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High rates of aggression do not predict rates of trauma in captive groups of macaques

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Abstract

Socially inflicted traumas are a major concern for the management of captive groups of rhesus macaques. Rhesus macaques are the most commonly used nonhuman primate in biomedical research, and social housing is optimal for promoting psychological well-being. However, trauma is frequent due to a strong reliance on aggression to establish and maintain hierarchical relationships. We studied six captive groups of rhesus macaques (*Macaca mulatta*) that underwent a variety of social perturbations and explored whether rates of aggression mapped onto rates of trauma using a fine-grained analysis that divided both aggression and trauma variables into specific, behaviorally-relevant categories (e.g., severe aggression by adult males relative to lacerations). Results did not show the expected positive relationship between aggression variables and trauma variables. Instead, rates of trauma (i.e., lacerations, moderate-severe trauma, total trauma) were negatively associated with the rate of impartial interventions (i.e., an intervention directed at both targets during an ongoing conflict) during baseline periods. Additionally, rates of trauma (i.e., lacerations, punctures, moderate-severe trauma, total trauma) were negatively associated with rates of total aggression following temporary knockouts of the individuals who commonly intervene impartially (i.e., conflict policers), and punctures and moderate-severe trauma were negatively associated with rates of severe aggression by adult males following permanent knockout of a high-ranked natal male. These results suggest that under homeostatic conditions, impartial interventions serve as a mechanism to reduce socially inflicted trauma but, following social manipulations of high-ranking males, an imbalance emerges. Our results underscore the importance of developing management strategies for rhesus macaque groups that promote internal social mechanisms of social stability such as maintaining conflict policing individuals (i.e., adult males) in social groups.

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Keywords

aggressive behavior; conflict management; injury; primates; social stability; wounding

1. Introduction

The housing of gregarious species in captivity can result in an assortment of socially inflicted traumas, such as tail biting in commercially raised pigs, feather pecking in laying hens (reviewed in Daigle, 2017), and outbreaks of severe aggression and traumas that disrupt social hierarchies in rhesus macaques (*Macaca mulatta*) (Ehardt and Bernstein, 1986; Beisner et al., 2015; Wooddell et al., 2017). Such circumstances can result in controversial procedures to reduce these traumas such as tail docking (Hunter et al., 2001), beak trimming (Duncan et al., 1989), and individual housing (Hannibal et al., 2016). Given that legislative and market forces have led to a growing pressure to house animals with conspecifics for social, agricultural, and research purposes, and that greater scrutiny is being aimed towards reducing socially inflicted traumas, the urgency to investigate the relationship between aggression (and other contributing factors) and trauma is well founded to both ensure productivity and enhance animal welfare.

Trauma is a major concern for the management of captive groups of rhesus macaques, which are the most commonly used nonhuman primate in biomedical research (McCowan et al., 2008; McCowan et al., 2017). Social housing is the best form of enrichment for captive primates (Lutz and Novak, 2005), because of their social and cognitive adaptations (Byrne and Whiten, 1988; Dunbar, 1998). To promote optimal welfare and utility as a biomedical research model, rhesus macaques are sometimes housed in naturalistic matrilineal social groups of 50–200 individuals (Hannibal et al., 2016). Because rhesus macaques are highly despotic, with steep linear hierarchies and a strong reliance on aggression (including biting) to regularly enforce the hierarchy (Sade, 1967; Missakian, 1972; Thierry, 2004), trauma occurs frequently. Some injuries can be fatal (Bernstein et al., 1974; Kaplan et al., 1980; Oates-O'Brien et al., 2010), but most are superficial lacerations, punctures, and abrasions (Judge et al., 1994). These injuries negatively impact the welfare of the injured animal, often require costly veterinary care, and may necessitate removing individuals from social housing (McCowan et al., 2008; McCowan et al., 2017). Such removals can pose further issues for the social group, as loss of high-ranking or keystone individuals (Modlmeier et al., 2014) can escalate social instability and trigger the onset of destabilizing hierarchical aggression that leads to severe wounding (McCowan et al., 2017; Wooddell et al., 2017) and likely group disbandment. Therefore, understanding the predictors of trauma is of key concern to managers of rhesus macaques to prevent escalated aggression, trauma, and social instability. Elucidating the relationship between aggression frequencies and trauma is thus a critical step in understanding whether management strategies aimed at reducing aggression may also reduce trauma.

Previous research has established a rich body of literature examining social predictors of trauma in captive groups of rhesus macaques, including seasonality (Wilson and Boelkins, 1970; Ruehlmann et al., 1988; Stavisky et al., 2018), sex ratio and conflict interventions

(Beisner et al., 2012), and cohesive matrilineal structures (Beisner et al., 2011; Stavisky et al., 2018). However, despite common expectations, studies have often failed to demonstrate a positive relationship between aggression rates and trauma. For example, male macaques received the most wounds in one comparative study despite reports in the literature that they engage infrequently in aggression (Ruehlmann et al., 1988), suggesting a disconnect between aggression and trauma frequencies. Further, removal of a trauma-inflicting matriline reduced traumas in a rhesus macaque group but aggression levels remained similar (Judge et al., 1994), and during the pairing process, subordinate behaviors (but not aggression) predicted lower rates of wounding (Pomerantz and Baker, 2017). However, most studies have taken a coarse-grained analytical approach e.g., using a summation of aggressive behavior and traumas over time (e.g., months to years), lumping together multiple types of trauma into a single outcome variable, or focusing only on traumas requiring veterinary treatment (Ruehlmann et al., 1988; Judge et al., 1994; Beisner et al., 2012; Stavisky et al., 2018). Cumulative metrics, however, may mask meaningful temporal variation in aggression and trauma rates or effects on specific types of trauma (e.g., lacerations and punctures; see Judge et al., 1994). We therefore explored whether rates of aggression map onto rates of trauma by utilizing a more fine-grain analysis. We hypothesized that if trauma is a consequence of biting aggression, then higher rates of severe aggression should be associated with higher rates of total trauma, moderate to severe trauma, and each different category of trauma. Further, higher rates of severe aggression by adult males should be associated with higher rates of male-pattern trauma, e.g., lacerations and punctures due to their sexually dimorphic canines. Alternatively, rates of trauma may be predicted by other socio-demographic factors such as rates of impartial interventions (interventions directed at both targets during an ongoing conflict; i.e., conflict policing), sex ratio, or the number and size of matrilines (Beisner et al., 2012; Beisner and McCowan, 2013; Stavisky et al., 2018) which we tested as alternative hypotheses.

2. Materials and Methods

2.1 Study groups and subjects

The study was conducted at the California National Primate Research Center (CNPRC) in Davis, CA, USA between March 2013 and August 2016 and was approved by the University of California Davis Institutional Animal Care and Use Committee. Six social groups of rhesus macaques housed in large 0.2-hectare outdoor enclosures were the subjects of this study (Table 1). Each enclosure contained multiple A-frame structures, suspended barrels, swings, and perches and animals were free to interact as they chose. Adult group size ranged from 55 to 101, and subject age ranged from 3 – 29 years (mean 7.2 years). Animals were fed a standard diet of monkey chow twice per day at approximately 0700 h and between 1430 and 1530 h. Fresh fruit or vegetables were provided once per week and seed mixture was provided daily. Water was available ad libitum. Outdoor enclosures were managed with a minimum level of disturbance.

2.2 Behavioral data collection

Groups were part of a larger study on social perturbations and welfare, and each group experienced a ‘knockout’ (i.e., removal; abbreviated KO) of some group members to test the

effects of removing certain individuals (i.e., high-ranked natal males; matriline fragments; conflict policers) on group stability and welfare. Thus, the KO perturbations were unrelated to the goals of the research presented in this paper. Study groups A-D experienced a permanent KO of either a natal male or several females from matriline 'fragments'(Beisner et al., 2011), and each group was observed for 20 consecutive weeks (6-week baseline, 6-week post perturbation, and 8-week follow-up period). Study groups E and F were observed for two 12-week periods (4-week baseline, 4-week perturbation, and 4-week post-perturbation), once for a conflict policer KO and once for a control KO. During the 4-week perturbation period of the conflict policer KO, a set of three high-ranked conflict policers was removed from the group for 6 hours each Monday (and returned late Monday afternoon), and for the control KO, a set of three high-ranked individuals that did not do conflict policing was removed each Monday. Conflict policers were defined as high-ranked individuals that frequently intervened to stop group members' fights (Flack et al., 2005b; Beisner and McCowan, 2013) by targeting both individuals in the aggressive interaction. Unexpected social and management events altered the study design in two groups: the baseline period was reduced by two days for group D, and the 4-week perturbation and 4-week post-perturbation of the control KO was cancelled for group E.

We used an event sampling design to collect all instances of aggressive interactions. Two observers collected data for 6 hours per day for 4 days per week from 0900–1200 h and 1300–1600 h in all phases of study except for the 8-week follow-up phase. During the 8-week follow-up phase for the permanent KOs, behavior data collection was reduced to 2 days per week for 6 hours per day. The observers moved around the outside of the enclosure, standing at least 5 feet from the chain link fence, to conduct their observations. Aggressive events were recorded as a series of dyadic interactions in which observers documented the identities of all participants, the type of aggressive or submissive behavior used by each, and the sequence of these interactions. Aggression was categorized according to severity and included simple threats (e.g., open mouth stare, brow flash, head bob), mild aggression which involved either a low-level of pursuit (e.g., threatening while approaching or following the recipient, lunge toward the recipient, or brief chase < 6 meters) or low-severity contact (e.g., mild push or slap), moderate aggression which involved either a long chase (> 6 meters) or contact aggression such as grapple or wrestle, and severe aggression which involved either a bite or preventing the recipient from running away (e.g., pin to the ground). Intervention was defined as a third-party entering an on-going fight by aggressing or approaching one (partial) or both (impartial) participants. Impartial interventions were those in which the intervener treated both participants the same, either by approaching or aggressing them. Data collection reliabilities were calculated using Krippendorff's alpha and ranged between 0.85 – 1.00 across all observers (Krippendorff, 2011).

From these behavioral data, we generated several variables representing rates of aggression (all rates scaled by adult group size and observation hours): (1) rate of all aggressive interactions, (2) rate of all severe aggressive interactions, (3) rate of all severe aggressive interactions by adult males (5+ years old), and (4) rate of all severe aggressive interactions by adult females (3+ years old). Based on male canine crown eruption age (Wang et al., 2016), the adult male age cut-off was defined as 5 years and older. In addition, we calculated

the rate of how many aggressive events were targeted with impartial interventions, to address the alternative hypothesis that trauma is lower when policing is more frequent.

2.3 Trauma recording

All instances of trauma were documented twice per week on both Mondays and Thursdays. Each of these days the observer identified and visually evaluated each subject (≥ 3 years old) for evidence of trauma. The following types of trauma were recorded: abrasions, crush/ bruising trauma, digit trauma, lacerations, nail avulsions, and puncture wounds (Table 2). Traumas of all types were categorized by severity. Minor injuries involved superficial tissue damage or reddish bruising and were unlikely to require further monitoring or veterinary care. Moderate injuries were defined as damage to the skin that passed through all layers of skin but were not initially large or deep enough to require veterinary care. Moderate injuries might involve blue/purple bruising and were monitored for possible infection or re-injury that would require veterinary care. Severe injuries were those that required medical attention, often involving damage to muscle, tendons, arteries or bones. All instances of severe trauma were treated by CNPRC veterinary staff. From these data, we obtained a count of traumas per group per week to generate five trauma variables: (1) total trauma, (2) moderate or severe trauma, (3) lacerations, (4) puncture wounds, and (5) abrasions. There were not sufficient observations of crush/ bruising trauma, digit trauma, or nail avulsions to examine these categories of trauma.

From these trauma and behavioral data, we tested the following: if trauma is an accidental consequence of aggressive interactions, then higher rates of total aggression should be associated with higher rates of total trauma and, potentially, higher rates of each different category of trauma. If trauma is a consequence of biting aggression, then higher rates of severe aggression should be associated with higher rates of total trauma, moderate to severe trauma, and each different category of trauma. Further, higher rates of severe aggression by adult males should be associated with higher rates of male-pattern trauma, e.g., lacerations and punctures due to their sexually dimorphic canines. Alternatively, rates of trauma may be predicted by other socio-demographic factors such as rates of impartial interventions (i.e., conflict policing), sex ratio, or the number and size of matrilines (Beisner et al., 2012; Beisner and McCowan, 2013; Stavisky et al., 2018) which we tested as alternative hypotheses.

2.4 Statistical Analyses

We fit generalized linear mixed-effects regression models (glmms) (McCullagh and Nelder, 1989) to each of five trauma outcome variables (total trauma, moderate-severe trauma, lacerations, punctures, abrasions), and these analyses were repeated for four different study conditions: (1) observation weeks during baseline phases (n=40), (2) observation weeks occurring after the permanent matriline fragment KO (n=28), (3) observation weeks occurring after the permanent natal male KO (n=28), and (4) observation weeks occurring after the temporary KO of conflict policers began (n=24). The unit of analysis for each was the count of traumas per week. We analyzed the baseline vs. post-perturbation weeks separately because the relationship between trauma and aggression had the potential to change in response to the social perturbation (e.g., Wooddell et al., 2016). All glmms were

run in R version 3.3.3 (R Core Team, 2017) using the *glmmADMB* package (Fournier et al., 2012) using a negative binomial family distribution, as the distribution of all trauma count variables showed over-dispersion. Adult group size was included as an exposure variable to account for the number of animals that could potentially receive trauma. We tested four predictor variables representing weekly rates of aggression for each outcome variable: total aggressive interactions, severe aggression, severe aggression by adult males, and severe aggression by adult females. To examine alternative hypotheses, we also tested the rate of impartial interventions and the number of matrilines per group, as well as control variables for season and the number of weeks that had passed since the KO began (for post-perturbation analyses only). A random effect for group was included in all models. We took an Information Theoretic (I-T) approach to model-fitting (Burnham and Anderson, 2002; Burnham et al., 2011), which uses information criterion scores, such as AIC, to select a candidate set of 'plausible' models, as opposed to using the P-values of individual predictors to decide whether a model is good. We fit all univariate and multivariate combinations of predictors, but due to small sample size, we limited these to a maximum of three predictors per model (in addition to the random effect) to avoid overfitting. For each analysis, we calculated AIC scores corrected for small sample size (i.e., AICc) for each model, and selected all models within 2 AICc points of the best model (i.e., dAIC <2) to be in the candidate model set (Burnham and Anderson, 2002). In keeping with the I-T approach, we did not choose a level of significance, and we report results from all models in the candidate set, including the beta coefficient and associated P-value for each predictor.

2. Results

A total of 1,956 injuries were documented across 508 subjects from six study groups: 455 abrasions, 34 instances of bruising or 'crush' trauma, 64 digit traumas, 870 lacerations, 20 nail avulsions, and 513 punctures. In four study groups, adult females (3+ years old) received less trauma than expected by chance. In five groups, subadult males (3–4 years old) received more trauma than expected, and in three groups adult males (5+ years old) received more trauma than expected (Table 3).

3.1 Baseline phase

Table 4 presents a summary of all trauma analyses, showing the predictors present in the top models for each outcome variable across the four different social conditions (i.e., baseline and after the matriline fragment, natal male, and policer social perturbation experiments).

Total trauma: There were four top models of baseline total trauma per week which included the rate of impartial interventions, the rate of severe aggression, or both. Models 1 and 3 indicated that weeks with higher rates of impartial interventions had less total trauma (model 1: $\beta = -13.5$, $P = 0.04$; model 2: $\beta = -11.2$, $P = 0.11$; Figure 1). Models 2 and 3 included the rate of severe aggression (model 2: $\beta = 0.63$, $P = 0.28$; model 3: $\beta = 0.86$, $P = 0.13$), suggesting that weeks with higher rates of severe aggression had higher rates of total trauma. Model 4 was the empty model (dAICc = 1.7).

Moderate-severe trauma: There were three top models of weekly moderate-severe trauma during baseline. Model 1 included the rate of impartial interventions and season, showing that moderate-severe trauma was less frequent during spring compared to fall, where fall coincides with the annual mating season ($\beta = -1.08$, $P = 0.02$), and during weeks with a higher rate of impartial interventions ($\beta = -17.5$, $P = 0.11$). Model 2 included season only (spring vs. fall: $\beta = -1.18$, $P = 0.02$) and model 3 included only the rate of impartial interventions ($\beta = -21.6$, $P = 0.08$). Aggression variables were not associated with moderate-severe trauma counts.

Lacerations: The best model of weekly lacerations during baseline included only the rate of impartial interventions such that weeks with more impartial interventions had fewer lacerations (AICc = 213.7, $\beta = -10.3$, $P = 0.05$). The second-best model was the empty model (dAICc = 1.4). Aggression variables were not associated with laceration counts.

Punctures: The weekly frequency of puncture wounds was not associated with any variables analyzed; the best model was the empty model with no predictors.

Abrasions: The weekly frequency of abrasions was not associated with any variables analyzed; the best model was the empty model with no predictors.

3.2 Permanent KO (matriline fragment)

Total trauma: The best model of weekly total trauma following the permanent removal of females in matriline fragments included season only (AICc = 176.8, compared to second-best model dAICc = 2). Total trauma was lower during spring compared to fall ($\beta = -0.48$, $P < 0.001$). Aggression variables were not associated with total trauma.

Moderate-severe trauma: The best model of weekly moderate-severe trauma following the permanent removal of females from matriline fragments included season and the number of weeks since the KO (AICc = 115.3, compared to second-best model dAICc = 5.4). Moderate-severe trauma was less frequent during spring compared to fall ($\beta = -1.43$, $P < 0.001$) and less frequent as the number of weeks since the KO increased ($\beta = -0.077$, $P = 0.002$).

Lacerations: There were three top models of weekly lacerations following the permanent removal of females from matriline fragments, and all three indicated that lacerations were less frequent as the number of weeks after the KO increased (model 1: $\beta = -0.048$, $P = 0.004$; model 2: $\beta = -0.067$, $P = 0.003$; model 3: $\beta = -0.056$, $P = 0.002$). Model 2 also included the rate of impartial interventions ($\beta = 13.4$, $P = 0.18$). Model 3 also included the rate of aggression ($\beta = -0.92$, $P = 0.24$).

Punctures: There was one best model of weekly puncture wounds which showed that punctures were less frequent during spring compared to fall ($\beta = -0.66$, $P = 0.006$).

Abrasions: There were three top models of weekly counts of abrasions following the permanent removal of females from matriline fragments, and all showed that abrasions were less frequent during weeks with more impartial interventions (model 1: $\beta = -5.53$, $P <$

0.001; model 2: β = −6.60, $P < 0.001$; model 3: β = 4.10, $P = 0.05$). Model 2 also included the rate of severe aggression by adult males (β = −98.4, $P = 0.12$), and model 3 also included season (spring vs. fall: β = −0.46, $P = 0.38$).

3.3 Permanent KO (natal male)

Total trauma: The weekly frequency of total trauma following the permanent removal of the natal male was not associated with any variables analyzed; the best model was the empty model with no predictors.

Moderate-severe trauma: The best model of moderate-severe trauma per week following the permanent removal of the natal male included season, number of weeks since the KO, and the rate of severe aggression by adult males (AIC = 135.0, compared to second-best model dAIC = 4.3). Moderate-severe traumas were less frequent when severe aggression by adult males was higher (β = −167.3, $P = 0.02$; Figure 2), as the number of weeks since the KO increased (β = −0.094, $P = 0.005$), and less frequent during spring compared to fall (β = −0.96, $P < 0.001$).

Lacerations: There were five top models of lacerations per week following the permanent removal of the natal male; three included the number of weeks since the KO, two included the rate of severe aggression, and one included the rate of total aggression. Models 1–3 showed that lacerations were less frequent as the number of weeks since the KO increased (model 1: β = −0.05, $P = 0.02$; model 2: β = −0.04, $P = 0.10$; model 3: β = −0.05, $P = 0.06$). Results were mixed regarding the relationship between aggression and lacerations. Model 1 suggested lacerations were more frequent when rates of overall aggression were higher, (β = 2.1, $P = 0.09$), whereas models 2 and 4 suggested lacerations were less frequent during weeks with higher rates of severe aggression (model 2: β = −21.2, $P = 0.12$; model 4: β = −25.6, $P = 0.07$). Model 5 was the empty model.

Punctures: The best model of weekly puncture wounds (AIC = 129, compared to second-best model dAIC = 2.0) showed that following the permanent KO of the natal male, puncture wounds were less frequent during weeks with higher rates of severe aggression by adult males (β = −198.1, $P = 0.02$).

Abrasions: The weekly frequency of abrasions following the permanent removal of the natal male was not associated with any of the variables analyzed; the best model was the empty model with no predictors.

3.4 Temporary KO (conflict policer)

Total trauma: There were two top models of the weekly frequency of total trauma during the weeks after the temporary KO of conflict policers started, and both included the rate of aggression. Total trauma was less frequent during weeks when the rate of aggression was higher (model 1: β = −3.42, $P = 0.009$; model 2: β = −3.88, $P = 0.005$). Model 1 also indicated that total trauma was more frequent during the weeks immediately after the KOs began (β = −0.125, $P = 0.04$).

Moderate-severe trauma: There were three top models of moderate-severe trauma during the weeks after the temporary KO of conflict policers started. Model 1 indicated that moderate-severe trauma was less frequent when rates of impartial interventions were higher ($\beta = -7.85$, $P = 0.02$). Model 2 indicated that moderate-severe trauma was less frequent when rates of aggression were higher ($\beta = -7.57$, $P = 0.004$). Models 1 and 3 showed that moderate-severe trauma was less frequent in summer compared to spring (model 1: $\beta = -1.06$, $P < 0.001$; model 3: $\beta = -0.776$, $P = 0.019$).

Lacerations: The best model (AIC = 131.1, compared to second-best model dAIC = 2.5) showed that during the weeks after the temporary KO of conflict policers started, lacerations were less frequent during weeks with higher rates of aggression ($\beta = -5.53$, $P = 0.004$).

Punctures: The best model (AIC = 123.3, compared to second-best model dAIC = 2.5) showed that during the weeks after the temporary KO of conflict policers started, punctures were less frequent when rates of aggression were higher ($\beta = -7.17$, $P = 0.003$) and when rates of severe aggression by adult males were lower ($\beta = 202.9$, $P = 0.03$).

Abrasions: There were three top models of abrasions during the weeks after the temporary KOs started. Model 1 included an interaction between the rate of impartial interventions and the number of weeks since the KOs started, indicating that as the number of weeks since the KOs increased, abrasions became less frequent during weeks with more impartial interventions (impartial: $\beta = 0.11$, $P = 0.96$, weeks since KO started: $\beta = -0.028$, $P = 0.82$, impartial × weeks since KO: $\beta = -4.99$, $P = 0.06$). Models 2 and 3 included the number of weeks since the KO (model 2: $\beta = -0.22$, $P = 0.008$; model 3: $\beta = -0.23$, $P = 0.005$), and model 3 also included impartial interventions ($\beta = -2.57$, $P = 0.33$).

3. Discussion

Socially-derived injuries are a key concern for managers of socially housed animals in captivity. Understanding the factors that lead to more versus less frequent trauma can improve colony management techniques. For socially housed rhesus macaques, wounding is a common problem due to their despotic dominance style – aggression is used to maintain dominance relationships and severe aggression is relatively frequent (Bernstein and Ehardt, 1985; Thierry, 2004). In macaques, socially-derived traumas such as punctures and lacerations are the result of aggression, and therefore observed rates of aggressive behavior should be predictive of trauma frequencies, particularly when fine-scale (e.g. weekly) measurements of aggression and trauma are analyzed and different types of trauma are examined separately. However, across six study groups examined during both baseline and perturbation phases of study, we did not find the expected positive relationship between aggression rates and trauma frequencies in the majority of our analyses. Rather, our most consistent findings were (1) rates of aggression were often negatively associated with trauma during the weeks following the natal male and policer KOs, and (2) impartial interventions were negatively associated with rates of trauma, particularly during baseline weeks of study. We discuss these findings in more detail below.

4.1 Aggression rates are not positively associated with trauma rates

Contrary to expectations, we found a positive relationship between rates of aggression and trauma in only two of the 20 different analyses conducted. During the baseline condition across all six study groups, aggression variables were not associated with any of the trauma outcome variables. Similarly, following the permanent removal of females from matriline fragments, no relationship between aggression rates and trauma frequency was found. Only two analyses (Table 4) showed the expected positive relationship–following the onset of repeated temporary KOs, puncture wounds were more frequent when rates of severe aggression by adult males was more frequent; and following permanent KO of a high-ranked natal male, there was a trend for lacerations to be more frequent when rates of total aggression were higher. Thus, our fine-grained week-to-week analysis of specific links between aggression and trauma, e.g., severe aggression by adult males relative to frequency of punctures and lacerations, failed to detect a consistent positive relationship between rates of aggression and trauma.

The lack of a positive relationship between aggression and trauma suggests that injuries are not an accidental outcome of aggressive interactions. This is consistent with several previous studies with more coarse-grained summaries of aggression and trauma. Ruehlmann et al. (1988) summarized the frequency of total trauma received for different age/sex classes over a year, finding that although adult male macaques (i.e., *M. arctoides, M. mulatta, M. nemestrina*) received the most trauma, they were not the most frequent targets of contact aggression or biting. Judge et al. (1994) summarized distinct categories of trauma (i.e., flayings, lacerations, digit loss) and compared receipt of these traumas with the rate of total aggression calculated over a 2-month period. No relationship was found between the rate of aggression and incidence of trauma, as removal of the trauma-inflicting matriline resulted in a reduction in all traumas but no change in the rate of total aggression (Judge et al., 1994).

The underlying social dynamics of trauma appear to be more complex than a simple positive correlation with biting aggression. Aggressors may moderate the intensity of their bites, thereby influencing the likelihood of injury. For example, the most vital regions of the body (e.g., abdomen, chest, and throat) are rarely targeted by aggressors despite covering nearly one fifth of the total body surface area, suggesting that aggressors avoid biting the most vulnerable parts of the body (Owens, 1975; Ruehlmann et al., 1988). Similarly, the ability to restrain aggressive behavior is evident from social play (e.g., play fighting) in which both adults and immature individuals show bite restraint to avoid injuring their playmates (Symons, 1978). In contrast, other circumstances are found where monkeys show a clear intention to injure their target, during very serious aggressive events when the target of aggression is pinned to the ground and bitten repeatedly for several minutes e.g., matrilineal overthrows (Gygax et al., 1997).

Objectively determining when aggressors do and do not moderate the intensity of their biting behavior may be difficult. However, future research on which individuals do (or do not) moderate their bites and the factors that determine this behavior, such as personality and temperament, kinship, or the strength of social bonds between the aggressor and target, would likely advance our understanding of the link between aggressive behavior and trauma.

4.2 Negative association between aggression and trauma following natal male and policer KOs

During the weeks following the permanent removal of a high-ranked natal male in two study groups, we found a negative relationship between severe aggression rates and multiple types of trauma. Specifically, both puncture wounds and moderate-severe trauma were more frequent during weeks when the rate of severe aggression by adult males was lower. In addition, there was a trend for lacerations to be more frequent during weeks when the overall rate of severe aggression was lower. Similarly, an unexpected negative relationship was found between rates of total aggression and multiple types of trauma in the study groups that experienced the temporary removal of conflict policers. Following onset of the policer KOs, all categories of trauma (except abrasions) were lower during weeks with higher rates of total aggression.

The type of social perturbation may partly explain this negative relationship. The natal male and policer KO experiments both involved removal of high-ranked individuals (primarily males) which likely impacted the stability of the hierarchy, at least temporarily. Thus, social perturbations that involve animals at the top of the hierarchy may cause rates of aggression to be negatively associated with rates of trauma. The underlying reason for the negative relationship between aggression and trauma rates is not entirely clear, however. Future research will investigate this relationship further, such as examining whether policers' use of aggression changed upon returning to their social groups (e.g., if policers used aggression more often, to reassert/ exercise their role as conflict policers, this policing aggression may have kept trauma rates down). Alternatively, rates of mild aggression may have changed following the experimental KOs such that animals increased mild aggression (thereby increasing rates of total aggression) to counteract the temporary hierarchical instability and maintain dominance relationships, with reduced rates of trauma being a byproduct of this maintenance.

4.3 Conflict policing via impartial interventions reduces trauma rates

During the baseline weeks of study, the predictor most frequently found in our top models was the rate of impartial interventions. The top models of baseline lacerations, moderate-severe trauma, and total trauma all indicated that trauma frequencies were lower during weeks with more impartial interventions. Furthermore, impartial interventions were negatively associated with certain types of trauma following the matriline fragment KO (i.e., abrasions) and policer KO (i.e., abrasions and moderate-severe trauma). The frequent appearance of impartial interventions in the top models of our analyses suggests that conflict policing behavior is a key social mechanism for reducing trauma. This is consistent with prior work which has highlighted the importance of conflict policing and the presence of adult males (i.e., the primary conflict policers) for the maintenance of social stability in macaques (Bernstein and Sharpe, 1966; Flack et al., 2005b; Beisner et al., 2012; McCowan et al., 2017) as well as other species (von Rohr et al., 2012). Notably, the rate of impartial interventions was negatively associated with some of the more serious types of trauma (e.g., counts of moderate-severe trauma and lacerations). This suggests that policing is particularly effective at reducing some of the most detrimental aggression among group members. Furthermore, it suggests that observations of dramatic and/or persistent increases in the

frequency of lacerations or moderate-severe trauma (as opposed to abrasions and puncture wounds) may signal a decrease in social stability if conflict policers are not keeping such trauma in check.

4.4 Trauma across different age/sex categories

Total trauma was unequally distributed across different age/sex classes. We found that adult and/or subadult males were injured more often than expected by chance in all study groups. Male macaques are often reported to receive more frequent and/or more severe trauma than females (Vandenbergh and Vessey, 1968; Wilson and Boelkins, 1970; Whitten and Smith, 1984; Ruehlmann et al., 1988), although sex differences are not always found (Mallow, 1980). The bias toward males in receipt of trauma in captivity may be associated with males' inability to emigrate from their natal groups without management intervention. In most macaque species, males disperse from their natal groups around sexual maturity (e.g., *M. fascicularis*: (Van Noordwijk and Van Schaik, 1985); *M. mulatta*: (Drickamer and Vessey, 1973); *M. nemestrina*: (Oi, 1990); but see (Marty et al., 2017)). However, males at the CNPRC remain in their natal groups unless or until they are removed for research or management purposes. Thus, higher rates of trauma received by subadult males in particular may be an indication that these males are no longer welcome in their natal group (perhaps because group members expect them to leave), and due to the boundaries of a captive enclosure, they cannot escape their attackers. However, the welfare benefits of outdoor social group housing for normal physiological and social health are great enough that males should be maintained in social groups unless they are instigators or recipients of repeated and severe trauma.

4.5 Management implications

The findings from this study have some implications for the management of macaque social groups in captivity. First, observed increases in the rate of aggression (even severe aggression) in macaque social groups likely provide little information about the risk of trauma for group members, particularly when groups have not experienced any recent social perturbations to the hierarchy. For the purposes of managing social groups of macaques, our results suggest that monitoring the underlying social dynamics of stability in macaque groups, i.e., rates of impartial interventions and policing, are much more informative with regard to trauma than rates of aggression (McCowan et al., 2017). This is not to say that rates of aggression contain no information; monitoring specific types of aggression, such as rates of bidirectional or insubordinate aggression toward specific individuals (e.g., the alpha matriline) may be indicators of social instability and therefore trauma risk (Wooddell et al., 2017). Regardless, it is desirable to reduce trauma rates in both stable as well as potentially unstable social groups. In lieu of behavioral monitoring, colony managers might aim to maintain sufficient numbers of adult males (particularly males with equable or tolerant personality and high social power) because these adult males are the primary conflict policers (McCowan et al., 2011; Beisner et al., 2012). However, maintenance of adult males in captive groups of rhesus macaques is challenging, and our finding that males receive more trauma than expected seems to underscore this fact. Second, our results suggest that enrichment or management strategies aimed at reducing rates of aggression will not

necessarily reduce rates of trauma. The value of management strategies for reducing trauma requires study of its impact on trauma directly.

5. Conclusion

Although socially inflicted traumas are a common consequence of social housing of highly gregarious species in captivity, e.g., tail biting in commercially raised pigs, feather pecking in laying hens, lacerations and punctures in macaques, the relationship between social aggression and trauma appears to depend upon the taxonomic group being studied. For instance, aggression and trauma tend to be related in pigs (Turner et al., 2006; Desire et al., 2015) but they have an unpredictable relationship in rhesus macaques. Furthermore, some traumas such as feather pecking in laying hens are not driven by aggression at all (Bessei et al., 2013; Daigle, 2017). Despite these differences, there are some other commonalities. The suppression and/or policing of group conflict by adult males is common to both macaques (Flack et al., 2005a; Beisner and McCowan, 2013) and pigs (Grandin and Bruning, 1992; Borberg and Hoy, 2009). Among pigs, boar presence is associated with reduced fighting in mixed pigs, and boars have been observed to walk between fighting pigs or intervene to stop fights (Grandin and Bruning, 1992; but see Seguin et al., 2006). Therefore, development of appropriate management strategies for socially-derived injuries is likely to be largely species-specific, but valuable insights can be gained from cross-species comparison.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- Trauma is an undesirable consequence of group housing rhesus macaques
- We tested if social aggression rates predict rates of different types of trauma
- Aggression shows an inconsistent, sometimes negative, relationship with trauma
- High rates of impartial conflict intervention predict low trauma rates

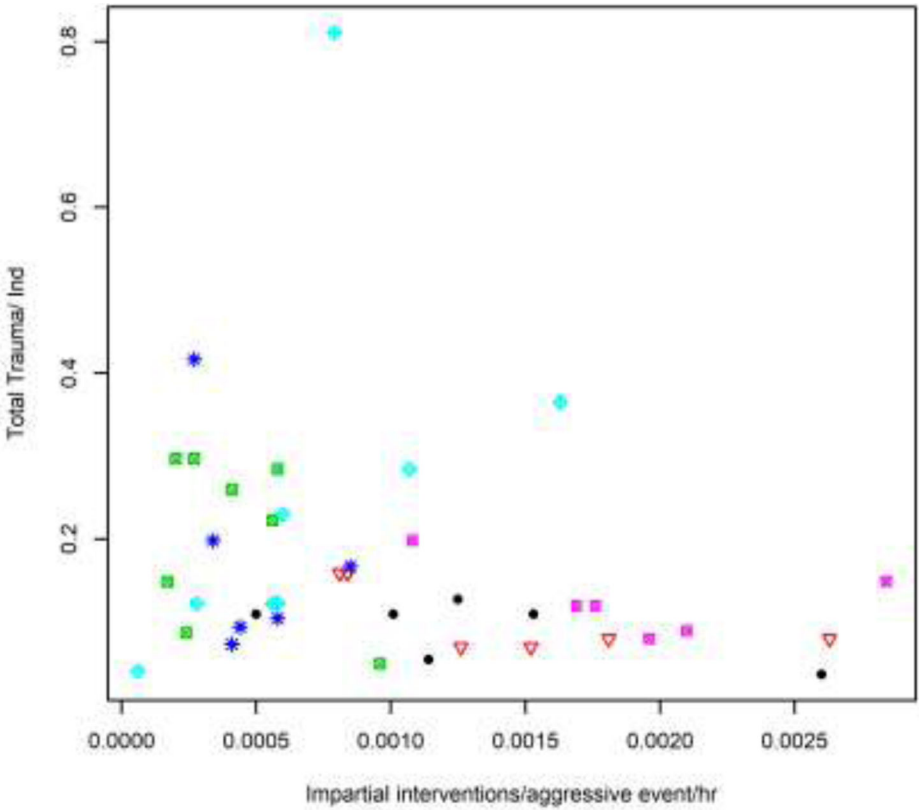

Fig 1.

Rate of total trauma relative to rate of impartial interventions (n = 40 weekly counts across six study groups; shapes and colors distinguish different study groups)

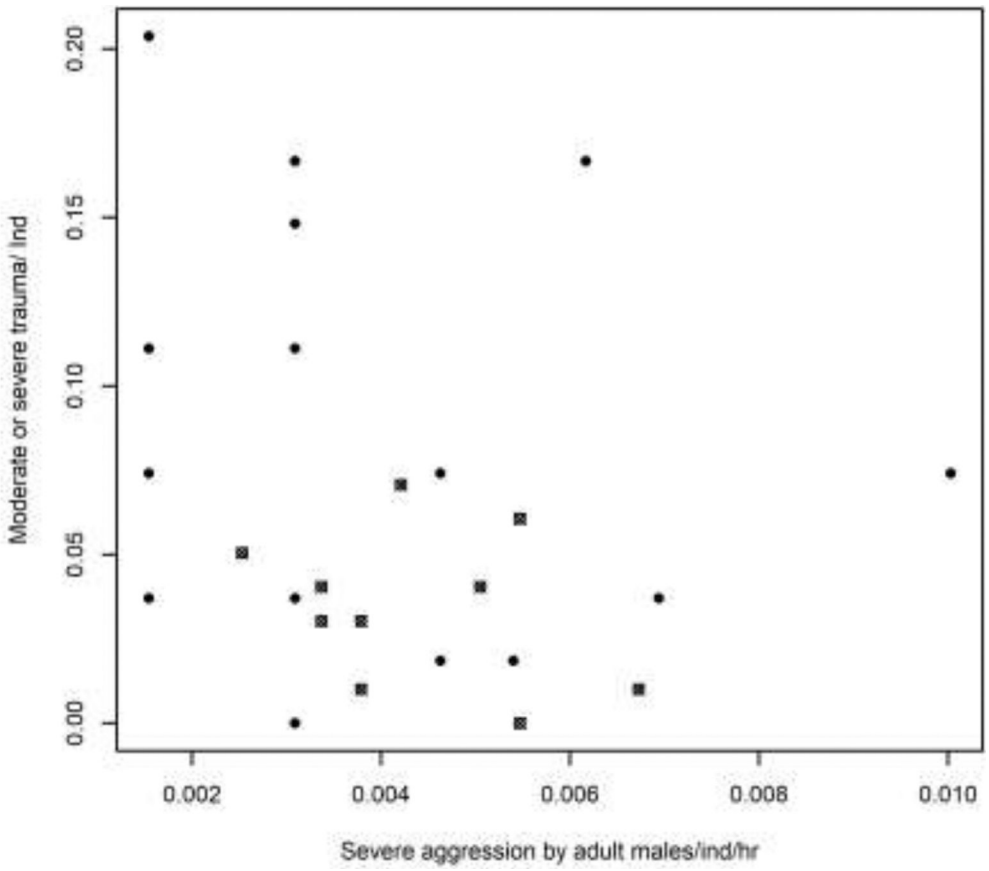

Fig 2.

Rate of moderate-severe trauma relative to the rate of severe aggression by adult males from two study groups (represented by circles and squares) that experienced a natal male KO

Table 1

Study groups' characteristics

Group	Group Size (adults)	Adult Sex Ratio (females:male)	Number of Matrilines (mean size)	Perturbation
A	132 (101)	4.7	13 (8.0 inds)	matriline fragment KO
B	185 (96)	4.9	13 (8.2 inds)	matriline fragment KO
C	204 (101)	5.6	40 (3.3 inds)	natal male KO
D	125 (55)	3.9	6 (13.7 inds)	natal male KO
E	156 (81)	11.4	30 (3.0 inds)	conflict policer KO
F	107 (74)	4.9	19 (3.7 inds)	conflict policer KO

Table 2

Definitions of trauma types

Trauma category	Definition	Observed severity
abrasion	superficial cuts or scraping of the skin	98.5% minor; 1.5% moderate
crush or bruising	injuries that cause bruising or other internal injury without piercing the skin	100% minor
digit trauma	any trauma to the digits, including punctures, lacerations, or crush, as well as removal of all or part of a digit, but not including trauma to the nail	50% minor; 28.5% moderate; 21.5% severe
laceration	injuries that tear or rip the skin	68.7% minor; 22.2% moderate; 9.0% severe
nail avulsion	trauma to the nngernail/toenail without additional digit trauma; includes removal of part or all of a nail	50% minor; 50% moderate
puncture	injuries directed straight into the skin, with no additional tearing/abrasion of the skin	81.3% minor; 18.7% moderate

Table 3

Observed (vs. expected [a]) frequencies of trauma across age/sex classes

	Group A	Group B	Group C	Group D	Group E	Group F
Adult females	144 (190.2)	203 (281.9)	195 (218.4)	79 (120.7)	190 (257.6)	267 (319.7)
Adult males	70 (41.1)	87 (55.6)	24 (39.1)	42 (30.6)	30 (22.1)	106 (65.7)
Subadult males	43 (25.7)	107 (59.5)	107 (68.5)	49 (18.7)	148 (88.3)	65 (52.6)
Chi-square	43.14	77.64	30.05	67.75	60.91	36.36
p-value	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Result	Less female trauma; more male trauma	Less female trauma; more male trauma	More subadult male trauma	Less female trauma; more male trauma	Less female trauma; more subadult male trauma	Less female trauma; more adult male trauma

[a] expected frequencies of trauma calculated from the proportion of each age/sex class in each study group

Table 4

Summary of group-level weekly trauma analyses, highlighting the predictors associated with trauma variables at $p < 0.10$

	Baseline	Matrihne fragment KO	Natal male KO	Temporary KO (conflict policers or high-ranked controls)
Total trauma	Impartial interventions**	Season**	none	[a]Aggression** Weeks since KO**
Moderate-Severe trauma	Season* Impartial interventions*	Weeks since KO** Season**	[a]Severe aggression by adult males** Weeks since KO** Season**	Impartial interventions** [a]Aggression** Season**
Lacerations	Impartial interventions**	Weeks since KO**	Aggression* [a]Severe aggression* Weeks since KO**	[a]Aggression**
Punctures	none	Season**	[a]Severe aggression by adult males**	[a]Aggression** Severe aggression by adult males**
Abrasions	none	Impartial interventions**	none	Impartial interventions* Weeks since KO**

*$0.05 < p < 0.10$

**$p<0.05$

[a]unexpected negative association with trauma