

# Utility of Automated Feeding Data to Detect Social Instability in a Captive Breeding Colony of Rhesus Macaques (*Macaca mulatta*): A Case Study of Intrafamily Aggression

Juliane R Johnston,<sup>1</sup> Tracy L Meeker,<sup>1</sup> Jacklyn K Ramsey,<sup>1</sup> Maria M Crane,<sup>1</sup> Joyce K Cohen,<sup>1,3</sup> and Kelly F Ethun<sup>1,2,4,\*</sup>

Some captive breeding colonies of rhesus macaques live in large outdoor multimale, multifemale social groups. These groups are composed of several matrilineal families, governed by a clear female dominance hierarchy. Aggression within the same or between different matrilineal families due to social instability can result in trauma and mortality. Therefore, a primary management goal is to detect emerging social unrest before the onset of significant fighting and wounding. Accordingly, groups are monitored routinely for changes in dominance and alliance relations as well as for increases in trauma frequency and severity. Decreased food intake is a normal physiologic response to acute stress; therefore, inappetence in key animals or groups of monkeys might be used as an indicator of increased social stress and emerging instability. An incident of intrafamily aggression occurred recently in a breeding group at our facility and resulted in considerable fighting. Because this compound was equipped with an automated feeding system that tracks the caloric intake of individual animals, we retrospectively analyzed feeding data to determine whether significant reduction in caloric consumption occurred prior to the onset of aggression, compared with baseline values. Neither the entire group nor individual families showed any significant differences in total caloric intake between baseline and previous 24 h values; however, the affected family exhibited a 20% reduction in total caloric during the 24 h prior to the aggression. Most notably, the deposed subfamily showed a marked 58% reduction in caloric intake during the prior 24 h, whereas remaining subfamilies showed no significant changes in intake. High-ranking animals of the group, including the  $\alpha$  female,  $\beta$  female, and  $\alpha$  male, similarly exhibited marked decreases in caloric intake during that period. These findings indicate that automated feeders can assist management staff with monitoring social stability in breeding colonies of rhesus macaque.

DOI: 10.30802/AALAS-JAALAS-18-000139

To simulate wild conditions and maximize breeding efficiency, some rhesus macaques bred for research are raised in large outdoor multimale, multifemale social groups.<sup>3</sup> These large breeding groups are often composed of several multigenerational matrilineal families. Several factors contribute to the social stability of these groups, including a clear dominance hierarchy,<sup>5,9,18</sup> a cohesive kinship structure within families,<sup>5,13</sup> and the presence of adult males or other high-ranking animals that effectively 'police' social conflicts.<sup>6,7,10,21</sup> Due to the despotic dominance style of rhesus macaques,<sup>16,41</sup> a low level of social aggression is expected,<sup>8,9</sup> however, increased rates of uncontrolled aggression among members of the same or different matrilineal families is indicative of social instability and can result in significant trauma and even mortality.<sup>18</sup>

Increased rates of aggression and trauma are a particular concern for rhesus macaque breeding programs due to the established link between social overthrows (maximal group instability) and poor reproductive output.<sup>17</sup> For these reasons, a primary goal in the management of these breeding groups is the detection of emerging social unrest before the onset of

significant fighting and wounding. Accordingly, large breeding groups of rhesus macaques are routinely monitored by management staff for changes in dominance and alliance relations at both the group- and matrilineal-level as well as for increases in trauma frequency and severity.<sup>5,36</sup>

In addition to its potential to result in significant wounding, social aggression in macaque groups can lead to increased psychosocial stress in all involved parties and particularly in the intended targets.<sup>2,25</sup> Glucocorticoids are elevated in response to acute psychosocial stress,<sup>26</sup> and the same central neuroendocrine pathways that control these hormonal changes also induce appetite suppression in animals exposed to acute stress.<sup>31</sup> Indeed, transient episodes of anorexia and inappetence commonly occur in experimental animal models of acute psychosocial stress<sup>11,12,28,34</sup> as well as in animals after housing changes (that is, location transfer or group composition change).<sup>15,35,44,45</sup> Therefore, it is reasonable to hypothesize that inappetence among socially housed macaques may be indicative of increased social stress and evident before the onset of overt aggression.

Automated feeders that reliably record the calorie consumption of individual animals among socially housed rhesus macaques are commercially available; however, little information is available regarding the value of this system in the management of colony social health. Recently, an incident of intrafamily fighting occurred involving a middle-ranked family

Received: 04 Dec 2018. Revision requested: 12 Feb 2019. Accepted: 29 Apr 2019.

Divisions of <sup>1</sup>Animal Resources and <sup>2</sup>Developmental and Cognitive Neurosciences, Yerkes National Primate Research Center, and Departments of <sup>3</sup>Psychiatry and <sup>4</sup>Pathology and Laboratory Medicine, Emory University School of Medicine, Atlanta, Georgia

\*Corresponding author. Email: Kelly.f.ethun@emory.edu

of a large established breeding group at the Yerkes National Primate Research Center that resulted in significant wounding. In this incident, animals from 2 different subfamilies incurred injuries. Because the compound housing this social group was equipped with automated feeders, feeding data were analyzed retrospectively to determine whether any significant reduction in daily caloric consumption occurred 24, 48, 72, or 96 h prior to the onset of overt aggression at the group-, family-, or subfamily-level compared with baseline values (that is, previous 30-d average). We hypothesized that no change in feeding activity would be observed at the group-level across time but that the affected family would exhibit a significant decrease in average caloric intake at least 24 h prior to the reported incident. Most notably, we hypothesized that the subfamily with the worse injuries would show the greatest percentage decrease in average caloric intake during this time period. Finally, we hypothesized that the percentage decrease in caloric intake from baseline to -24 h in these 'most-affected' animals would significantly predict the severity of their wounds received during the fighting incident and baseline period. Findings from this study validate the usefulness of automated feeding systems in the monitoring of social stability among compound-housed rhesus macaques, particularly when analyzed in conjunction with wounding and social behavior data.

## Materials and Methods

**Study population.** The rhesus macaque (*Macaca mulatta*) breeding colony at the Yerkes NPRC (Lawrenceville, GA) is primarily maintained in large multimale, multifemale breeding groups (18 to 169 animals), comprising multiple multigenerational matrilineal, and housed in 0.06- to 0.38-acre outdoor compounds with attached indoor enclosures. This case study describes changes in feeding patterns and trauma scores associated with an incident of intrafamily aggression within one of these large breeding groups. At the time of the reported incident, group membership was 126 animals, including 2 breeding adult males, 63 breeding-age females, 40 juvenile and yearling offspring (1 to 3 y old), and 21 infants (younger than 12 mo).

The adult females and their offspring were organized into 8 different families (Table 1) and multiple subfamilies (Table 2). For the purpose of this report, subfamily refers to a branch in the pedigree of a matriline. Each subfamily is represented by the oldest (and most commonly highest-ranked) adult female that is the daughter or granddaughter to the common maternal ancestor of the family. Animals referred to as the 'α female' and 'β female' in this report represent the 1st- and 2nd-ranked adult females in the entire linear hierarchy of the social group. The α and β females are members of the α (1st-ranked) family of the group. The α and β females, as well as other adult female members of the α (1st-ranked) and β (2nd-ranked) families, are referred to as 'high-ranking animals of the social group' in this report. At our facility, genetically related juvenile males are removed from their natal groups by 36 mo of age, and unrelated adult males are rotated among the breeding groups every 3 y. Therefore, no adult males were present in this social group, other than the 2 unrelated adult breeding males. Due to their role in controlling aggression among adult females of the social group, adult breeding rhesus macaque males (along with adult females of the α and β families) are referred to as 'high-ranking animals' of the social group, or specifically as 'α male' or 'β male,' in this report.

This large breeding group was established in 1996; therefore, these animals were housed together for 21 y prior to the incident. An overthrow of the α family of this group occurred in December

**Table 1.** Number of breeding females and offspring per family

Family rank	Adult females	Offspring <sup>a</sup>	Total
1	11	5	16
2	4	2	6
3	7	7	14
4	3	3	6
5	16	9	25
6	17	13	30
7	2	1	3
8	3	0	3
Total	63	40	103

<sup>a</sup>1 to 3 y of age.

**Table 2.** Composition of 5th-ranked family

Subfamily	Adult females	Offspring <sup>a</sup>	Total
A	4 <sup>b</sup>	2	6
B	2	1	3
C	3	2	5
D	5 <sup>c</sup>	3	8
E	2	1	3
Total	16	9	25

<sup>a</sup>1 to 3 y of age.

<sup>b</sup>One adult female in the A subfamily and <sup>c</sup>2 adult females in the D subfamily were out of the group at the time of the fighting incident.

2011, but no other major social changes occurred in the 6.5 y prior to the current incident. Management of this social group was consistent with other compound-based breeding groups at our facility. Routine group observations were conducted by experienced colony management staff to monitor for changes in social dominance and alliance ties. Social rank data of each family were available in colony records and determined by the frequency of submissive behavior and aggression received by nonfamilial group mates.<sup>40</sup> Matrilineal coefficient of relatedness was based on genetic data available at the time of the fighting incident.

All animals had continuous access to fresh drinking water and unrestricted access to a commercial monkey diet (LabDiet 503A, Purina Mills International, St Louis, MO) dispensed by an automated feeder system (NHP BioDAQ version 6, Research Diets, New Brunswick, NJ). LabDiet 503A is the pelleted (3/8 in. × 1/2 to 3/4 in.) version of the standard LabDiet 5038 Monkey Diet and is compatible with the NHP BioDAQ system. Routine enrichment provided to all animals included fresh produce, climbing structures, foraging devices, and other manipulanda. All animals were free of SIV, simian T-lymphotropic virus, simian type D retroviruses, and herpes simian B virus. The facility and its programs are fully AAALAC-accredited. Procedures involving all animals were approved by the Emory University IACUC and were conducted in accordance with USDA Animal Welfare Regulations,<sup>1</sup> the *Guide for the Care and Use of Laboratory Animals*,<sup>39</sup> and institutional policies.

**Automated feeders and caloric intake analyses.** Caloric intake data for each macaque in the group was quantified by using an automated feeding system with radiofrequency identification technology (NHP BioDAQ version 6, Research Diets, New Brunswick, NJ). As animals obtain food pellets, the computer-controlled system records the weight (in grams) obtained in real-time by detecting radiofrequency identification microchips (DataMar, Temple, TX) implanted subcutaneously

in each hand of individual animals. Validation studies have revealed that animals waste less than 5% of food obtained. In addition, because food is continuously available and because each compound is equipped with multiple feeders, dominant macaques do not restrict the access of more subordinate animals to feeders.<sup>43</sup> Therefore, all animals in the group have free access to a standard monkey diet.

Feeding bout data generated by the feeding system were simultaneously stored and managed on a local and remote server. The software associated with this system (BioDAQ Online DataViewer) can summarize feeding bouts of individual animals over a specified time period (as HH:MM:SS) as the total number of kilocalories obtained. In addition, daily feeding reports are sent to veterinary and colony management staff via email, identifying animals that have not been scanned within the past 24 h (0500:00 to 0500:00 the previous morning), macaques that have eaten less than a predetermined number of daily kilocalories according to their age, and those that consumed 75% less calories than their 7-d average. The minimal daily kilocalorie requirement—but not the percentage change in caloric intake parameter and baseline average interval—can be changed by the user. These parameters are encoded in the software, because they were originally intended to identify animals with missing or broken radiofrequency identification microchips and to alert husbandry staff to malfunctioning feeders.

After the intrafamily fighting incident described in this case report, retrospective analyses of caloric intake data from this compound were conducted. Using the feeding system software, total caloric intake values for each animal in the group (older than 12 mo of age) were calculated 24, 48, 72, and 96 h prior to the fighting incident ( $t = 0$ , 2000:00). The average daily number of kilocalories consumed by each animal for 30 d prior to the incident (96 h to 34 d) was considered their baseline value. Infants younger than 12 mo were excluded from the feeding data analyses, because of the large variations in the timing of weaning in this NHP species.<sup>38</sup> In addition, all feeding data from animals not present in the group at the time of the fighting incident or those with a history of chronic illness (for example, diarrhea) were excluded. Once generated, all feeding data were exported into a spreadsheet program (Excel, Microsoft, Redmond, WA) for summarization and statistical analyses. In addition, the feeding data were screened for quality assurance prior to any analyses. Because the feeding system contains a light sensor, we also compared the nighttime and daytime feeding patterns of individual animals. Feeding bout heatmaps displayed in the results were generated by using the BioDAQ Online DataViewer. Because they use a color system, each consumption heatmap graphically represents the number of feeding bouts that occurred during each hour of the day (0 to 24) over a specified number of days (for example, 0 to 6 d prior to the fighting incident). The density or darkness of the green blocks used in these graphs is positively related to the number of feeding bouts that occurred during that hour of the day (for example, a darker green block represents a greater number of feeding bouts than a lighter green block; a white block for a particular hour of the day represents no feeding activity or zero calories consumed).

**Wound scoring.** To examine the relationship between inappetence and trauma severity, all trauma cases that occurred during the fighting incident and baseline period among the 5th-ranked family members were scored retrospectively according to wound descriptions recorded in their clinical records by using a 5-point trauma severity scale (Figure 1). When an individual trauma case had multiple injuries, the

trauma severity score for that incident was equivalent to the product of the worse injury score and the number of injuries. A final trauma severity score sum was then calculated for each animal by summing the scores for each trauma incident associated with each animal in the 5th-ranked family during the baseline period and fighting incident.

The highest score on the trauma severity scale was reserved for the occurrence of severe female-inflicted crush trauma wounds with evidence of rhabdomyolysis. Rhabdomyolysis is a serious consequence of crushing wounds because elevated blood levels of creatine kinase, myoglobin, electrolytes, purines, and other enzymes caused by trauma-inflicted muscle damage can lead to acute kidney injury, marked metabolic acidosis, and decreased survival.<sup>27,30,37</sup> As such, primary lab parameters evaluated in these cases included venous blood pH, lactate, base excess, bicarbonate, and serum creatine kinase levels. According to previously published data for rhesus macaques, normal ranges for these parameters were: lactate, 0 to 2.0 mmol/L; pH, 7.35 to 7.45; bicarbonate, 15 to 23 mmol/L; and base excess, -2 to 3 mEq/L. Any acid-base value outside of these normal ranges that was in the direction of acidosis (that is, lactate greater than 2.0 mmol/L; pH less than 7.350; bicarbonate less than 15 mmol/L; or base excess less than -2 mEq/L) was considered indicative of metabolic acidosis, a hallmark of rhabdomyolysis.<sup>27</sup> Peak serum creatine kinase values greater than 1000 U/L, measured 6 to 12 h after injury, were indicative of muscle damage.<sup>14</sup> Slash-type injuries with muscle involvement (scores 2 to 5) were considered to be male-inflicted wounds.<sup>3</sup>

**Statistical analyses.** Feeding data analyzed for this case study included the total number of kilocalories consumed by each animal in the group (older than 12 mo of age) within 24, 48, 72, and 96 h prior to the intrafamily fighting incident ( $t = 0$ , 2000:00) involving the 5th-ranked family of the group. The average daily number of kilocalories consumed by each animal in the group 30 d prior to the incident (96 h to 34 d before) was considered the baseline value. In addition, the percent changes in caloric intake from baseline to 24 and 48 h prior to the intrafamily fighting event were calculated for each animal in the group. By using statistical software JMP 13 Pro (SAS Institute, Cary, NC), all feeding and trauma severity score data were evaluated to confirm normality and equality of variance. Data not normally distributed were transformed to improve normality for analysis.

Total kilocalorie intake data were normally distributed after square-root transformation; however, significant Levene and Bartlett tests ( $P$  values = 0.001 to 0.04) indicated unequal variance by group-family (ranks 1 to 8), subfamily of 5th-ranked family (A through E), and time. Therefore, a repeat-measures linear mixed-effect model with a Toeplitz unequal variance structure was chosen to determine whether the total number of kilocalories consumed by the whole group and individual families changed across the study timepoints. Fixed-effect terms for this repeated-measures model included time, family (ranks 1 to 8), and their interaction. A similar model was used to determine whether the 5th-ranked family of the group experienced a significant decrease in kilocalorie intake at 24 and 48 h prior to the fighting incident compared with their baseline values. Fixed-effect terms for this caloric intake model included time, subfamily (A through E), and their interaction. All percent change in caloric intake data from baseline to 24 h prior to the event were normally distributed and had equality of variance (nonsignificant Levene and Bartlett tests) between group-families (ranks 1 to 8) and 5th-ranked family subfamilies (A through E); therefore, separate least square means models with

Score	Degree	Wound Description
1	Minor	Superficial laceration, abrasion, or puncture wound to body or extremities (digits/tail), < 3 cm in length
2	Mild	Laceration or puncture wound with or without minor muscle involvement (breaks fascia only), 3–6 cm in length.
3	Moderate	Laceration, puncture, or degloving wound with muscle involvement ( $\leq 0.5$ cm in depth) and > 6 cm in length. Bite wounds or other soft tissue injuries with mild swelling.
4	Marked	Deep laceration or puncture wound with muscle involvement (> 0.5 cm in depth), any length. Crush trauma bite wounds with no evidence of rhabdomyolysis. Other soft tissue injuries with moderate swelling.
5	Severe	Severe crush trauma bite wounds with evidence of rhabdomyolysis. Other soft tissue injuries with marked swelling. Deep ( $\geq 0.5$ cm) muscle laceration of any length, involving multiple muscle bodies.

**Figure 1.** Numerical scoring system for trauma severity. All trauma cases that occurred during the incident of intrafamily aggression and baseline period among 5th-ranked family members were scored retrospectively, according to wound descriptions in clinical records. A trauma severity score sum was then calculated for each animal.

a fixed-effect term of family or subfamily was used to determine whether individual families of the group or subfamilies of the 5th-ranked family exhibited different degrees of inappetence within 24 h of the main social aggression incident, respectively.

The percent change in kilocalorie intake data from baseline to 48 h prior to the event were normally distributed but had unequal variance between individual families and subfamilies; therefore, separate linear mixed-effect models with Toeplitz unequal variance structures were used with family or subfamily as fixed-effect terms. Tukey Honest Significant Difference tests were used for all posthoc comparisons. To determine whether percent change in caloric intake from baseline to 24 h prior to the fighting event in targeted animals significantly predicted the severity of their wounds, severity scores of injuries received by 5th-ranked family members during the fighting incident and their trauma severity score sums were analyzed in separate univariate regression analyses. An  $\alpha$  level of less than 0.05 was considered significant for all analyses. For simplicity, raw data are displayed in the results.

### Case Study

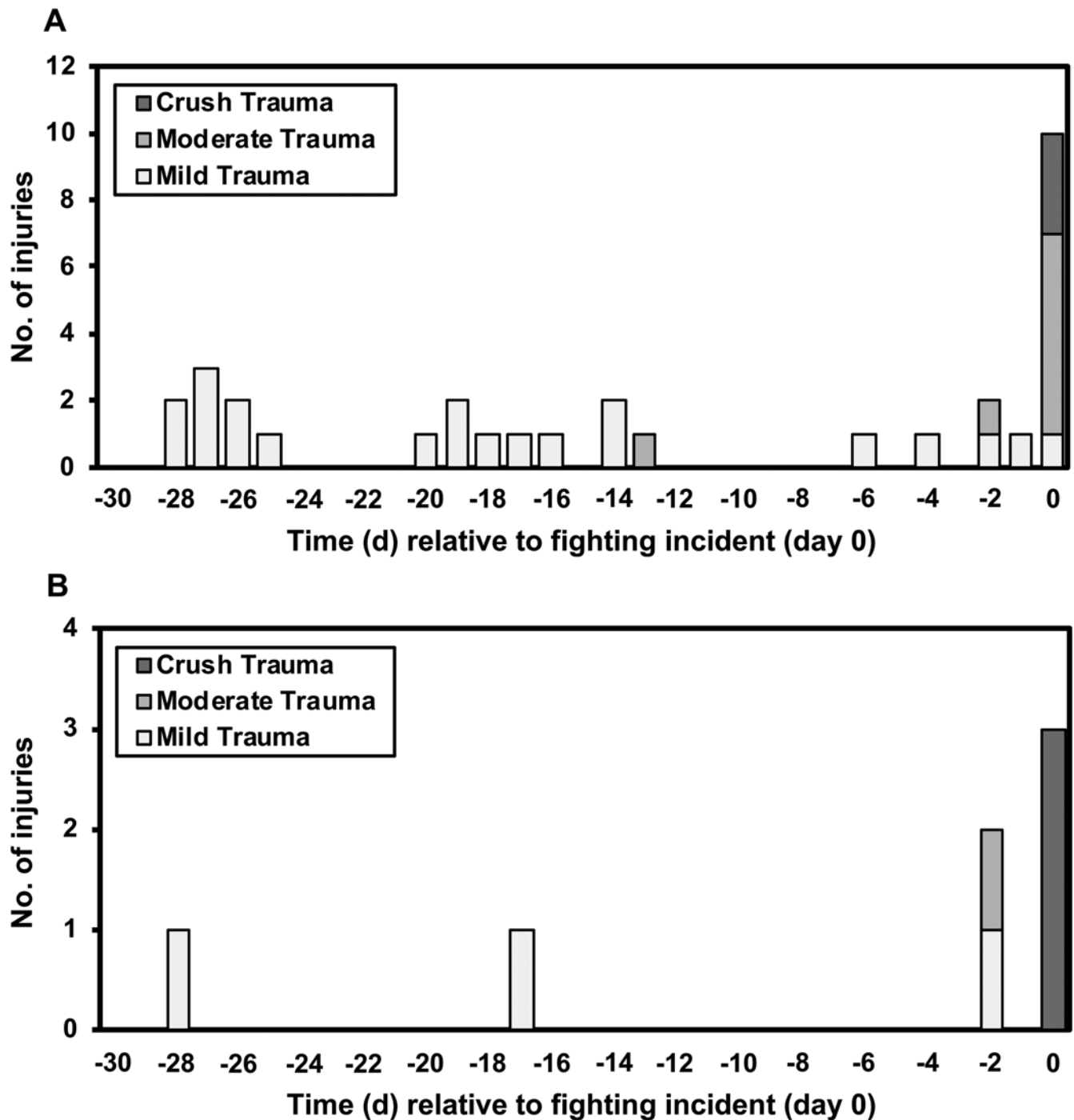
At 2000 on a Monday evening in early spring, a nighttime animal care technician reported significant fighting among members of the 5th-ranked family of rhesus macaques that were living in a large established breeding group at our facility (Yerkes National Primate Research Center Field Station). Several adult females from the  $\alpha$  and  $\beta$  families of the group and the 2 breeding males were also observed to be involved. Although group-level trauma rates in the 4 wk prior to this incident were relatively low (Figure 2 A), this incident of social unrest resulted in a total of 3 cases of crush trauma, 6 cases of moderate male- and female-inflicted trauma, and one case of mild male-inflicted trauma. All macaques survived and were immediately cared for according to the severity of their wounds.

The 5th-ranked family of the group had 5 subfamilies (A through E), comprising a total of 16 adult females and 9 juveniles

(Table 2). The intrafamily fighting incident involved the top-ranked A subfamily ( $n = 4$  adult females) and middle-ranked C subfamily ( $n = 3$  adult females) of the 5th-ranked family. Similar to group-level trauma rates, the number of previously reported injuries involving subfamily A members in the 4 wk prior to this incident were relatively low (Figure 2 B). However, at 2 d prior to the incident, a colony management technician observed 3 high-ranking females from the  $\alpha$  and  $\beta$  families of the group briefly aggress the highest-ranking female of subfamily A of the 5th-ranked family of the group and her oldest daughter. The highest-ranking female of subfamily A experienced a minor ear wound only; however, her daughter received moderate female-inflicted injuries and was removed from the group for treatment. No additional aggression nor other social concerns were noted during follow-up observations of this social group conducted that day (Saturday afternoon) and the next day (Sunday morning). During the main fighting event (Monday evening), all 3 of the remaining adult females of subfamily A of the 5th-ranked family received crush trauma injuries, including the highest-ranked female of subfamily A that received minor ear trauma at 2 d previously. Indeed, this highest-ranking female of the subfamily A sustained the worst crush trauma injuries, consisting of multiple soft tissue injuries with moderate swelling and bruising. Lab work revealed serum creatine kinase levels greater than 1100 U/L at approximately 12 h after injury and normal acid–base and lactate values, consistent with muscle injury but not to the extent of rhabdomyolysis. The highest-ranking female of subfamily C had female-inflicted wounds of moderate severity as well as 2 mild male-inflicted wounds. Five adult females in the  $\alpha$  family, including the  $\alpha$  and  $\beta$  females of the group, and one adult female from the  $\beta$  family were found to have mild to moderate male-inflicted trauma injuries.

### Results

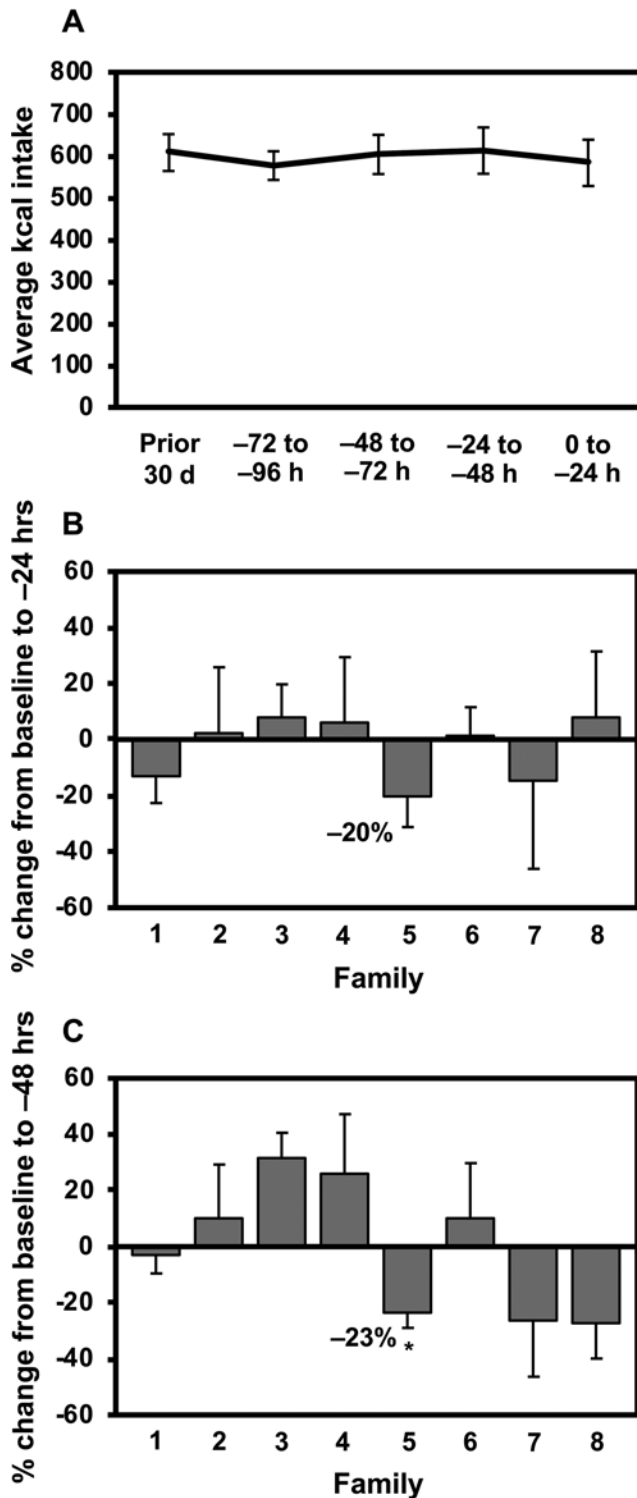
**Caloric intake analyses by social group and family.** Feeding data in this study were analyzed retrospectively due to a 15-h



**Figure 2.** Trauma frequencies for (A) the social group ( $n = 103$  macaques) and (B) targeted subfamily A of the 5th-ranked family of the social group ( $n = 4$  adults and  $n = 2$  juveniles). All 3 of the adult females of subfamily A of the 5th-ranked family present in the group during the intra-family fighting incident ( $t = 0$ ) received crush trauma injuries. Two days before this fighting incident, the highest-ranking female of subfamily A and her oldest daughter were aggressed by females belonging to the  $\alpha$  and  $\beta$  families of the group and received mild and moderate trauma, respectively. The adult female with moderate female-inflicted trauma was removed from the group for treatment. This same adult female received mild trauma 17 d prior to the intrafamily fighting event. No other social aggression-related injuries were reported for other members of this subfamily.

time difference between the occurrence of the fighting incident ( $t = 0, 2000$ ) and generation of the last daily email feeding report received by management ( $t = 15$  h prior to event, 0500 to 0500 the previous morning, see methods). Specifically, feeding data were analyzed by compound and family to determine whether significant reduction in caloric consumption occurred within the 24, 48, 72, or 96 h prior to the onset of fighting, compared with baseline values (prior 30-d daily average). Results revealed no

significant difference in caloric consumption for the whole social group and individual families across time (time:  $F_{4,169} = 0.64$ ,  $P = 0.64$ , Figure 3 A; family $\times$ time:  $F_{28,260} = 1.07$ ,  $P = 0.37$ , data not shown). In addition, the percent change in caloric intake from baseline to  $-24$  h prior to the fighting event was not significantly different between individual families (Figure 3 B; family rank,  $F_{7,82} = 0.60$ ,  $P = 0.75$ ); however, the affected 5th-ranked family exhibited 20% and 23% decreases in caloric intake from baseline



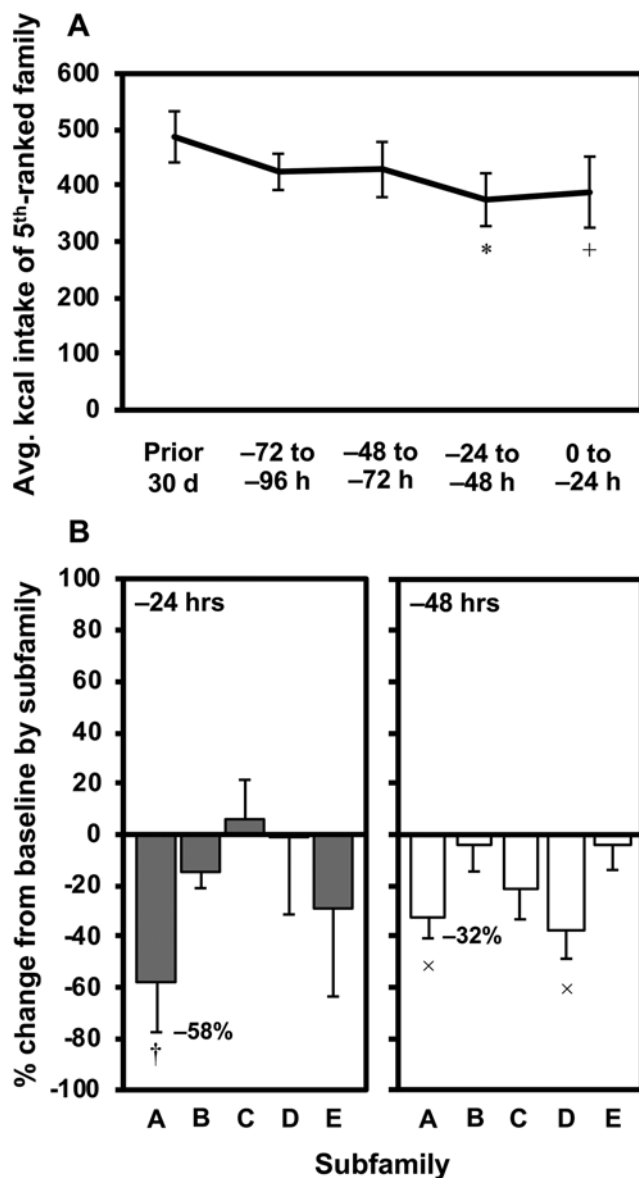
**Figure 3.** Average caloric intake by social group and family. (A) No significant changes in caloric intake at the group-level were observed prior to the intrafamily fighting incident among 5th-ranked family members (0 h). (B) The percentage change in caloric intake from baseline to -24 h before this social incident was not significantly different among individual families. However, the affected 5th-ranked family of the group exhibited a 20% decrease in food intake during this period ( $F_{7,82} = 0.60$ ,  $P = 0.75$ ). (C) The 5th-ranked family also exhibited a 23% decrease in appetite at -48 h before the incident; this feeding level was significantly different from the food intake of the 1st- ( $\alpha$ ), 3rd-, and 6th-ranked families ( $^*$ ,  $P < 0.001$ – $0.05$  for all comparisons at -48 h prior). In addition, the lowest-ranking families of the group (7th- and 8th-ranked) showed moderate decreases in appetite during this period, but these changes did not reach statistical significance at the family level. Data are expressed as mean  $\pm$  SEM.

to -24 and -48 h before the fighting incident, respectively (Figure 3 B and C). In agreement, analyses of the number of calories consumed by this affected 5th-ranked family revealed moderate decreases in caloric intake from baseline to 24 and 48 h before the event, respectively (Figure 4 A; time,  $F_{2,21} = 4.84$ ,  $P = 0.02$ ; posthoc pairwise comparisons  $P = 0.09$  and  $\bar{P} < 0.05$  from baseline to -24 and -48 h before the incident, respectively). Most notably, the targeted A subfamily of this 5th-ranked family showed a marked 58% decrease in average caloric intake in the 24 h prior to the main fighting incident (Figure 4 B;  $P = 0.007$  compared with baseline), whereas the remaining subfamilies (B through E) of this same family showed no statistically significant changes in intake during this period. When the same feeding data was expressed as a consumption heatmap (Figure 5), the affected A subfamily had fewer and smaller feeding bouts from -24 to 0 h compared with the previous 6 d.

Both the 7th and 8th-ranked families of the group ( $n = 3$  per family) showed a 27% decrease in caloric intake from baseline to -48 h. These moderate changes in appetite however, did not reach statistical significance. Moreover, the 7th-ranked family exhibited a mild 14% reduction in caloric intake from baseline to -24 h that did not reach statistical significance (Figure 3 B and 3 C). Although the percent change in caloric intake from baseline to -48 h was not statistically different among the subfamilies of the 5th-ranked family of the group, the D subfamily (Table 2;  $n = 6$  in group at time of incident) exhibited a significant 37% decrease in caloric intake during this period (Figure 4 B; posthoc pairwise comparison from baseline to -48 h,  $P = 0.04$ ). In addition, the E subfamily of the 5th-ranked family of the group ( $n = 3$ ) showed a moderate reduction in caloric intake (29%) from baseline to -24 h; however, this change in food intake did not reach statistical significance (Figure 4 A). None of the members of the 7th- and 8th-ranked families or the D and E subfamilies of the 5th-ranked family of the group received trauma during the main intrafamily event or during the brief episode of social aggression noted at 2 d before the primary incident. Furthermore, colony management staff did not observe animals of these families to be involved in noncontact aggressive interactions during this period.

**Feeding patterns of high-ranking animals.** The  $\alpha$  and  $\beta$  females as well as the  $\alpha$  and  $\beta$  breeding males of the social group exhibited changes in their feeding patterns prior to the reported social unrest incident. Specifically, the  $\alpha$  female and male had large percent decreases in caloric intake during the 24 and 48 h prior to the intrafamily fighting incident (Figure 6 A), consuming 32% to 48% fewer calories than their baseline values. Similarly, the  $\beta$  female consumed 32% fewer calories than her baseline values from -48 to -24 h and consumed zero calories from -24 h to 0 (Figure 6 B). In addition, the other adult female members of the  $\alpha$  family ( $n = 9$ ) exhibited a mean percent decrease in caloric intake of 16% and 7% at -24 and -48 h, respectively. Although the  $\alpha$  male of the social group showed an overall percent decrease in caloric intake from baseline to -24 and -48 h, he fed more frequently at night during this period (Figure 6 C). Specifically, the  $\alpha$  male consumed 38% of his total daily calories at night from -24 to 0 h and 36% from -48 to -24 h, compared with consuming 18% (on average) of his total caloric intake at night during the 30-d baseline period. In addition, the  $\beta$  male of the social group exhibited more nighttime feeding in the 24 h prior to the intrafamily fighting incident, consuming 46% of his total daily calories at night during this period compared with 30% (on average) during the baseline period.

**Trauma severity and percent change in caloric intake.** To test our hypothesis that the percent decrease in caloric intake from baseline to -24 h in targeted animals would significantly predict



**Figure 4.** Average caloric intake by the affected 5th-ranked family of the social group. (A) The affected 5th family of the group showed a notable reduction in average caloric intake within -48 h of the intrafamily fighting incident (Time,  $F_{(2,21)} = 4.84$ ,  $P = 0.02$ ; pairwise comparisons from baseline values to -24 and -48 h, †,  $P = 0.09$  and \*,  $P < 0.05$ , respectively). (B) The percent change in caloric intake from baseline to -24 h was not significantly different among the subfamilies of the 5th-ranked family; however, the targeted A subfamily showed a marked -58% reduction in average caloric intake from baseline to -24 h prior to the main social event (†,  $P = 0.007$ , compared with baseline), whereas the remaining subfamilies (B through E) exhibited no statistically significant changes in food intake during this period. Similarly, the percent change in caloric intake from baseline to -48 h was not significantly different among the subfamilies of the 5th-ranked family; however, subfamilies A and D exhibited significant decreases in caloric intake from their baseline values (×,  $P = 0.02$  and  $0.04$ , compared with baseline, respectively). All data expressed as mean ± SEM.

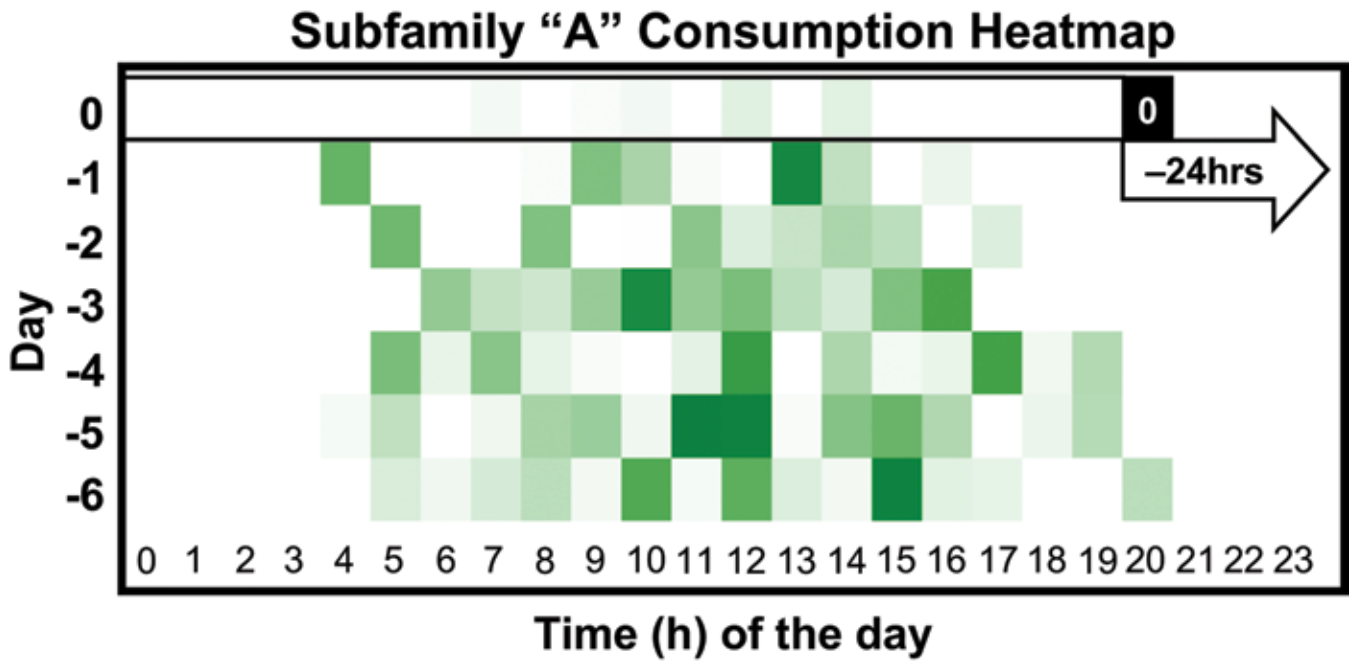
the severity of their wounds, we used univariate regression analysis to evaluate severity scores of injuries received by 5th-ranked family members during the fighting incident. Results revealed a negative relationship between trauma severity and preceding inappetence, in which greater percent decreases in caloric intake from baseline to -24 h predicted higher severity scores of wounds received during the fighting incident ( $R^2 = 0.37$ ,  $\beta = -0.632$ ,  $P < 0.01$ ). Similarly, percent change in caloric

intake from baseline to -24 h significantly predicted the trauma severity score sum of injured animals in this family ( $R^2 = 0.35$ ,  $\beta = -0.618$ ,  $P < 0.01$ ; Figure 7). As expected, most of the animals with high trauma-severity sum scores and large negative percent changes in caloric intake at -24 h were members of the deposited A subfamily of the 5th-ranked family of the group.

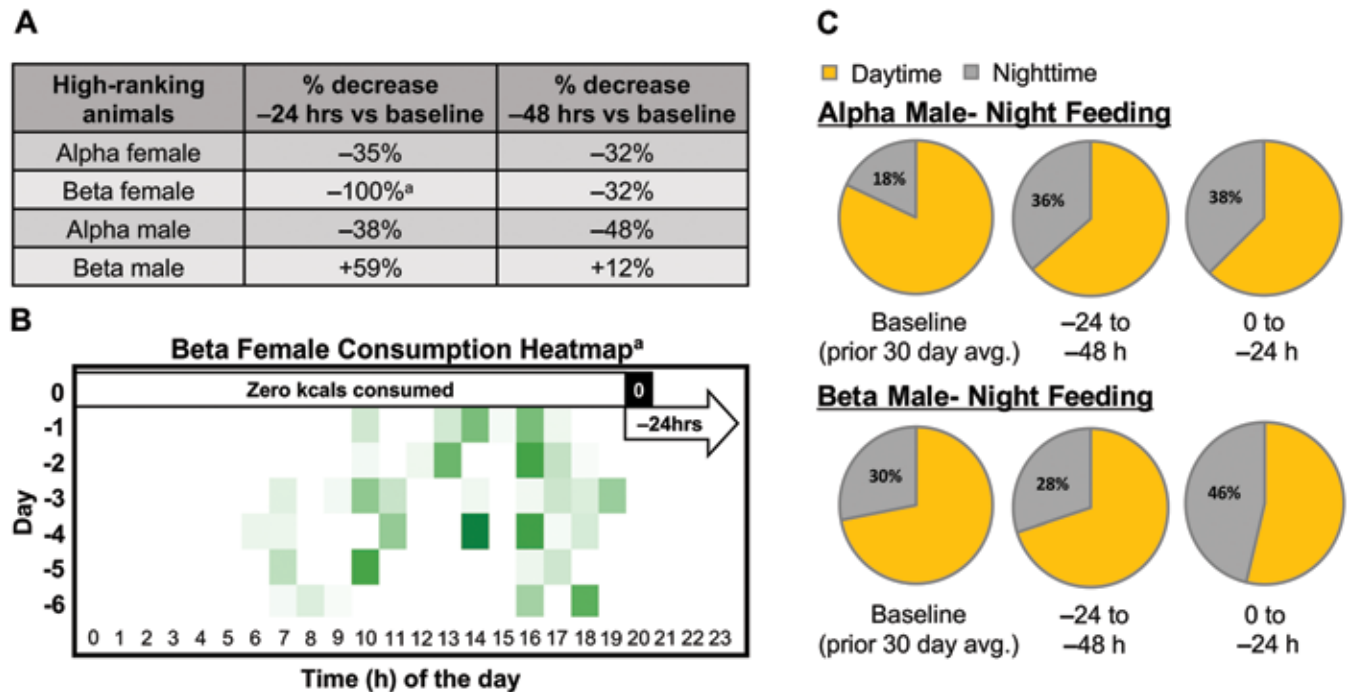
## Discussion

Many studies have provided information regarding the underlying sources of social instability in macaque societies, including fragmented matrilineal dominance and kinship structures<sup>5,13,18</sup> and impaired conflict management mechanisms.<sup>6,20,21</sup> The absence of one or more of these factors, at either the family or group level, can lead to increased aggression and fighting that may result in significant wounding—and even mortality—in despotic species, such as rhesus macaques.<sup>16,41</sup> Captive groups of rhesus macaques are routinely monitored for changes in dominance ranks, alliance relations, and rates of trauma to detect emerging social instability. Despite these efforts, however, the precise timing of severe outbreaks of aggression (overthrows or other major fighting events) is largely considered unpredictable to captive macaque managers.<sup>7,32</sup> Transient inappetence in animals is a common consequence of exposure to an acute stressor.<sup>11,28,35</sup> However, the present data suggest that cues leading up to social aggression in rhesus monkey groups may serve as a psychosocial stressor in specific animals. Because feeding bout data can be collected in real-time by means of automated feeders using radiofrequency identification technology, it is reasonable to hypothesize that aberrant changes in food intake in key individuals or groups of animals could be used as indicators of emerging instability and promptly alert managers to impending outbreaks of intense aggression. In this case study of intrafamily fighting, we found marked reductions in feeding activity among the targeted animals of the 5th-ranked family as well as the  $\alpha$  female,  $\beta$  female, and  $\alpha$  male of the group at least 24 to 48 h prior to the onset of significant wounding. Thus, these findings support the concept that feeding data can be used to predict the timing of deleterious outbreaks of aggression in captive groups of rhesus macaques.

This case study reports an intrafamily fighting incident involving 2 different subfamilies of the 5th-ranked family of a large breeding group: a first-ranked subfamily A and a third-ranked subfamily C. Based on limited behavioral observations conducted during and immediately after this evening incident, it was assumed by management that subfamily C attempted to contest subfamily A, with support from high-ranking females of the social group. This assumption was based on the observation that female members of subfamily A received the worse injuries during this conflict. It is well known that adult recipients of social aggression in macaque groups experience increased psychosocial stress, but group interactions prior to the onset of overt aggression may also affect specific animals. Therefore, we hypothesized that marked reductions in average caloric intake would be observed in this 5th-ranked family, but particularly in the 'most affected' subfamily A, at least 24 h prior to the occurrence of significant fighting. Results revealed moderate decreases in average caloric consumption in the 5th-ranked family from baseline to -24 and -48 h; however, only the deposited subfamily A exhibited reductions in caloric intake that reached statistical significance at both -24 and -48 h (-58% and -32% from baseline values,  $P = 0.007$  and  $0.02$ , respectively). No statistically significant change in appetite in subfamily C was observed during this time period. Moreover, the percent change in caloric intake of subfamily A members of the 5th-ranked family



**Figure 5.** Consumption heatmap for subfamily A. Fewer and smaller feeding bouts (represented by light green boxes) occurred in the targeted subfamily A of the 5th-ranked family during the -24 h before the intrafamily fighting incident (t = 0 to 2000 the previous day), compared with the previous 6 d. Consumption heatmap was generated by using BioDAQ Online DataViewer (labels added for display by authors).



**Figure 6.** Feeding patterns of high-ranking animals of the social group. (A) Large percentage decreases in caloric intake were noted in the  $\alpha$  female,  $\beta$  female, and  $\alpha$  male of the entire social group in the -24 hrs and -48 hrs prior to the intrafamily fighting incident. (B) A heatmap of the feeding bouts of the  $\beta$  female of the social group revealed that this animal consumed zero calories from the automated feeders within -24 h of this incident (t = 0 to 2000 the previous day). (C) Examination of the nighttime compared with daytime feeding patterns of the  $\alpha$  and  $\beta$  males of the social group revealed increased night-feeding by both males at least -24 h prior to the intrafamily fighting incident. Most notably, the percentage of nighttime feeding of the  $\alpha$  male during the -24 h and -48 h before the incident nearly doubled compared with his baseline feeding pattern. The consumption heatmap and the nighttime vs. daytime feeding patterns were calculated by using the BioDAQ Online DataViewer (labels added for display by authors).

from baseline to -24 h significantly predicted the severity of their wounds. Together, these changes in food intake support behavioral observations that members of subfamily A of the 5th-ranked family of the group were the intended targets of this episode of intense aggression.

The occurrence of this intrafamily fighting incident was largely not anticipated by management staff. First, aggressive behavior among female macaques is more frequently seen during the breeding season;<sup>42</sup> however, this incident of intense aggression occurred during the birthing season. Secondly, a brief



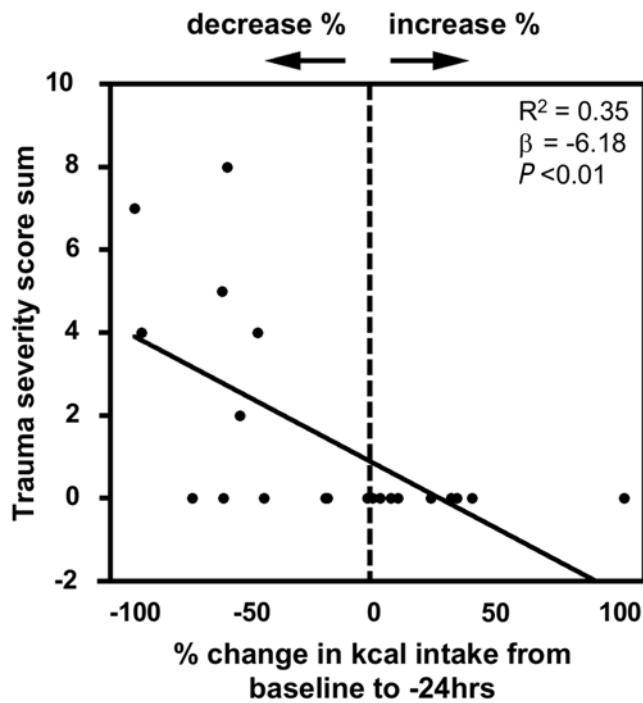


Figure 7. Regression of percentage change in caloric intake from baseline to -24 h before the fighting incident and trauma severity score sum of 5th-ranked family members.

incident of contact aggression was observed at -2 d involving 3 high-ranking females from the  $\alpha$  and  $\beta$  families of the group, the highest ranked female of the 5th-ranked family of the group, and her oldest daughter; however, no additional aggression nor other social concerns were noted by experienced colony management staff during follow-up observations of this social group over the next 48 h. In addition, low rates of contact and noncontact aggression were observed in several weeks prior to this fighting incident. These findings are consistent with the historical belief that the precise timing of social overthrows and other forms of intense aggression in captive macaque groups are largely unpredictable by managers.<sup>32</sup> Indeed, some suggest that simple rates of female-female agonistic behavior (aggression and submission) offer little or no predictive power for the detection of social instability.<sup>7,32</sup> In this study, however, retrospective analyses revealed marked inappetence in the targeted subfamily A of the 5th-ranked family and high-ranking females from the  $\alpha$  and  $\beta$  families of the group during the 2 d following their initial agonistic interaction, suggesting that this social conflict was not immediately reconciled and social unrest persisted.

In macaque societies, high-ranking members of the group, but particularly males, play important conflict control or 'policing' roles to maintain group stability.<sup>4,10,22</sup> The term 'policing' refers to a conflict management mechanism that involves a third-party intervention that functions to stop intragroup fighting.<sup>20</sup> Several prior studies report that successful intervention behavior in rhesus macaques is associated with lower group-level conflict severity and wounding.<sup>4,33</sup> Policing interventions, however, are operationally defined as either 'impartial policing' (policer shows no preferential behavior toward any particular conflict participant)<sup>7</sup> or 'partial policing' in support of nonkin subordinates (policer directs more aggression toward the dominant conflict participant(s)).<sup>6</sup> In this main fighting incident, several  $\alpha$ -family females and the highest-ranking female of subfamily C of the 5th-ranked family of the group were found to have male-inflicted wounds,

indicating that the adult males of the group exhibited partial policing toward these females to stop them from further aggressing members of subfamily A of the 5th-ranked family. Retrospective analyses of the feeding data of both breeding males revealed a large decrease in food intake in the  $\alpha$  male, but not the  $\beta$  male of the group, within -24 to -48 h of the main fighting incident. Both the  $\alpha$  and  $\beta$  males of the group, however, fed more frequently at night during the same period. Most notably, during the 2 nights prior to the main event, the percentage of nighttime feeding by the  $\alpha$  male of the group nearly doubled compared with his baseline values. Collectively, these findings suggest that, during periods of high social tension, the adult males of the group may forgo feeding during daylight hours to spend more time policing the adult females. These changes in adult breeding male feeding patterns also provide additional evidence that the brief discordance that occurred 2 d prior to the main fighting event between high-ranking females of the group and subfamily A members of the 5th-ranked family was not fully reconciled and increased in intensity within an approximately 48 h period.

Also noteworthy in this case study is the percent decrease in caloric intake from baseline to -24 h by the targeted subfamily A members of the 5th-ranked family of the group significantly predicted the severity sum scores of their wounds received during the main fighting incident and the baseline period. This finding suggests that rhesus macaques can anticipate contact aggression from group mates and have stress-induced inappetence as a consequence of this anticipation. It is also consistent with existing models of primate social conflict that assume primates recognize individuals and remember the outcome of past interactions.<sup>24,29</sup> It is likely that the same relationship between inappetence and trauma severity would be observed among individuals or subgroups of animals living in different social environments (for example small harem or peer groups). What is unknown, however, is the precise nature of the social cue animals use as predictors of eventual aggression.

Although stress hormones were not measured in this study, it is well-established that social aggression in rhesus macaque groups leads to increased psychosocial stress in all involved parties.<sup>2,25,44</sup> Transient inhibition of food intake is also a normal adaptive response to acute stress mediated by the hypothalamic neuropeptide corticotropin-releasing factor through the HPA axis.<sup>26</sup> The degree of appetite inhibition depends on the intensity of the stressor, caloric content of the diet, relative increase in corticotropin-releasing factor, activation of CRF1 receptors instead of CRF2 receptors in the hypothalamus, and degree of negative feedback from glucocorticoids released from the adrenal glands. Glucocorticoids induced by acute stress also affect leptin and insulin release, which can modulate feeding behavior through corticotropin-releasing factor and other hypothalamic appetite regulatory neuropeptides.<sup>23,31</sup> Given this evidence, it stands to reason that deposed members of subfamily A of the 5th-ranked family of the group experienced stress-induced inappetence; however, no hormonal data is available from this study to confirm this assumption.

Mild to moderate decreases in caloric intake were observed in the D and E subfamilies of the 5th-ranked family as well as in the 7th- and 8th-ranked families of the group at -24 h and -48 h; however, no members of these subfamilies and families received trauma nor were observed to be involved in aggressive interactions during this period. Moreover, with the exception of a reduction in appetite in the D subfamily of the 5th-ranked family at -48 h, none of these negative percent changes in caloric intake reached statistical significance. Failure to observe

significant decreases in appetite at the subfamily- and family-level was likely due to small sample size ( $n = 3$  animals per subfamily or family) and high within-group variability. These animals represent either the lowest-ranking animals in their family or the whole social group. Because socially subordinate rhesus macaques (by definition) receive higher rates of aggression than more dominant animals, it is possible that these low-ranking animals had mild to moderate stress-induced inappetence based on their prior social experience. The D subfamily of the 5th-ranked family of the group showed a 37% decrease in caloric intake from baseline to -48 h that did reach statistical significance. In addition, 2 of the 5 adult females in this subfamily were not present in the group at the time of the main fighting incident; therefore, it is possible that this lack of social support led the remaining subfamily members to be more susceptible to noncontact aggression and stress-induced inappetence.

Automated feeders can be used to enhance the monitoring of individual animals living in large social groups, because the daily caloric intake of individual animals can be monitored routinely by management for large decreases in appetite and other changes in feeding activity. Indeed, our group has previously shown that individual animals with reduced appetite, can be identified from daily feeding reports, alerting veterinarians to possible subclinical health problems (for example enteritis) before the development of more serious clinical signs (for example lethargy, dehydration).<sup>19</sup> In regard to the detection of social issues in these groups, however, untargeted feeding queries and alerts tend to be less informative than more targeted analyses. For instance, no significant changes in food intake for the whole group were observed in the current study. Subfamily A animals of the 5th-ranked family of the group were also not identified on the feeding report received by management the morning of the main fighting event, but large decreases in caloric intake by this subfamily were found when feeding queries targeted the post-conflict period following their initial aggressive interaction with high-ranking females. Moreover, the  $\beta$  male of this social group exhibited an overall 59% increase in total caloric intake at 24 h prior to the main fighting incident, but consumed the majority of these calories at night instead of during daylight hours. Thus, here, we propose that feeding data are most efficiently used in the social management of large macaque groups when feeding queries and alert parameters inclusively target: 1) matrilineal families at identifiable risk for social instability; 2) key members with significant social power or 'control' roles in the group; and 3) sensitive time periods for escalating aggression and fighting. Feeding queries defined by these social parameters may also help management disentangle stress-induced inappetence from clinical inappetence caused by a physical health issue.

Matrilineal families identified by management to be at increased risk for social instability may include those with low genetic relatedness, weak social relationships, and/or high trauma severity sum scores. For example, the 5th-ranked family of this group could have been identified to be at-risk because: 1) their matrilineal coefficient of genetic relatedness was less than 0.20 at the time of the fighting incident, which has been previously identified as a risk factor for increased matrilineal instability in rhesus macaque groups;<sup>5</sup> and 2) removal of the oldest daughter of subfamily A from the group for trauma treatment at -2 d may have led to less social support for the remaining adult females of subfamily A and/or weakened social relationships between subfamilies A and C, which may have precipitated the opportunity for more aggression.<sup>45</sup> Once identified, targeted feeding alerts can be implemented to more closely monitor each at-risk family, subfamily, or key individual (for example matriarch or another adult female with a high

trauma severity sum score) for large reductions in caloric intake. As suggested by findings in this study, the days following aggressive interactions involving at-risk families are sensitive periods for the detection of stress-induced inappetence in these animals and increased night feeding by 'policing' animals. Thus, targeted feeding queries during these time periods can alert management to aggressive interactions (of varying degrees of intensity) with inadequate conflict resolution and identify groups at imminent risk for escalating aggression. Management staff can then use this timely information to increase observations and possibly intervene prior to the onset of more intense fighting and wounding.

The inclusion of feeding data generated by automated feeders into the social management of captive rhesus macaque groups offers a few advantages over traditional practices. First, feeding bout data are collected in real-time and summarized in an automated unbiased manner. Moreover, feeding bouts are collected continuously from every group member with hand microchips, representing a rich and dynamic dataset that can be queried for individual changes in food intake with available software. In contrast, social and wounding data are not collected and analyzed automatically by any available means. Indeed, the interactions that define the dominance and affiliative relationships in these groups are sparse; thus, the gathering of enough observational behavioral data to unequivocally detect social instability is often time-consuming and requires well-trained staff. The efficiency with which observational behavioral and wounding data are collected to detect instability in at-risk families or groups, however, may be improved through the utilization of targeted feeding queries and alerts.

Despite these benefits, further research is needed to fully evaluate the utility and cost benefits of automated feeders in primate social management. At a minimum, findings from this case study should be confirmed in larger studies using rhesus monkeys housed in different group sizes and social configurations. As previously mentioned, it is expected that the same relationship between trauma severity and preceding inappetence would be observed among individual animals or subgroups of rhesus monkeys living in other social environments, including other multimale breeding groups, small harem groups, or peer groups (exclusively, male or female); however, this hypothesis needs to be tested. It is also not known whether individual incidents of trauma during periods of relative social stability are associated with immediately preceding inappetence. Furthermore, larger studies will help optimize feeding alert queries for the early detection of social stability among at-risk groups or subgroups of animals and provide the opportunity for cost-benefit analyses. The equipment and software associated with the automated feeding system described in this case study, and the infrastructure that supports it, are very expensive and resource-demanding. It is currently less clear, however, whether these expenses are off-set (or at least justified) by improvements in colony management efficiency and animal welfare (by reducing wounding and maintaining individual animals and families in their social groups for longer periods of time than previously possible), and cost savings in veterinary care related to the reduced occurrence and severity of trauma. Nonetheless, information gained from these future cost-benefit analyses should be useful to other primate facilities interested in implementing automated feeders in their captive colonies.

The current case study is not without limitations. Due to the limited number of animals within each involved family and subfamily, there was insufficient statistical power to analyze the data for changes in caloric intake by age category (adults compared with juveniles compared with yearlings). The adult females of subfamily A of the 5th-ranked family of the group, however, received the

worst injuries and exhibited the largest average percent decreases in caloric intake at -24 h (-87% for 3 adults). In contrast, the average change in caloric intake among the offspring in this subfamily was -12% at -24 h ( $n = 2$ ). Based on this limited information, a significant effect of age on caloric intake may have been found with a larger sample size. Further, because both the initial and main social event involving subfamily A of the 5th-ranked family occurred outside of normal work hours, limited behavior observations were conducted by management staff to determine whether a conflict resolution had been reached between participants. It is also not completely clear which adult female(s) initiated the main fighting event and elicited the most intense aggression toward subfamily A of the 5th-ranked family. Based on the wounding data, however, we assumed that subfamily C attempted to contest subfamily A, with support from high-ranking females of the  $\alpha$  and  $\beta$  families of the group. A significant relationship between wounding and percent change in caloric intake at -24 h was also found in the contested animals. Thus, this case study is a good example of how automated feeding data can be used to enhance the social management of captive macaques by providing supplemental information to behavioral and trauma data.

In summary, findings from this case study of intrafamily fighting in a large breeding compound of rhesus macaques suggest that stress-induced inappetence and/or increased night-feeding in key individuals may help management detect emerging social instability prior to the onset of significant aggression and wounding. Early detection of social instability in these groups may, in turn, lead to improvements in animal welfare via reduced wounding and pain/distress as well as possibly negating the need to remove animals from their social group. Aberrant changes in food intake among socially housed animals, however, are not readily identifiable on untargeted daily feeding alerts designed to capture individual animals with marked anorexia over a rigid time period (see methods). Here, we propose that feeding data is most efficiently used in the social management of captive primates and has the greatest potential to improve animal welfare when feeding data is analyzed in conjunction with behavioral and trauma data. Specifically, we propose that feeding alert parameters are best defined by the user and inclusively target: 1) matrilineal animals at identifiable risk for social instability; 2) high-ranking individuals with control roles in the group; and 3) sensitive time periods for increased aggression (for example postconflict or -changes in group composition). Real-time analyses of feeding data by these parameters can possibly alert management to agonistic interactions (of varying degrees of intensity) with inadequate conflict resolution. Management staff can then use this timely information to increase observations and possibly intervene prior to the escalation of additional aggression and trauma. Although further research is needed to fully validate these targeted alert queries, the utility of automated feeding data in the social management of captive colonies of rhesus macaques represents a paradigm shift from more conventional practices. This technology used in the context of social health surveillance is novel and has the potential to improve animal wellbeing and management efficiency, which in turn, fosters the conduct of high-quality science using NHP.

### Acknowledgments

This project was funded in part by NIH ORIP/OD P51OD011132 to Yerkes NPRC and NIH G20 OD 20272-01. We thank the Yerkes Field Station animal care staff, colony management staff, veterinarians, and veterinary technicians for their assistance in maintaining the automated feeders, monitoring the social group, and caring for the injured animals. We also thank Ed Ulman, Matthew Williams, Nicholas Denkowycz, and Doug Compton of Research Diets for the design and manufacture of

the automated feeders as well as their excellent software and technical support. Finally, we thank Mark E Wilson for his critical review of the manuscript.

### References

1. **Animal Welfare Regulations**. 2008. 9 CFR § 3.129.
2. **Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland T Jr, Sapolsky RM**. 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm Behav* **43**:67–82. [https://doi.org/10.1016/S0018-506X\(02\)00037-5](https://doi.org/10.1016/S0018-506X(02)00037-5).
3. **Abee CR, Mansfield K, Tardiff S, Morris T**. 2012. Nonhuman primates in biomedical research: biology and management, 2nd ed. San Diego (CA): Elsevier.
4. **Beisner BA, Jackson ME, Cameron A, McCowan B**. 2012. Sex ratio, conflict dynamics, and wounding in rhesus macaques (*Macaca mulatta*). *Appl Anim Behav Sci* **137**:137–147. <https://doi.org/10.1016/j.applanim.2011.07.008>.
5. **Beisner BA, Jackson ME, Cameron AN, McCowan B**. 2011. Detecting instability in animal social networks: genetic fragmentation is associated with social instability in rhesus macaques. *PLoS One* **6**:1–11. <https://doi.org/10.1371/journal.pone.0016365>.
6. **Beisner BA, McCowan B**. 2013. Policing in nonhuman primates: partial interventions serve a prosocial conflict management function in rhesus macaques. *PLoS One* **8**:1–13. <https://doi.org/10.1371/journal.pone.0077369>.
7. **Beisner BA, Wooddell LJ, Hannibal DL, Nathman A, McCowan B**. 2019. High rates of aggression do not predict rates of trauma in captive groups of macaques. *Appl Anim Behav Sci* **212**:82–89. <https://doi.org/10.1016/j.applanim.2019.01.003>.
8. **Bernstein IS**. 1976. Dominance, aggression, and reproduction in primate societies. *J Theor Biol* **60**:459–472. [https://doi.org/10.1016/0022-5193\(76\)90072-2](https://doi.org/10.1016/0022-5193(76)90072-2).
9. **Bernstein IS, Gordon TP**. 1974. The function of aggression in primate societies. *Am Sci* **62**:304–311.
10. **Bernstein IS, Sharpe LG**. 1966. Social roles in a rhesus monkey group. *Behaviour* **26**:91–104. <https://doi.org/10.1163/156853966X00038>.
11. **Calvez J, Fromentin G, Nadkarni N, Darcel N, Even P, Tomé D, Ballet N, Chaumontet C**. 2011. Inhibition of food intake induced by acute stress in rats is due to satiation effects. *Physiol Behav* **104**:675–683. <https://doi.org/10.1016/j.physbeh.2011.07.012>.
12. **Casey R**. 2009. Fear and stress, p 144–153. In: Horwitz D, Mills D, Heath S, editors. *BSAVA manual of canine and feline behavioural medicine*. Dorset (United Kingdom): Gloucester.
13. **Chapais B**. 1992. Role of alliances in the social inheritance of rank among female primates, p 29–59. In: Harcourt AH, de Waal FB, editors. *Coalitions and alliances in humans and other animals*. New York: Oxford University Press.
14. **Chen CY, Lin YR, Zhao LL, Yang WC, Chang YJ, Wu KH, Wu HP**. 2013. Clinical spectrum of rhabdomyolysis presented to pediatric emergency department. *BMC Pediatr* **13**:1–6. <https://doi.org/10.1186/1471-2431-13-134>.
15. **Crockett CM, Bowers CL, Sackett GP, Bowden DM**. 1990. Appetite suppression and urinary cortisol responses to different cage sizes and tethering procedures in longtailed macaques. *Am J Primatol* **20**:184–185.
16. **De Waal FBM, Luttrell L**. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stump-tail monkeys. *Am J Primatol* **19**:83–109. <https://doi.org/10.1002/ajp.1350190203>.
17. **Dettmer AM, Woodward RA, Suomi SJ**. 2015. Reproductive consequences of a matrilineal overthrow in rhesus monkeys. *Am J Primatol* **77**:346–352. <https://doi.org/10.1002/ajp.22350>.
18. **Ehardt CL, Bernstein IS**. 1986. Matrilineal overthrows in rhesus-monkey groups. *Int J Primatol* **7**:157–181. <https://doi.org/10.1007/BF02692316>.
19. **Ethun KF, Dicker S, Hughes B, Johnson ZP, Wilson ME**. 2015. Use of automated feeding stations to enhance the veterinary care and management of socially housed rhesus macaques (*Macaca mulatta*).

- p 661. Association of Primate Veterinarians workshop. Phoenix, Arizona: American Association for Laboratory Animal Science.
20. **Flack JC, de Waal FB, Krakauer DC.** 2005. Social structure, robustness, and policing cost in a cognitively sophisticated species. *Am Nat* **165**:E126–E139. <https://doi.org/10.1086/429277>.
  21. **Flack JC, de Waal FB.** 2004. Dominance style, social power, and conflict, p 157–182. In: Thierry B, Singh M, Kaumanns W, editors. *Macaque societies: a model for the study of social organization*. Cambridge (United Kingdom): Cambridge University Press.
  22. **Flack JC, Girvan M, de Waal FB, Krakauer DC.** 2006. Policing stabilizes construction of social niches in primates. *Nature* **439**:426–429. <https://doi.org/10.1038/nature04326>.
  23. **Foster MT, Warne JP, Ginsberg AB, Horneman HF, Pecoraro NC, Akana SF, Dallman MF.** 2009. Palatable foods, stress, and energy stores sculpt corticotropin-releasing factor, adrenocorticotropin, and corticosterone concentrations after restraint. *Endocrinology* **150**:2325–2333. <https://doi.org/10.1210/en.2008-1426>.
  24. **Gouzoules S.** 1984. Primate mating systems, kin associations, and cooperative behavior: evidence for kin recognition? *Yearb Phys Anthropol* **27** S5:99–134. <https://doi.org/10.1002/ajpa.1330270506>.
  25. **Gust DA, Gordon TP, Hambright MK, Wilson ME.** 1993. Relationship between social factors and pituitary-adrenocortical activity in female rhesus monkeys (*Macaca mulatta*). *Horm Behav* **27**:318–331. <https://doi.org/10.1006/hbeh.1993.1024>.
  26. **Herman JP, McKlveen JM, Ghosal S, Kopp B, Wulsin A, Makinson R, Scheimann J, Myers B.** 2016. Regulation of the hypothalamic–pituitary–adrenocortical stress response. *Compr Physiol* **6**:603–621. <https://doi.org/10.1002/cphy.c150015>.
  27. **Hobbs TR, O'Malley JP, Khuangsathiene S, Dubay CJ.** 2010. Comparison of lactate, base excess, bicarbonate, and pH as predictors of mortality after severe trauma in rhesus macaques (*Macaca mulatta*). *Comp Med* **60**:233–239.
  28. **Hotta M, Shibasaki T, Arai K, Demura H.** 1999. Corticotropin-releasing factor receptor type 1 mediates emotional stress-induced inhibition of food intake and behavioral changes in rats. *Brain Res* **823**:221–225. [https://doi.org/10.1016/S0006-8993\(99\)01177-4](https://doi.org/10.1016/S0006-8993(99)01177-4).
  29. **Lee ED, Daniels BC, Krakauer DC, Flack JC.** 2017. Collective memory in primate conflict implied by temporal scaling collapse. *J R Soc Interface* **14**:1–6.
  30. **Malinoski DJ, Slater MS, Mullins RJ.** 2004. Crush injury and rhabdomyolysis. *Crit Care Clin* **20**:171–192. [https://doi.org/10.1016/S0749-0704\(03\)00091-5](https://doi.org/10.1016/S0749-0704(03)00091-5).
  31. **Maniam J, Morris MJ.** 2012. The link between stress and feeding behaviour. *Neuropharmacology* **63**:97–110. <https://doi.org/10.1016/j.neuropharm.2012.04.017>.
  32. **McCowan B, Beisner BA.** 2017. Utility of systems network analysis for understanding complexity in primate behavioral management, p 157–186. In: Schapiro SJ, editor. *Handbook of primate behavioral management*. Boca Raton (FL): CRC Press.
  33. **McCowan B, Beisner BA, Capitanio JP, Jackson ME, Cameron AN, Seil S, Atwill ER, Fushing H.** 2011. Network stability is a balancing act of personality, power, and conflict dynamics in rhesus macaque societies. *PLoS One* **6**:e22350. <https://doi.org/10.1371/journal.pone.0022350>.
  34. **Meerlo P, Overkamp GJ, Koolhaas JM.** 1997. Behavioural and physiologic consequences of a single social defeat in Roman high- and low-avoidance rats. *Psychoneuroendocrinology* **22**:155–168. [https://doi.org/10.1016/S0306-4530\(96\)00047-9](https://doi.org/10.1016/S0306-4530(96)00047-9).
  35. **Meyer JS, Hamel AF.** 2014. Models of stress in nonhuman primates and their relevance for human psychopathology and endocrine dysfunction. *ILAR J* **55**:347–360. <https://doi.org/10.1093/ilar/ilu023>.
  36. **Oates-O'Brien RS, Farver TB, Anderson-Vicino KC, McCowan B, Lerche NW.** 2010. Predictors of matrilineal overthrows in large captive breeding groups of rhesus macaques (*Macaca mulatta*). *J Am Assoc Lab Anim Sci* **49**:196–201.
  37. **Oestern HJ, Trentz O, Hempelmann G, Trentz OA, Sturm J.** 1979. Cardiorespiratory and metabolic patterns in multiple trauma patients. *Resuscitation* **7**:169–183. [https://doi.org/10.1016/0300-9572\(79\)90024-8](https://doi.org/10.1016/0300-9572(79)90024-8).
  38. **Reitsemma LJ, Partrick KA, Muir AB.** 2016. Interindividual variation in weaning among rhesus macaques (*Macaca mulatta*): serum stable isotope indicators of suckling duration and lactation. *Am J Primatol* **78**:1113–1134. <https://doi.org/10.1002/ajp.22456>.
  39. **Institute for Laboratory Animal Research.** 2011. *Guide for the care and use of laboratory animals*, 8th ed. Washington (DC): National Academies Press.
  40. **Stammen RL, Cohen JK, Meeker TL, Crane MM, Amara RR, Hicks SL, Meyer JS, Ethun KF.** 2018. Effect of chronic social stress on prenatal transfer of antitetanus immunity in captive breeding rhesus macaques (*Macaca mulatta*). *J Am Assoc Lab Anim Sci* **57**:357–367. <https://doi.org/10.30802/AALAS-JAAL-AS-17-000102>.
  41. **Thierry B.** 1985. Patterns of agonistic interactions in 3 species of macaque (*Macaca mulatta*, *M. fascicularis*, *M. tonkeana*). *Aggress Behav* **11**:223–233. [https://doi.org/10.1002/1098-2337\(1985\)11:3<223::AID-AB2480110305>3.0.CO;2-A](https://doi.org/10.1002/1098-2337(1985)11:3<223::AID-AB2480110305>3.0.CO;2-A).
  42. **Vandenbergh JG, Vessey S.** 1968. Seasonal breeding of free-ranging rhesus monkeys and related ecological factors. *J Reprod Fertil* **15**:71–79. <https://doi.org/10.1530/jrf.0.0150071>.
  43. **Wilson ME, Fisher J, Fischer A, Lee V, Harris RB, Bartness TJ.** 2008. Quantifying food intake in socially housed monkeys: social status effects on caloric consumption. *Physiol Behav* **94**:586–594. <https://doi.org/10.1016/j.physbeh.2008.03.019>.
  44. **Wooddell LJ, Kaburu SS, Rosenberg KL, Meyer JS, Suomi SJ, Dettmer AM.** 2016. Matrilineal behavioral and physiologic changes following the death of a nonalpha matriarch in rhesus macaques (*Macaca mulatta*). *PLoS One* **11**:1–15. <https://doi.org/10.1371/journal.pone.0157108>.
  45. **Wooddell LJ, Kaburu SS, Suomi SJ, Dettmer AM.** 2017. Elo-rating for tracking rank fluctuations after demographic changes involving semifree-ranging rhesus macaques (*Macaca mulatta*). *J Am Assoc Lab Anim Sci* **56**:260–268.