediately following the introduction of the new male when compared to the original condition. This effect did not remain in the PA period (Figure 1 and Table 3). We also found significantly lower frequencies of passive interventions following the introduction of the novel male when compared to the period following MR (Figure 1 and Table 3), as well as lower frequencies of passive interventions under low-density social conditions compared to high-density social conditions (Figure 2 and Table 4).

4 | Discussion

Inherent aspects of captivity such as a lack of escape promote the escalation of aggression (Hosey, 2005; McCowan et al., 2008). As routine interventions could disrupt natural, behavioral mechanisms of conflict management, it is essential that animal managers understand how decisions influence the behavior, health, and welfare of their animals (Beisner et al., 2016; Honess & Marin, 2006; Hosey, 2005; Morgan & Tromborg, 2007). Here, we highlight how changes to social group composition and social density in a captive group of Sulawesi crested macaques affect mechanisms of conflict management.

Despite the lack of a significant change in conflict-related behavior immediately following each intervention, each intervention could contribute to the decrease in conflict observed in the PA period. For example, though contraception as a tool to manage aggression has predominantly focused on its application in males (Penfold et al., 2005), its application in females may also result in...
changes to conflict behavior. Fertile females are more frequently the recipients of male sexual aggression and female mate competition (Baniel et al., 2018; Clark & Melfi, 2005, July; Dixson, 2009; Huchard & Cowlishaw, 2011; Reed et al., 1997). Female *M. nigra* have conspicuous sexual swellings when fertile (Higham et al., 2012), and maximally swollen females receive more aggression from both males and females (Clark & Melfi, 2005, July). Contraceptive implants will eliminate or significantly decrease sexual swellings, which may contribute to the reduction in aggression during the last observation period.

Similarly, the change in enclosure may have also contributed to our findings as more naturalistic and complex enclosures are associated with a reduction in conflict behaviors (Little & Sommer, 2002; Maple & Stine, 1982; O’Neill et al., 1991; Ross et al., 2011), as well as with an increase in species-typical behavior (Chang et al., 1999; Maple & Finlay, 1989; Maple & Perkins, 1996). Visibility of the macaques was also reduced in the new enclosure, which may have resulted in a decrease in the number of conflict events we were able to observe. However, as we only observed significant differences in behavior following the introduction of the novel male and the period of acclimation, rather than immediately following the move to a new enclosure or access to the outdoor enclosure, it is less likely that the observed effects were driven by a reduction in visibility. Factors such as social cohesion (McCowan et al., 2008), individual personality (McCowan et al., 2011), and individual identity may also contribute to differences in aggressive and intervention behavior across conditions, but were outside the scope of this study.

We observed significant decreases in the intensity and frequency of aggression when the macaques were given outdoor access. Under high social densities, captive primates mitigate against increased conflict as a result of social tension by increasing rates of affiliative behavior or by reducing the frequency of all social interaction (Aureli & de Waal, 1997; de Waal, 1989; Judge & de Waal, 1997; Nieuwenhuijsen & de Waal, 1982; Novak et al., 1992; van Wolkenten et al., 2006; Videan & Fritz, 2007). Previous research has illustrated that short-term increases in grooming interactions occurred following the introduction of the novel male (Cowl et al., 2020), which may be used to offset aggression (Bercovitch & Lebrón, 1991; Crast et al., 2015; de Waal, 1989; Nieuwenhuijsen & de Waal, 1982). Under high social densities, more subtle forms of agonistic behavior, like submission or displacements, are more likely to occur (de Waal, 1989; Judge & de Waal, 1997; Judge, 2000). However, we were unable to determine whether there were any changes to these behaviors as a result of the interventions due to our focus on overt, contact aggression. Moreover, as the frequency of aggression decreased significantly, and remained low following the introduction of the novel male, regardless of being given outdoor access or not, the reduction in aggression may also be driven by other effects, such as the introduction of the novel, reproductive male.
Breeding programs frequently use surgical or hormonal contraception in males to manage reproduction, however, these methods can also be used to manage aggressive behavior (Asa & Porton, 2005; de Nys et al., 2010; Muller, 2017; Penfold et al., 2005). Previous results in primates have been mixed (Carbajal et al., 2018; Fernández-Bellon et al., 2013; May; Takeshita et al., 2017). Variation in the efficacy for behavioral management may lie with the age at which the procedures occur. If sexually mature males are contracepted, individual aggression can remain unchanged as behavioral repertoires may already be established in individuals (Asa, 2005; Eppl, 1978; Wallace et al., 2016). If, on the contrary, immature males are contracepted, as in this study, male sexual behavior, body size, temperament, and the development of secondary sexual characteristics will be affected (Nagarajan et al., 2013; Porton & Demateo, 2005; Wallace et al., 2016). These males are less likely to be socially dominant than intact males (Dröschler & Waitt, 2012; Michael & Zumpe, 1993; Reed et al., 1997; Richards et al., 2009), which may result in them being less effective at successfully intervening in conflict (Flack, de Waal, et al., 2005; McCowan et al., 2011), and aggression directed towards treated individuals may even increase (Dixson, 1993; Wallace et al., 2016). As the frequency of aggression was lowest during periods when a reproductively active male was present, our results suggest that males who are surgically sterilized when sexually immature could be less effective at mitigating conflict in mixed-sex groups than intact males. As simply the presence of individuals perceived as “conflict interveners” can prevent the initiation of conflict without intervening, these individuals may not be perceived as “conflict interveners” by other group members (Flack, Krakauer, et al., 2005). The efficacy of contraception or castration for group management is, therefore, likely related to a combination of individual age and group composition, among other variables.

There was a decrease, rather than an increase in conflict behavior following the introduction of the novel male. Immigration events can elicit extreme increases in aggression as new individuals attempt to establish themselves within the social hierarchy (Alberts et al., 1992; Bernstein, 1971; Bernstein, 1974; Brent et al., 1997; McCowan et al., 2008; Pusey & Packer, 1987; Teichroeb et al., 2011). In captivity, changes to group membership elicit more severe increases in aggression than either crowding or food withdrawal (Bercovitch & Lebrón, 1991; Bernstein, 1974; de Waal, 1989; Nieuwenhuijsen & de Waal, 1982; Southwick, 1967), therefore mitigating aggression during the introduction of novel individuals to a group is a concern for captive managers. That there were no significant differences in aggression following the introduction of the new male in the present study suggests that the new male integrated himself quickly and may reflect an absence of competition for dominance (Cowl et al., 2020).

Aggressive interventions occurred frequently in this study and may highlight a degree of social instability as a result of the management interventions. Aggressive interventions constitute a high risk to the intervener due to the risk of retaliation but may allow the intervener to reinforce social relationships, or to obtain a better
position in the social hierarchy than an individual involved in the conflict (Chapais, 1995; Das, 2000; Petit & Thierry, 1994). These interventions only occurred after the removal of the males and may indicate competition for social rank. Passive interventions also occurred significantly more than expected. These types of interventions present relatively little risk to the intervener and may preserve existing social relationships by not favoring one individual involved in the conflict over the other (Das, 2000).

In captivity, aggression in primates is influenced by various factors including the presence of visitors, management, a limited ability to escape conflict, and enclosure design (Beisner & Isbell, 2011; Honess & Marín, 2006; Hosey, 2005; Morgan & Tromborg, 2007; Theil et al., 2017). Although most management decisions in captivity are designed with specific breeding or welfare outcomes in mind (Glatston, 1997), resulting social changes may impact mechanisms of conflict management. As aggression can compromise animal health and wellbeing, it is particularly important for captive animal managers to identify practical methods to mitigate excessive conflict (Beisner & Isbell, 2011). Our results highlight how both differences in male reproductive status and social density may influence group rates of aggression. These changes, however, may incur a period before they are effective. Castration at a young age may successfully allow for all-male groups by mitigating sexually driven aggression and by altering male temperament, in mixed-sex groups, however, undesired social consequences may occur. As we were unable to fully separate effects driven by sexual status and social density, further research should be undertaken to fully evaluate the effects of each type of management intervention on behavior.

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CONFLICT OF INTERESTS
The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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