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Elo-rating for Tracking Rank Fluctuations after Demographic Changes Involving Semi-free–ranging Rhesus Macaques (*Macaca mulatta*)

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Rhesus macaques (*Macaca mulatta*) are gregarious primates that form despotic societies characterized by frequent and intense aggression. Within long-term social groups, demographic changes may influence hierarchical stability, potentially resulting in conflict and violently abrupt hierarchical changes. This conflict can result in serious implications for animal welfare, and thus, predictive tools would be invaluable to captive managers in determining social instabilities. Using the method Elo-rating to track rank changes and dominance stability, we predicted that demographic changes to a population of semi-free ranging rhesus macaques would result in changes in hierarchical stability. Over a 3 y period, dominance data were recorded on all troop members to track the hierarchy. Throughout the 3 y, significant changes occurred to the population (mainly due to health and colony management reasons; no changes specifically occurred for this study) including permanent removal of a large group of natal males, temporary and permanent removal of top-ranking females, and depositions of top-ranking families. Our retrospective study suggests that removing natal males was beneficial in promoting overall troop stability (that is, stability of dominance relationships), although remaining males opportunistically attempted to increase in rank, perhaps due to limited competition. Our results also suggest that removing top-ranking females, even temporarily, destabilized dominance relationships; consequently adjacently ranked females opportunistically increased in Elo-rating, both before and after the depositions of the α families. Thus, these challenges to the established hierarchy can be predicted by increases in Elo-rating within the β families after demographic changes to the α families. Our results suggest that the presence of natal males and the removal of top-ranking females should be minimized to maintain stable dominance relationships. In addition, longitudinal data reflecting dominance ranks, collected by using Elo-rating, may help managers of captive colonies in predicting dominance instabilities before they occur.

The breeding of animals in captive or semi-free ranging conditions can serve multiple functions, from the maintenance of demographic viability and genetic diversity for conservation purposes,[46] to the rearing of subjects for biomedical research,[33] or the study of behaviors that are difficult to observe and study in more naturalistic environments (for example, social learning[49]). One of the biggest challenges in the management of captive or semi-free ranging colonies lies in the correct understanding of the sociodynamics of a population to prevent the surge of unpredicted conflicts and social instabilities.[6] In this context, it is necessary to identify special measures that can help track the sociodynamics of a population to improve the management of captive colonies.

In particular, rhesus macaques (*Macaca mulatta*) are the most widely used NHP in biomedical research[24] and are often housed in large breeding groups throughout the world.[37] Female macaques are philopatric and form stable linear hierarchies both within their matrilines and within the troop.[41,42] Given that rank is transmitted to juveniles through coalitionary support from mothers and close kin,[12] the hierarchy can remain stable for years and decades.

Occasionally, however, specific events can undermine such stability, such as the prolonged presence of natal males,[7] removal or death of high-ranking members,[4,39] and seemingly unanticipated overthrows.[19,23,43] More specifically, increasing evidence indicates that the presence of natal males can potentially undermine troop stability[31] through high levels of aggression and maternal kin support that results in increases in rank.[7] In free-ranging conditions, males commonly transfer to neighboring communities,[35] whereas in captivity, males are unable to leave their natal group. Limited research in captivity suggests that increased densities of natal males are associated with ultimate levels of instability,[44] and the experimental removal of natal males from the α matriline may alter status signaling networks, promoting increased social stability.[9] However, the extent to which troop stability benefits from the culling of a large group of natal males remains unclear.

In addition, maximal instability may affect the troop as a whole, and as such, may accumulate in bouts of escalated aggression. Overthrows are particular events in which lower-ranking NHP jointly aggress top-ranking animals, resulting in changes to the social order, long-term reproductive consequences[18] and subsequent infant bio-behavioral development,[26] loss of research subjects, and pose a significant issue regarding animal well-being. Research can be severely disrupted and ultimately terminated, resulting in considerable loss of resources and research productivity.

Given the devastating consequences that these events can have on the whole colony, investigating how demographic changes,[13] such as removals, influence the social hierarchy is critical to minimize the risk of conflict. Previous research has

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indicated that removal of top-ranking females may predict matrilineal overthrows in rhesus macaque groups,[23,39] probably because dominants play a vital role in the stability of a troop by controlling conflicts,[20] or because it may result in vacancies in the hierarchy. Accordingly, decreases in the number of adult females in the α matriline preceded their overthrows, suggesting that relative size of the α matriline may signal relative social power.[40] Thus, the number of females in the α matriline appears to be critically important for the stability of the group. Nevertheless, the effects of the loss of high-ranking individuals on the troop hierarchical dynamics are still unclear.

To date, the consequences of these demographic changes on the troop stability are still relatively understudied, and conventional analyses rely on matrix-based interactions, which do not readily track rank changes over time. Recent developments have been made in the assessment of dominance hierarchies,[27] such as Elo-rating,[21,38] which may provide more detailed information on hierarchical dynamics after demographic changes.

By taking advantage of Elo-rating,[38] a method devised to track rank changes and troop stability, our retrospective study aimed to explore variations in rank and group stability (measured via levels of rank changes) after specific demographic changes. More specifically, we predicted that: 1) after the removal of natal males, troop stability will increase, because the presence of natal males can result in unstable dominance relationships;[7] 2) after the temporary or permanent removal of high-ranking females, troop stability will decrease, because females ranked immediately below those removed opportunistically attempt to increase in rank; 3) the deposition of top-ranking females will result in opportunistic increases in Elo-rating for adjacently ranked females as they assume dominance; and 4) depositions will occur after a period of maximal instability and may be a stabilizing mechanism and thus, after an overthrow, troop stability will increase.

Materials and Methods

Subjects and housing. The study population comprised 111 rhesus macaques (*M. mulatta*) born between 1997 and 2015 at the NIH Animal Center at the Laboratory of Comparative Ethology field station (Poolesville, MD). The field station was a 5-acre (2.0-ha) outdoor, open-air enclosure with natural foliage (cedar trees, honeysuckle bushes, tall grasses, and so forth), and a pond measuring 0.9 ha.[17] Corncrib shelters and 3 indoor enclosures (2.74 × 5.79 × 4.27m) were continuously available for inclement weather. Inside, lighting was maintained on a 12:12-h cycle (0700 to 1900) and a temperature of approximately 25 °C, but the outside portion was exposed to both ambient temperature and lighting.

Commercial lab diet (Monkey Chow no. 5038, Purina, St Louis, MO), natural vegetation, and water were available without restriction and were supplemented with fresh fruits and vegetables daily. All procedures adhered to the Animal Welfare Act,[5] the American Association of Laboratory Animal Science Position Statement for the Humane Care and Use of Laboratory Animals,[3] and the *Guide for the Care and Use of Laboratory Animals*[29] and were approved by the National Institute of Child Health and Human Development Animal Care and Use Committee.

The troop consisted of 3 matrilines (Figure 1). Matriline 3 occupied the top rank since 2009, after a matrilineal overthrow[18] of the previously dominant matriline 1 (dominant since troop formation in the early 1980s). Matriline 4 occupied the intermediate rank between matrilines 3 and 1 (matriline 2 was removed in 2004 due to management reasons). Matriline 3 comprised 6 major families (mothers and offspring)—E, H, B, Y, UR, and UL (in that hierarchical order)—and matriline 4 comprised 4 major families—N, XA, X, and L (in that hierarchical order). Matriline 1 was analyzed as a whole due to the small sample size (only 2 adult females).

Demographic changes. *Permanent removal of natal males.* According to protocols to maintain a population threshold, 9 natal males (age [mean ± SEM], 3.67 ± 0.58 y) were removed from the troop in February 2015. Males between the ages of 2 and 4 y, who often become the target of aggression around puberty, typically are selected for removal to both minimize the risk for injury and to approximate the male emigration that occurs in the wild.[35] Of the natal males removed, 6 were juveniles (all 3 y of age), and 3 were adult males (two 4-y-olds and one 8-y-old). Most of the males removed were mid-ranking males (6 were from matriline 4); in addition, 2 notable males from matriline 3 were removed. One of these 2 animals was a juvenile male (age, 3 y) whose mother (CX) underwent a major rank increase[50] in 2014 and ranked within the α family at the time (family H). Given his maternal support, he was quickly ascending the hierarchy. In addition, the adult male (age, 8 y) had continuously fallen in rank (from the β male to the fourth-ranking male) after an altercation with the α male. The other males were relatively stable in their ranks.

Temporary removal of α and β females in 2013. In October 2013, the α female, in family E, was temporarily removed for unrelated health procedures. A month later in November, the β female was temporarily removed for breeding purposes to increase genetic diversity within the troop.

In December 2013, the α family, family E, was deposed, and all family members in family E were permanently removed. The next-ranking family (family H) assumed dominance for the next 2 y.

Permanent removal of the third-ranking female in 2015. In the fall of 2014, the third-ranking female (part of family H; age, 6 y) was displaced to the 4th rank by her 2.5-y-old sister, similar to previous observations.[16] The younger sister remained the third-ranking female for the next year.

In September 2015, the third-ranking female was permanently removed from the troop for unrelated health concerns. Approximately 3 mo later, in late December 2015, family H was deposed, and all family H members were permanently removed from the troop. The following 2 overthrows occurred within a relatively short time period (within 6 wk of family H's overthrow), likely stemming from the onset of this initial outbreak of aggression.

Permanent removal of the top-ranking matriarch in 2016. Three days after the onset of aggression in late December 2015, a decision was made to permanently remove the matriarch of family B (the β family, also the α female at the time).

After the removal of family B's matriarch, her daughters assumed dominance, with the youngest daughter (age, approximately 5.5 y) as the α female. In January 2016, this family was deposed, and all family B members were permanently removed.

Final overthrow of α female. After the overthrow of Family B, family Y (the next-ranking family) assumed dominance. In February 2016, family Y was overthrown, and all family members were permanently removed. At this point, the troop was confined to the indoor portions of the habitat for the remainder of the study, in which family UR remained the α family until the study ended in May 2016.

Dominance interactions, Elo-rating, and troop stability. A total of 15,933 dominance interactions were recorded from February 2013 through May 2016 during all observed occurrences

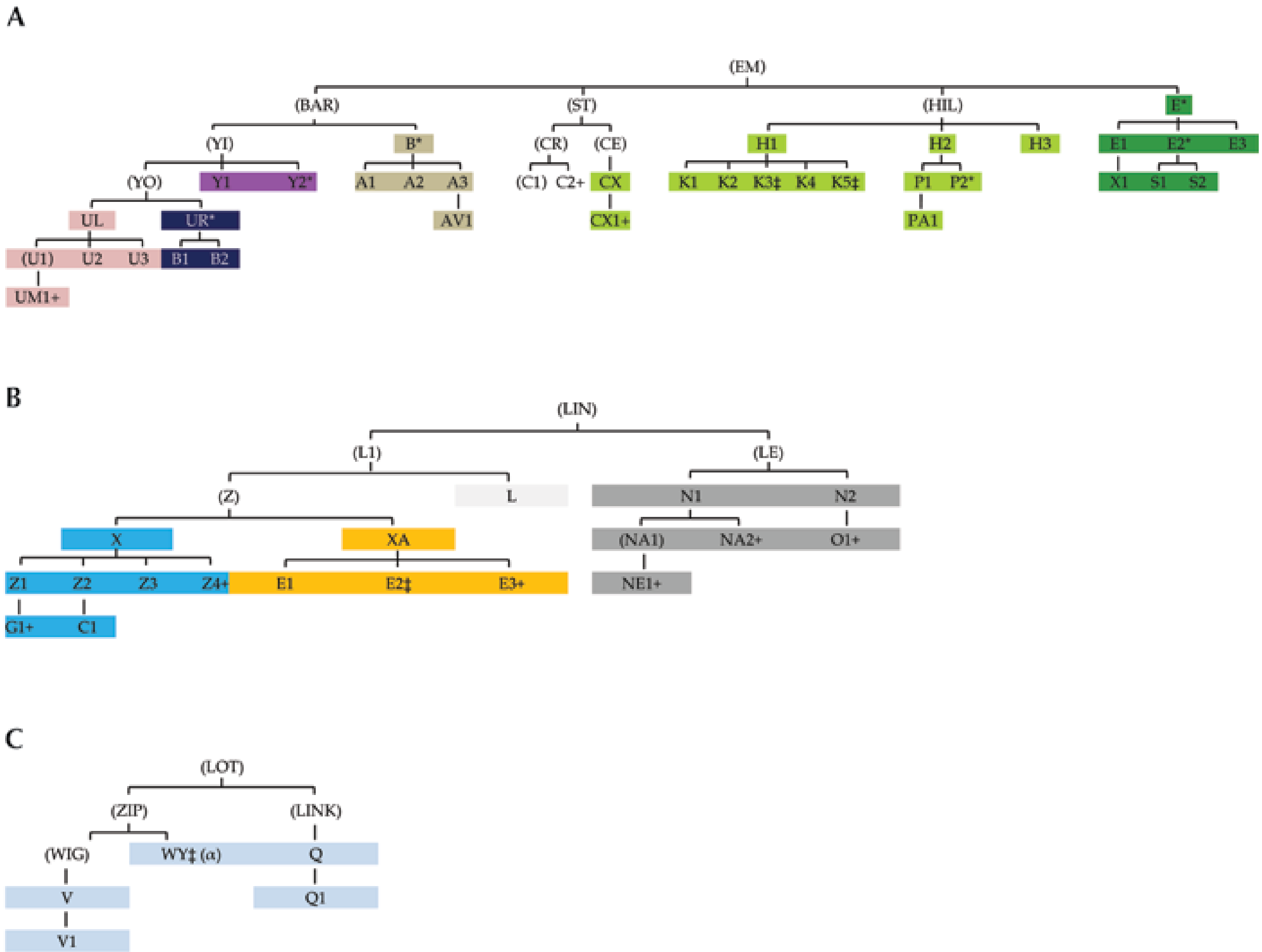

Figure 1. Troop pedigree for the LCE field station in 2013. Offspring are arranged in birth order, with the oldest to the left. Therefore, ranks flow from right to left, following the youngest ascendancy rule. Families are denoted by similar colors; parentheses indicate animals no longer in troop; +, male removed in 2015; ‡, adult male remaining in 2015. (A) Matriline 3. UR*, α family until cessation of data collection. Y2*, only close kin were juveniles; overthrown February 2016 by family UR (dark blue) after a ~25-d tenure. B*, observed overthrowing family H in 2015 (removed 23 December 2015); family overthrown January 2016 by family Y (purple) and matriarch UR (dark blue) after a ~18-d tenure. CX was unusual in that she ranked within family H beginning in 2014. Although not closely related, she was analyzed as part of family H beginning in 2015, due to her rank (no. 5 in 2015; she also was overthrown with family H). P2* was the no. 3 female (permanently removed September 2015); family overthrown December 2015 by family B (tan) and likely family X (matriline 4) after a ~730-d tenure. E* and E2* were the α and β females at the beginning of the study in 2013; temporarily removed October 2013 and November 2013, respectively; family overthrown December 2013 by family H (light green) after a ~1460-d tenure (since 2009). (B) Matriline 4. Family X were instigators of bidirectional aggression to α family in 2015 (family H) and likely were involved in their overthrow. E2 was the lowest-ranking male. After the male cull, E2 rapidly increased in rank by aggressing higher-ranking females. He was chased out of the troop only 1 mo later. (C) Matriline 1. Except for WY, who was the troop's α male, this matriline was the lowest ranking.

and focal animal sampling.[2] Dominance interactions included displacements, threats, chases, attacks, and fear grimaces.[50]

Dominance ranks were established via Elo-rating, a numerical system that tracks rank changes over time by constantly updating values according to wins and losses.[1,21,38,50] In brief, Elo-ratings are calculated based on the expectation of winning, where few points are attributed to winners or losers in which the expectation of winning is high (that is, the animal is higher rated before the interaction). Conversely, more points are attributed to winners or losers in which the expectation of winning is low (that is, animal is lower-rated beforehand). Therefore, large increases in Elo-rating over time thus can signal winning interactions with relatively lower probabilities of winning (closely ranked or lower ranking beforehand). Two main advantages of the use of Elo-rating over matrix-based analyses include the abilities to accommodate variations in study population and to track rank changes over time,[38,50] thus making Elo-rating ideal for studying how changes in sociodynamics relate to rank changes.

Elo-ratings were generated by using the elo.sequence function[38] in R software (version 3.1.2). Each animal's initial rating was set at 1000, and the k factor (a constant based on the probability of winning) was set at 200. A total of 31,866 Elo-ratings were generated based on 15,933 troop interactions (2 Elo-ratings are generated for every interaction, one for the winner and one for the loser).

Because Elo-ratings fluctuate, large differences can reflect changes in ordinal ranks within the troop. Therefore large fluctuations in Elo-ratings are associated with decreased stability (that is, the lack of stable dominance relationships). To assess whether demographic changes were associated with changes in overall troop stability, we used the stability.index function.[38]

This function measures the ratio of rank changes per individuals present over a given time period. Stability index values typically range from 0 to 0.5,[38] with higher values reflecting a greater ratio of rank changes per animals present and thus decreased stability, and lower values reflecting lower ratios of rank changes per animals present and thus increased stability.[38]

Statistical analyses. Time blocks were created for each event that reflected the entire time after the event and before the occurrence of another major event (such as in 2015 and 2016, when multiple overthrows occurred soon after each other). For each event, average Elo-ratings were compared across each time block by using paired samples *t* tests for both the immediate family members and the next ranking family (to examine opportunistic changes in the next ranking families). As a control, we also examined changes in matriline 4, which was presumably unaffected by the demographic changes, given that the changes occurred within matriline 3. In addition, stability index values were calculated for each major event and the same time points. All results are reported as mean ± SEM. All analyses were performed with SPSS 22 (IBM, Armonk, NY). Differences were considered significant when the *P* value was less than 0.05.

Permanent removal of natal males. Average Elo-ratings were compared for the 4 remaining adult males a month before and after removal of the 9 natal males. We compared these changes in Elo-rating to those of similarly ranked adult females ($n = 4$) as a control, with the prediction that only males would show a significant change in Elo-rating. Because the males may have changes in Elo-rating in opposite directions (that is increases or decreases), we then used ANOVAs with time as the between subjects variable to examine individual male responses. Troop stability was measured a month before and a month after the male removals, with the prediction that troop stability should increase following their removal.[7]

Temporary removal of α and β females in 2013. Elo-ratings were extracted 2 mo before and after the temporary removal of the α and β females (because the family was overthrown after approximately 2 mo) for the α family (family E), β family (family H), and matriline 4 (as a control). We predicted that the α family would decrease in Elo-rating as a result of decreased troop stability and increased rank changes within the troop. Similarly, we predicted that the β family would opportunistically increase in Elo-rating as a result of the temporary absence of top-ranking females. Stability was calculated for the 60 d preceding and following the temporary removals, with the prediction that rank changes in the troop would increase, resulting in decreased troop stability.

In addition, during the 3 mo before and after the α family's deposition, we predicted that the β family would endure a significant increase in Elo-rating to become the α family. We also predicted an increase in troop stability after the overthrow, because overthrows may serve as a 'boiling point' after a period of sustained instability followed by a relatively calm period, as anecdotally observed in our troop.

Permanent removal of third-ranking female in 2015. After the removal of the third-ranking female in 2015 (part of family H), Elo-ratings were extracted for the α family (family H), the second-ranking family (family B), and matriline 4 as a control. We predicted that the α family would receive greater insubordination and more frequent challenges due to losing a top-ranking female and thus would have a decrease in Elo-rating. More frequent challenges to the α family would therefore result in decreased troop stability. In addition, frequencies of bidirectional aggression (aggression yielding no clear winner; significant retaliated aggression from subordinate monkey) and insubordination (lower-ranking monkeys aggressing monkeys from a higher-ranking family) to the α and β families were compared by using χ^2 tests. We predicted an increase in Elo-rating for the β family after the removal of the third-ranking female due to opportunities to increase in the hierarchy. We used 3-mo time blocks for these analyses, because the α family was overthrown 3 mo later.

After the α family (family H) was overthrown, we compared Elo-ratings for the β family (family B) and matriline 4 (as a control) during the 2 wk before and after this event (because another overthrow occurred 2 wk afterward), with the prediction that the β family would increase opportunistically in Elo-rating to become the α family. In addition, we predicted an increase in troop stability after the takeover of family H, owing to this boiling-point hypothesis.

Permanent removal of top-ranking matriarch in 2016. After the removal of the top-ranking matriarch of family B (who was ranked as the α female at that time due to the overthrow), we compared Elo-ratings for her family and the next ranking families (Y and UR) during the 2 wk before and after her removal (because the family was overthrown after 2 wk), using matriline 4 as a control. We predicted that, after the removal of the matriarch in family B, her daughters would assume dominance, as indicated by an increase in Elo-rating. However, because losing a top-ranking female can signal an opportunity of ascension for adjacently ranked females, we also predicted an increase in Elo-rating for the next-ranking individuals (Y and UR). We also calculated family-level stability (that is, family-level hierarchies) in addition to troop stability, because the loss of aged matriarchs can be detrimental to the stability of families.[50]

After the takeover of family B, Elo-ratings were compared for the next-ranking family, family Y, with matriline 4 as a control, in the month before and after (as the final overthrow occurred after a month). We predicted family Y would assume dominance, and similarly, troop stability would again increase.

Final overthrow of α female. After the overthrow of Family Y, Elo-ratings were extracted for the next ranking family, Family UR, in the 3 mo before and after (until the cessation of data collection), as well as matriline 4 as a control. Troop stability was also calculated for this time. We predicted that Family UR would assume the top rank, and stability would again increase.

Results

Removal of natal males. After the removal of a large cohort of natal males, the remaining 4 adult males displayed no collective change in Elo-rating (mean ± SEM; before, 1409.91 ± 352.80; after, 1515.08 ± 319.34; paired *t* test, $t_3 = -0.86$, $P = 0.45$); neither did similarly ranked females (before, 1692.80 ± 284.79; after, 1703.19 ± 257.40; paired *t* test, $t_3 = -0.30$, $P = 0.78$). However, when examining individual males, further analyses revealed significant changes for each male (Figure 2). The α and β males both had significant increases in Elo-rating (α male: before, 2273.38 ± 5.59; after, 2366.00 ± 3.07; ANOVA: $F_{1,150} = 175.53$, $P < 0.001$; β male: before, 1394.52 ± 16.40; after, 1605.73 ± 9.51; ANOVA, $F_{1,83} = 55.27$, $P < 0.001$). However, the third-ranking male experienced a significant decrease in Elo-rating (before, 1426.45 ± 39.89; after, 1199.58 ± 16.89; ANOVA, $F_{1,46} = 19.56$, $P < 0.001$) due to aggression from the β male (after the removal, the third-ranking male only lost 5 interactions, all from the β male). The lowest ranking male, which rose to become the fourth-ranking male, demonstrated a rapid and significant increase in Elo-rating (before, 545.30 ± 12.43; after, 889.02 ± 27.80; ANOVA: $F_{1,66} = 92.28$, $P < 0.001$), mainly as a result of his persistent targeting of females. Approximately 1 mo after the removal, this

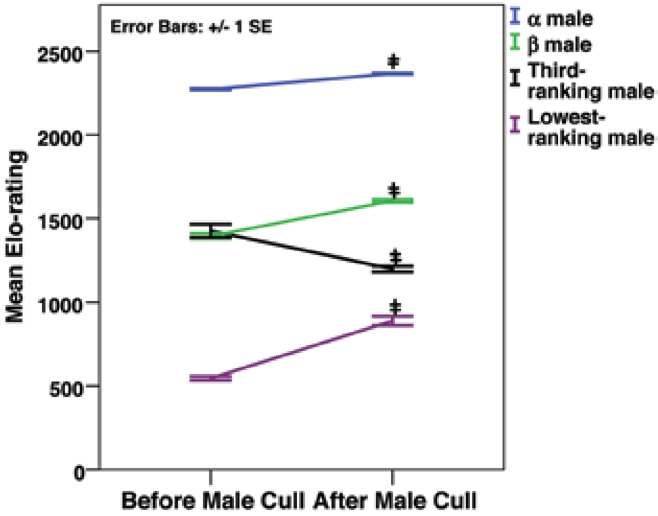

Figure 2. All males had significant (‡, $P < 0.001$) changes in Elo-rating after the culling of natal males.

Figure 3. Sister rank reversal. The third-ranking female (age, 6; part of family H) was outranked by her 2.5-y-old sister, which then became the third-ranking female until her removal in September 2015.

male was permanently removed from the troop after receiving intense aggression from other troop members in response to his rapid rank ascension. After the permanent removal of the group of males, the stability index value decreased from 0.47 to 0.27 (supporting the prediction that the removal of natal males would result in increased troop stability), indicating higher levels of troop stability and lower levels of overall rank changes after their removal (Figure 2).

Temporary removal of α and β females in 2013. The α family exhibited a significant increase in Elo-rating after the temporary removal of the α and β females in family E in October and November 2013 and their reintroduction (before, 1476.33 ± 43.44; after, 1626.83 ± 65.23; paired *t* test, $t_5 = -3.12$, $P = 0.01$). The β family (family H) likewise exhibited a significant increase in Elo-rating after the α family's absence and reintroduction (before, 1245.13 ± 24.04; after, 1406.63 ± 27.49; paired *t* test, $t_7 = -4.96$, $P = 0.002$), supporting prediction 2. Matriline 4 had no significant changes in Elo-rating (before= 894.43 ± 56.67 after= 884.62 ± 42.92; paired *t* test, $t_8 = 0.25$, $P = 0.81$). Troop stability decreased in the months surrounding the α family's absence, as the stability index increased from 0.08 to 0.29, revealing greater rank changes (supporting our prediction that the removal of top-ranking females would result in decreased troop stability).

Accordingly, in the months after the temporary absences, the α family was overthrown by the next-ranking family, family H. In doing so, family H became the α family (before, 1180 ± 92.25; after, 1312.94 ± 122.86; paired *t* test, $t_7 = -2.59$, $P = 0.04$, supporting our prediction that after the overthrow of the α family, the β family would become dominant), and the stability index decreased from 0.22 to 0.11 (supporting our prediction that overthrows are a stabilizing mechanism), reflecting greater hierarchical stability. Matriline 4 had no significant changes in rank (before, 849.95 ± 36.95; after, 802.54 ± 39.95; paired *t* test, $t_8 = 1.18$, $P = 0.27$). This hierarchy remained intact for the next approximately 2 y.

Permanent removal of third-ranking female in 2015. In fall 2014, the third-ranking female was displaced to the 4th rank by her younger sister after a sister rank reversal, as demonstrated by the observed reversal in Elo-ratings (Figure 3).

Surprisingly, after the removal of the third-ranking female in September 2015, the α family (family H) had a significant increase in Elo-rating (before, 1602.79 ± 208.34; after, 1749.97 ± 186.84; paired *t* test, $t_9 = -3.78$, $P = 0.004$). The next-ranking family (family B) similarly had a significant increase in Elo-rating (before, 1121.85 ± 156.3 after, 1295.69 ± 111.48; paired *t* test: t_7=-3.29, $P = 0.01$, supporting the prediction that the removal of top-ranking females would result in decreased troop stability as the β family increases in rank). Matriline 4 had no significant change in Elo-rating (before, 653.70 ± 58.28; after, 708.94 ± 69.56; paired *t* test, $t_{19} = -1.45$, $P = 0.16$). Unsurprisingly, the fourth-ranking female, the sister recently deposed after a sister rank reversal, regained her position as the 3rd female once her younger sister was removed. Troop stability decreased, as the stability index increased from 0.54 to 0.75 after the removal, leading just days up to the start of the conflict (supporting prediction 2: the removal of top-ranking females will result in decreased troop stability).

After the removal, bidirectional aggression toward the α family increased from 6 occurrences to 41 occurrences, and insubordination increased from 69 occurrences to 124 occurrences ($x^2 = 8.26$, df = 1, $P = 0.0041$). The β family (family B) had no significant changes in the receipt of bidirectional and insubordinate aggression ($x^2 = 0.668$, df = 1, $P = 0.42$). Approximately 66% of the bidirectional aggression toward the α family occurred from family X, a low-ranking (but large) family in matriline 4, which displayed a significant increase in Elo-rating after the third-ranking female's removal (before, 542. 12 ± 82.14; after, 655.70 ± 90.08; paired *t* test, $t_8 = -3.80$, $P = 0.005$). Two weeks prior to the overthrow, family X retaliated aggression to the α and β females—the first occurrence of bidirectional aggression observed directed toward them.

Although the initial events on the morning of the overthrow remain unknown, the β female in Family H was observed fear-grimacing to the matriarch in family X (at 15 y old, the second oldest matriarch in the troop), although no direct altercations were observed. Later, the matriarch in the β family (at 18 y, the oldest matriarch in the troop), family B, was observed aggressing the remaining family members in family H. Family B then assumed the role as the α family (before, 1385.08 ± 100.62; after, 1592.36 ± 131.23; paired *t* test, $t_7 = -3.71$, $P = 0.008$, supporting the prediction that after the overthrow of the α family, the β family would become dominant), resulting in an increase in hierarchical stability, because the stability index decreased from 0.73 to 0.61 (supporting our prediction that overthrows are a stabilizing mechanism). Matriline 4 had no significant changes in Elo-rating after the overthrow (before, 731.67 ± 74.42; after, 756.13 ± 65.78; paired *t* test, $t_{19} = -0.83$, $P = 0.42$).

Permanent removal of top-ranking matriarch in 2016. Following the removal of family B's matriarch after the defeat of family H, the β family (family B) assumed dominance (before, 1319.14 ± 87.76; after, 1514.40 ± 121.82; paired *t* test: $t_6 = -3.11$, $P = 0.02$), with the youngest daughter (approximately 5.5 y old) assuming the α-female role. The next-ranking families (Y and UR) also exhibited a significant increase in Elo-rating after the matriarch's removal (before, 988.24 ± 108.98; after, 1103.07 ± 120.84; paired *t* test, $t_9 = -3.87$, $P = 0.004$, supporting the prediction that the removal of top-ranking females would result in decreased troop stability as the β family increases in rank), whereas matriline 4 had no significant changes in Elo-rating (before, 739.85 ± 76.23; after, 750.87 ± 64.81; paired *t* test, $t_{19} = -0.36$, $P = 0.73$). Hierarchical stability decreased, because the stability index increased from 0.69 to 0.75 (supporting our prediction that the removal of top-ranking females would result in decreased troop stability).

In the second week after the rise of family B, aggression started occurring between the juvenile males in the family, which would determine who would be the troop's third-ranking male. The mothers frequently aided their offspring, which resulted in severe fighting within the entire family and the destabilization of the family hierarchy (the stability index for family B increased from 0.03 to 0.06; all other families within matriline 3 had perfectly stable family units, with S = 0 both before and after). The number of within-family contact aggression in family B increased from 1 to 22 (and was absent in all other families). After the third day of severe intra-family fighting, a decision was made the next day to remove the juvenile males in an attempt to restore stability.

However, family B was deposed in January 2016 before this removal could be accomplished. The third-ranking female in family B displayed clear signs of submission (fear grimace) to the matriarch in family UR and was aggressed by the matriarch in family Y (the next-ranking female after family B) as well. Consequently, all family members in family B were permanently removed. After the overthrow, the next-ranking family, family Y, became the α family (before, 1051.61 ± 173.24; after, 1373.48 ± 240.64; paired *t* test, $t_3 = -3.22$, $P = 0.04$, supporting our prediction that after the overthrow of the α family, the β family would become dominant), with family UR ranking below them. Matriline 4 did not significantly change in Elo-rating (before, 746.18 ± 67.24; after, 736.06 ± 67.99; paired *t* test, $t_{19} = -0.29$, $P = 0.78$). After the overthrow of family B, the stability index decreased from 0.70 to 0.44, reflecting an increase in troop stability (supporting our prediction that overthrows are a stabilizing mechanism).

Final overthrow of α female. In February 2016, the matriarch of family UR (the next-ranking family) overthrew family Y. Family UR then assumed dominance (before, 1010.24 ± 159.89; after, 1498.54 ± 126.25; paired *t* test, $t_5 = -7.28$, $P = 0.001$, supporting the prediction that after the overthrow of the α family, the β family would become dominant) until the cessation of data collection in May 2016. Matriline 4 had a significant decrease in Elo-rating after the takeover (before, 735.65 ± 69.27; after, 655.43 ± 78.95; paired *t* test, $t_{19} = 2.10$, $P = 0.05$). The overthrow of family Y improved troop stability once again, because the stability index decreased from 0.70 to 0.22 (supporting prediction that overthrows are a stabilizing mechanism; Figures 4 and 5).

Discussion

We sought to determine the extent to which demographic changes to a population of semi-free ranging rhesus macaques influenced hierarchical stability. Using troop dominance interactions and Elo-rating over a 3-y period, we found that demographic changes resulted in significant changes to hierarchical stability.

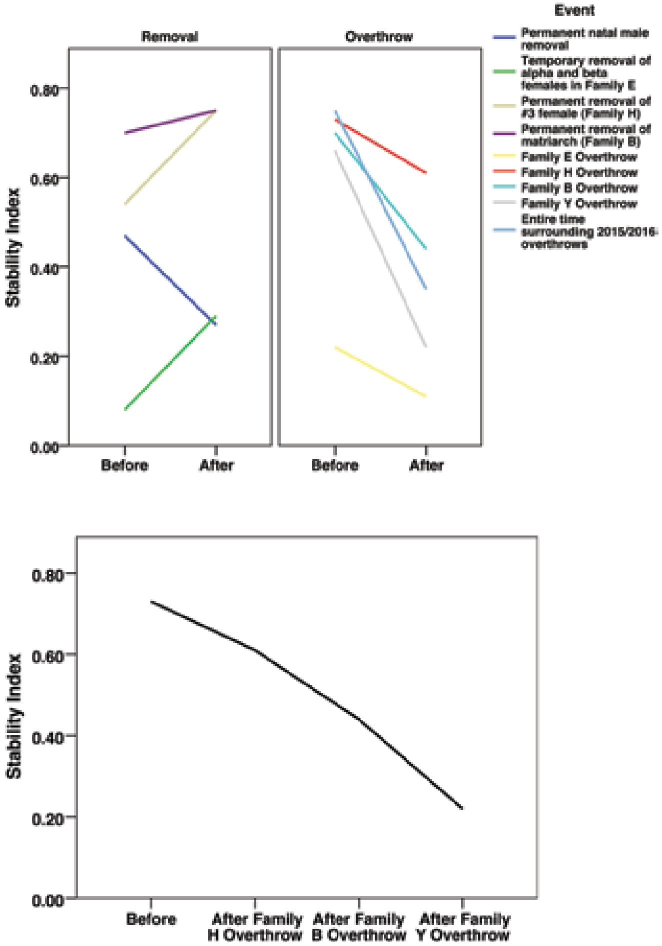

Figure 4. Troop stability after major demographic changes. Higher values reflect less stability (higher ratios of rank changes), and lower values reflect greater stability (lower ratios of rank changes). The removal of natal males resulted in improved troop stability. The removal of top-ranking females resulted in decreased troop stability, which preceded the overthrows of the α families. However, the overthrows resulted in increased troop stability and acted as a stabilizing mechanism.

Troop stability increased after the removal of natal males. Owing to kin support, natal males follow their matrilineal ranks, similar to females. However, as the males mature, they often rely on kin support to increase in rank.[7] This rise in rank by natal males results in hierarchical changes and instability but also can be highly beneficial for the males (resulting in delayed dispersal and greater reproductive success in free ranging populations[48]). Consequently, after the removal of natal males in our troop, troop stability increased, providing further evidence of their tendency to induce instability. It is possible that the troop stability improved because 2 of the natal males (a high-ranking juvenile male and the 8-y-old adult male) had somewhat unstable dominance positions, given that the juvenile male increased in rank along with his high-ranking mother, and the adult male fell in rank after an altercation with the α male. Therefore, their removal could have been highly effective in improving troop stability. However, which specific attributes (rank, age, etc.) of the natal males resulted in improved troop stability after their removal cannot be discerned completely,

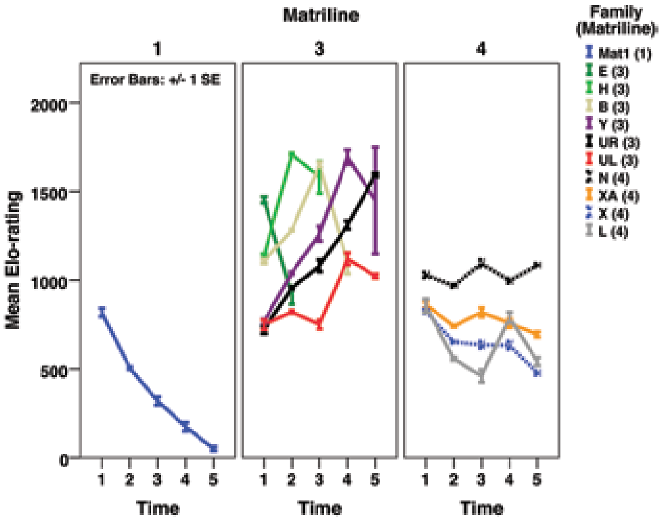

Figure 5. Progression of the α family from 2013 until 2016. Throughout the 3 y of data collection, the troop's α family (in the dominant matriline 3) changed dramatically. By the end of the study, 5 of the 6 families in matriline 3 had become the troop's α family. The relative hierarchies for matrilines 4 and 1 remained relatively stable., Time 1, February 2013 to 28 December 2013 (family E tenure); time 2, January 2014 until 20 December 2015 (family H tenure); time 3, 21 December 2015 to 7 January 2016 (family B tenure); time 4, 8 January 2016 to 1 February 2016 (family Y tenure); and time 5, 2 February 2016 to 1 May 2016 (family UR tenure).

because all males were removed on the same day. Therefore, we could not examine differences between the removal of high- compared with low-ranking natal males or different age categories. Indeed, recent research suggests that not all natal males are the same and that young high-ranking natal males may especially contribute to social instability.[9] Future research should investigate experimental removal of natal males that vary in age and rank.

However, the removal of males was not without consequence. Although there were no significant differences for collective male Elo-ratings, all males had significant fluctuations in Elo-rating (albeit in different directions), likely due to the decreased competition of other males.[25] In addition, the lowest-ranking male significantly increased in Elo-rating and, as a result of this rapid rank ascension, was permanently chased out of the troop only 1 mo later. Although the removal of natal males may have troop-wide benefits, other males should be monitored to minimize risks of aggression as they attempt to increase in rank (particularly when the removed males were adjacent in rank, because there tends to be a dominance-succession rule[22]).

Unsurprisingly, the temporary removal of top-ranking females resulted in decreased troop stability. We predicted that after temporary removal of top-ranking females, the α family would decrease in Elo-rating, as a result of decreased troop stability. In contrast, we found the α family increased in Elo-rating after their return, likely as an attempt to preserve the established social order and warn potential challengers of their willingness to fight.[11] In support of this explanation, in another captive group of rhesus macaques, the α matriline engaged in high levels of trauma-inflicting wounds, after the death of their matriarch, which the authors hypothesized to be a result of "enforcing their dominance positions in a period of perceived threat."[30] Even so, in our study, the β family also increased in Elo-rating, and the troop stability decreased 3-fold after the temporary removals. Thus, the increases in Elo-rating for the β family after the removals may have been a potential indicator of an impending challenge to the social order, further augmented by their involvement in the depositions. Similar to previous research,[39] we find evidence that the temporary removal of top-ranking females can render a troop vulnerable to social upheaval.

The removal of the third-ranking female in 2015 resulted in a cascade of events that collectively resulted in the collapse of the troop. After her removal, the α family received higher levels of insubordinate and bidirectional aggression (although bidirectional aggression was not included in the Elo-rating analyses, given that no clear winner was observed) but surprisingly had an overall increase in Elo-rating, namely due to the family members immediately adjacent in rank, who moved up in the hierarchy. Unstable dominance relationships emerged, as evidenced by decreased troop stability and family X's actions, which initiated 66% of the bidirectional aggression to the α family. After heightened insubordinate aggression and troop instability, the α family was deposed approximately 3 mo later. Although the preceding events were unobserved, soon after the onset of her family's overthrow, the β female was observed fear grimacing toward the matriarch in family X, reflecting a dramatic change in the status signaling. Soon afterward, the matriarch of family B (the β family) was initiating altercations. We speculate that, given the evidence preceding the overthrow (bidirectional aggression from family X and submissive signaling toward the matriarch of family X upon arrival), family X likely initiated the strife, which was then escalated by the β family's opportunistic involvement. We therefore conclude that the 2 oldest matriarchs in the troop (ages 15 and 18 y, respectively) in family X and family B, jointly targeted the α family (family H) and that this outcome might have been predicted given their increases in Elo-rating after the removal of the third-ranking female. Indeed, elderly females are more likely to initiate insubordinate aggression, especially when they have access to social support.[45] A collaborative effort may therefore have ensued among the 2 eldest matriarchs, who had the 2 largest families in the troop (and therefore the most social support).

Social support is critical in rank ascension,[14] and after the removal of the matriarch in family B (who ranked as the α female after the overthrow of family H), her daughters' dominance positions were now contestable without the presence and support of their matriarch. Severe fighting occurred within the family, thus destabilizing the family hierarchy. Increased intense aggression among members of the same family may have indicated changes in alliances,[8] prompting adjacently ranked females to opportunistically overthrow the weakly bonded family unit, which was less likely to fight back in unison, especially owing to the fact that the α female (the youngest daughter, 5.5 y) was young and inexperienced.[45] Consonantly, 2 of the 3 adult sisters were seen fighting each other, even after they had been deposed, indicating little allegiance to one another. These findings provide further evidence for the importance of matriarchs, which play an important role in family cohesion and stability in rhesus troops.[50] Furthermore, the bouts of severe aggression within family B were all instigated by juvenile male macaques and then escalated by maternal support. Although a decision was made to remove the males, the family was overthrown before this could be executed, providing further support that natal males can induce instability, especially in an already unstable family.

Removal of top-ranking females resulted in decreased troop stability and preceded their overthrows, which involved the β families. Animals of nearly equal rank are likely to challenge established social hierarchies,[11] and therefore these challenges might have been predicted in light of the β family's increases in Elo-rating before each overthrow. However, notably, we found that after each overthrow, troop stability increased. At first this situation seems counterintuitive, because we would expect heightened instability while ranks are reestablished and fighting occurs. However, during the altercations, ranks were established rapidly,[11] and upheavals were limited to only a few days, followed by a seemingly sudden pacifism. In addition, the overall troop hierarchy was not in total shambles, because there tended to be a dominance-succession rule,[15] and uninvolved matrilines remained stable in their ranks.[19]

Our results suggest that overthrows in rhesus troops are preceded by a period of sustained instability,[8,10,34] such as after the loss of keystone individuals, and an overthrow may act as a catalyst to restore dominance stability. However, this is not to say that overthrows only occur after demographic changes, because matrilineal fragmentation,[8] changes in socio-dynamics[32] and status signaling networks,[10] growing sizes of β families,[18] and female competition during the breeding season are also potentially influential.[28,47] Regardless, in each of our troop's overthrows (in 2009,[18] 2013, and 2015–2016), the absence (temporarily or permanently) of a top-ranking female was a common thread, similar to other captive[10,19,39] and free-ranging populations.[32] Here, we have demonstrated for the first time the changes in hierarchical dynamics that occur after the loss of top-ranking females, namely perturbations in troop stability. We found that our troop generally collapsed when the stability index value reached 0.7 and, as a consequence, was actually improving in dominance stability after each overthrow (down to 0.22 by the cessation of the study). Although this stability threshold value is likely unique to our troop, understanding the baseline stability for each captive troop can allow researchers and managers to address when the troop is becoming too unstable and reaching a potentially critical threshold. The question then becomes, if overthrows act as a mechanism to restore dominance stability, is there a way to restore stability without the occurrence of an overthrow? Simply removing animals may intensify, rather than resolve, conflicts. Answering these questions requires further research and the collaboration of multiple facilities, given that we are only beginning to address this issue.

One limitation to the current study is that these data were analyzed retrospectively. Although these results indicate likely predictors of an overthrow, the lack of analysis in real time prevented any acknowledgment of the potential indicators, because even insubordination occurred in typically fewer than 5% of all aggressive interactions[36] and therefore was overshadowed by the sheer amount of 'normal interactions.' Of course, inducing overthrows in a prospective study is not possible and certainly is not recommended. However, we do recommend that managers of large groups of captive rhesus macaques, as well as other despotic primates, track rank changes and dominance stability in real time through the use of Elo-rating. These changes, although subtle, might provide invaluable clues to the likelihood of a potential social collapse. Moreover, we urge an active communication between researchers, behavioral managers, and veterinarians when undertaking decisions regarding population removals. Unilateral decisions regarding troop composition should be avoided, because crucial information can be overlooked without a collaborative discussion. Finally, our study was unable to address the consequences of the removal of low-ranking animals or matrilines, because these changes did not occur. We hypothesize that the removal of low-ranking females would result in little change to hierarchical stability, similar to what has been observed with the immigration of low-ranking males.[38] Future research should evaluate a number of demographic changes that vary in their characteristics, to fully examine the hierarchical consequences and predictability for captive managers.

Our study highlights the efficacy of Elo-rating in tracking rank changes over time, especially after demographic changes. This tool has tremendous value and applicability to a wide range of facilities. Further research should evaluate a variety of different demographic changes and resultant effects on hierarchical stability. This information will then allow multiple facilities to predict the consequences of removals and guide future management decisions, thus collectively enhancing the well-being of primates in captivity.

Taken together, our findings underscore the consequences of demographic changes to a population of semi-free ranging rhesus macaques. Adjacently ranked monkeys may opportunistically take advantage of both temporary and permanent removals to increase in rank. When these removals consist of top-ranking females, these opportunistic changes may result in combative episodes. The consequences of population removals therefore should be considered carefully. In conclusion, Elo-rating is a very powerful tool in monitoring these changes and thus provides a valuable contribution to managers of captive NHP colonies in predicting and monitoring dominance instabilities.

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References

1. **Albers P**, **de Vries H**. 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. Anim Behav **61:**489–495.
2. **Altmann J**. 1974. Observational study of behavior: sampling methods. Behaviour **49:**227–267.
3. **American Association for Laboratory Animal Science.** 2015. AALAS position statement on the humane care and use of laboratory animals. J Am Assoc Lab Anim Sci **54:** 350–350.
4. **Anderson EJ, Weladji RB, Paré P**. 2016. Changes in the dominance hierarchy of captive female Japanese macaques as a consequence of merging 2 previously established groups. Zoo Biol **35**: 505–512.
5. **Animal Welfare Act as Amended.** 2008. 7 USC §2131–2156.
6. **Ballou JD, Lees C, Faust LJ, Long S, Lynch C, Lackey LB, Foose TJ.** 2010. Demographic and genetic management of captive populations. p 219. In: Kleiman DG, Thompson K, Kirk-Baer C, editors. Wild mammals in captivity: principles and techniques for zoo management. Chicago (IL): University of Chicago Press.
7. **Beisner BA**, **Jackson ME**, **Cameron AN**, **McCowan B**. 2010. Effects of natal male alliances on aggression and power dynamics in rhesus macaques. Am J Primatol **73:**790–801.
8. **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:**e16365.
9. **Beisner BA**, **McCowan B**. 2014. Experimental removal of high-ranking natal males alters the structure of silent-bared teeth display networks in captive groups of rhesus macaques. Abstract presented at the American Society of Primatologists 37th Annual Meeting, Decatur, Georgia, 12–15 September 2014. Am J Primatol **76 S1:**52.
10. **Beisner BA**, **Jin J**, **Fushing H**, **McCowan B**. 2015. Detection of social group instability among captive rhesus macaques using joint network modeling. Curr Zool **61:**70–84.

11. **Bernstein IS, Gordon TP**. 1974. The function of aggression in primate societies. Am Sci **62:**304–311.
12. **Bernstein IS**, **Williams LE**. 1983. Ontogenetic changes and the stability of rhesus monkey dominance relationships. Behav Processes **8:**379–392.
13. **Brotcorne F**, **Fuentes A**, **Wandia N**, **Beudels-Jamar RC, Huynen MC.** 2015. Changes in activity patterns and intergroup relationships after a significant mortality event in commensal long-tailed macaques (*Macaca fascicularis*) in Bali, Indonesia. Int J Primatol **36:**548–566.
14. **Chapais B**. 1988. Rank maintenance in female Japanese macaques: experimental evidence for social dependency. Behaviour **104:**41–58.
15. **Clarke FM**, **Faulkes CG**. 1997. Dominance and queen succession in captive colonies of the eusocial naked mole-rat, *Heterocephalus glaber.* Proc Biol Sci **264:**993–1000.
16. **Datta S**. 1988. The acquisition of dominance rank among free-ranging rhesus monkey siblings. Anim Behav **36:**754–772.
17. **Dettmer AM**, **Novak MA**, **Meyer JS**, **Suomi SJ**. 2014. Population density-dependent hair cortisol concentrations in rhesus monkeys *(Macaca mulatta).* Psychoneuroendocrinology **42:**59–67.
18. **Dettmer AM**, **Woodward RA**, **Suomi SJ**. 2015. Reproductive consequences of a matrilineal overthrow in rhesus monkeys. Am J Primatol **77:**346–352.
19. **Ehardt CL**, **Bernstein IS**. 1986. Matrilineal overthrows in rhesus monkey groups. Int J Primatol **7:**157–181.
20. **Flack JC**, **Girvan M**, **de Waal FB**, **Krakauer DC**. 2006. Policing stabilizes construction of social niches in primates. Nature **439:**426–429.
21. **Franz M**, **McClean E**, **Tung J**, **Altmann J**, **Alberts SC**. 2015. Self-organizing dominance hierarchies in a wild primate population. Proc Biol Sci **282**.
22. **Georgiev AV**, **Christie D**, **Rosenfield KA**, **Ruiz-Lambides AV**, **Maldonado E**, **Emery Thompson M**, **Maestripieri D**. 2016. Breaking the succession rule: the costs and benefits of an α-status takeover by an immigrant rhesus macaque on Cayo Santiago. Behaviour **153:**325–351.
23. **Hambright MK**, **Gust DA**. 2003. A descriptive analysis of a spontaneous dominance overthrow in a breeding colony of rhesus macaques (*Macaca mulatta*). Laboratory primate newsletter. **1:**8–10.
24. **Hannibal DL**, **Bliss-Moreau E**, **Vandeleest J**, **McCowan B**, **Capitanio J**. 2017. Laboratory rhesus macaque social housing and social changes: implications for research. Am J Primatol **79:**1–14.
25. **Hector AK**, **Raleigh MJ**. 1992. The effects of temporary removal of the α male on the behavior of subordinate male vervet monkeys. Am J Primatol **26:**77–87.
26. **Herrington JA**, **Del Rosso LA**, **Capitanio JP**. 2016. Biobehavioral consequences of prenatal exposure to a matrilineal overthrow and relocation in captive infant rhesus (*Macaca mulatta)* monkeys. Am J Primatol **78:**895–903.
27. **Holekamp KE**, **Strauss ED**. 2016. Aggression and dominance: an interdisciplinary. Behav Ecol **12:**44–51.
28. **Huchard E**, **Cowlishaw G**. 2011. Female–female aggression around mating: an extra cost of sociality in a multimale primate society. Behav Ecol **22:**1003–1011.
29. **Institute for Laboratory Animal Research.** 2011. Guide for the care and use of laboratory animals, 8th ed. Washington (DC): National Academies Press.
30. **Judge PG**, **de Waal FB**, **Paul KS**, **Gordon TP**. 1994. Removal of a trauma-inflicting α matriline from a group of rhesus macaques to control severe wounding. Lab Anim Sci **44:**344–350.
31. **Koford CB**. 1963. Rank of mothers and sons in bands of rhesus monkeys. Science **141:**356–357.
32. **Larson SM**, **Ruiz-Lambides A**, **Platt ML**, **Brent LJ**. [Internet]. 2016. Social network dynamics before a group fission event in Cayo Santiago rhesus macaques. Proceedings of the Joint Meeting of the American Society of Primatologists and International Primatological Society in Chicago, Illinois, 21–26 August 2016. Abstract 6518. Am J Primatol [Cited 08 December 2016]. Available at: https://www.asp.org/IPS/meetings/2016abstracts.pdf.
33. **Mansfield K**. 2003. Marmoset models commonly used in biomedical research. Comp Med **53:**383–392.
34. **McCowan B**, **Anderson K**, **Heagarty A**, **Cameron AN**. 2008. Utility of social network analysis for primate behavioral management and wellbeing. Appl Anim Behav Sci **109:**396–405.
35. **Melnick DJ**, **Pearl MC**, **Richard AF**. 1984. Male migration and inbreeding avoidance in wild rhesus monkeys. Am J Primatol **7:**229–243.
36. **Missakian EA**. 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta)* on Cayo Santiago. Primates **13:**169–180.
37. **Mitruka BM**. 1976. Introduction. p 1–21. In: Mitruka BM, Rawnsley HM, Vadehra DV, editors. Animals for medical research: models for the study of human disease. New York (NY): Wiley and Sons.
38. **Neumann C**, **Duboscq J**, **Dubuc C**, **Ginting A**, **Irwan AM**, **Agil M, Widdig A, Engelhardt A.** 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim Behav **82:**911–921.
39. **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.
40. **Raper J**, **Stephens BZ**, **Wallen K**. 2006. Matrilineal manipulations surrounding power shifts in socially housed groups of rhesus macaques (*Macaca mulatta*). Abstract presented at the American Society of Primatologists 29th Annual Meeting, San Antonio, Texas, 16–19 August 2006. Am J Primatol **68:**77.
41. **Sade DS**. 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. p 99–114. In: Altmann, SA, editor. Social communication among primates, Chicago (IL): University of Chicago Press.
42. **Sade DS**. 1969. An algorithm for dominance relations among rhesus monkeys: rules for adult females and sisters. Am J Phys Anthropol **31:**261.
43. **Samuels A**, **Henrickson RV**. 1983. Brief report: outbreak of severe aggression in captive *Macaca mulatta.* Am J Primatol **5:**277–281.
44. **Sanchez DM**, **Herman R**, **Wallen K**. 2014. Matrilineal overthrows in captive groups of rhesus macaques (*Macaca mulatta*): a retrospective analysis. Abstract presented at the American Society of Primatologists 37th annual meeting, Decatur, Georgia, 12–15 September 2014. Am J Primatol **76:**86.
45. **Seil SK**. [Internet]. 2014. Contra-hierarchical aggression among female rhesus macaques (*Macaca mulatta).* (Master's dissertation). [Cited 15 August 2016]. Available at: http://pqdtopen.proquest.com/doc/1665309227.html?FMT=ABS.
46. **Snyder NFR**, **Synder HA**. 1989. Biology and conservation of the California condor. p 175–267.In: Power DM, editor. Current ornithology, vol 6.
47. **Walker ML**, **Wilson ME**, **Gordon TP**. 1983. Female rhesus monkey aggression during the menstrual cycle. Anim Behav **31:**1047–1054.
48. **Weiß BM**, **Kulik L**, **Ruiz-Lambides AV**, **Widdig A**. 2016. Individual dispersal decisions affect fitness via maternal rank effects in male rhesus macaques. Sci Rep **6:**32212.
49. **Whiten A**, **Horner V**, **de Waal FB**. 2005. Conformity to cultural norms of tool use in chimpanzees. Nature **437:**737–740.
50. **Wooddell LJ**, **Kaburu SSK**, **Rosenberg KL**, **Meyer JS**, **Suomi SJ**, **Dettmer AM**. 2016. Correction: matrilineal behavioral and physiologic changes following the removal of a nonalpha matriarch in rhesus macaques (*Macaca mulatta*). PLoS One **11:**e0167739.