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Predictors of Matrilineal Overthrows in Large Captive Breeding Groups of Rhesus Macaques (*Macaca mulatta*)

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The purpose of this retrospective case-control study was to identify and assess biologically plausible variables that may predispose a captive rhesus macaque breeding colony to a matrilineal overthrow. Matrilineal overthrows are the result of members of multiple matrilines jointly attacking the highest-ranking matriline. Matrilineal overthrows in captive rhesus macaque colonies result in significant morbidity, mortality, and loss of genetic diversity. The following variables were investigated as potential determinants of overthrows: season, cage density, demographics, sex ratio, age of the alpha and beta animals, absence of the alpha and beta animals, pregnancy status of the alpha and beta females, number of adult females in the alpha matriline, recent changes in the male hierarchy, time since group formation, and number of adolescent males in the alpha matriline. Data were collected from January 1996 through January 2007. Univariate analysis indicated that absence of the alpha female from the group was associated with matrilineal overthrows, but multivariate analysis was not totally supportive. Conditional logistic regression identified number of juvenile males and number of adolescent males as associated with an overthrow; exact logistic regression was supportive. Principal component analysis followed by multivariate logistic regression identified 2 marginally nonsignificant predictors (the density and alpha factors). Our results suggest a possible association between the occurrence of a matrilineal overthrow and the following factors: absence of the alpha female, decreased housing density, number of juvenile males, and number of adolescent males.

Rhesus macaques are a social species and live in the wild in large multimale, multifemale groups ranging from 18 to 65 members.[14,19] Within these groups, male and female dominance hierarchies function independently.[7] The female family units are called matrilines. The top-ranked male and female macaques are designated as alpha animals, and the next highest ranking designated as beta animals. The alpha and beta females are usually from the same matriline. Females inherit the rank of their dam. Females remain tightly bonded with their matriline, whereas males over time will become independent of their family unit.[11] Top-ranking males may or may not be related to each other or to the alpha matriline; these animals assume the important social role of minimizing intragroup aggression.[3]

Matrilineal overthrows are the result of members of multiple matrilines jointly attacking the highest-ranking matriline.[7] During the past 15 y at our institution (the California National Primate Research Center), there have been more than 30 overthrows. Matrilineal overthrows in captive rhesus macaque colonies result in significant morbidity, mortality, and loss of genetic diversity.

Only a small number of matrilineal overthrows have been documented in the literature.[1,5,7,16] Although several hypotheses have been proposed relating to potential predictors of overthrows, no single predictor appears to be linked to all overthrow events described in the literature. One potential cause of an overthrow is the removal or reintroduction of high-ranking animals. Introduction of unfamiliar animals to, reintroduction of animals to, or removal of animals from an established group are all known to elicit intense excitement and increased aggression.[2,9,10,17]

Crowding or increased social density is another potential determinant of overthrow events. In some other species, such as rats, increased density can result in abnormal patterns of behavior, including decreased maternal ability, abnormal sexual behaviors, and increased aggression.[4] Early studies in nonhuman primates appeared to support a simple density–aggression relationship; however, this point is now debated in the literature, and a direct link between density and aggression has not been established.[8]

Another potential determinant is pregnancy status of the alpha and beta females. In one report, the alpha female was near-term at the time of the overthrow, and her pregnancy may have decreased her ability to defend herself and to maintain a strong bond with the alpha male.[5]

Population structure may also be a contributing factor to overthrow events. The simultaneous maturation of a large cohort of young females may have led to an overthrow.[16] In a separate report, the sexual maturation of a single subadult female appeared to contribute to an overthrow event.[5] In addition, the number of adolescent males (between 2 to 6 y of age) within the alpha matriline has been postulated as an important determinant. These young males inherit the rank and protection of their dam, and due to the captive environment, they are not able to migrate from their natal group, as they would in nature. In some instances, they have been observed harassing animals from other matrilines, and subsequent protection from retali-

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ation by their high-ranking dams has resulted in social unrest and, in some cases, an overthrow event.[7]

Still another report[1] suggests that changes in the male hierarchy may initiate an overthrow event, particularly when the top-ranking females resist the change in male rank. In the cited report[1], a young male attained maturity and climbed the dominance hierarchy. The 2 highest-ranking females resisted, and one of them was found dead. The young male appeared to be supported by the younger animals and eventually established himself as the alpha male.

Sex ratio is another demographic characteristic that has been considered as contributory to overthrow events. As previously mentioned, top-ranking males have the important role of minimizing intragroup aggression. If the sex ratio is askew, with too many females per male, female aggression may increase unchecked. The average sex ratio observed in the wild is 1 male:2.4 females.[18]

Variables that contribute to increased social stability seem plausible factors in matrilineal overthrows, too. The ages of the alpha and beta males and females may be important demographic variables, because older animals will have experienced more social interactions, which may influence their responses and result in increased social stability. The length of time since group formation is another plausible potential determinant of overthrow events, in that a group of animals that have been living together for a prolonged period of time are likely to have some degree of increased social stability. Similarly, the total number of adult females in the dominant matriline may play a role, as a larger matriline may provide more support and social stability.

Finally, seasonality is believed to play a role in matrilineal overthrows, in that increased levels of aggression and wounding during the breeding season are well documented.[6] Rhesus macaques are seasonal breeders, and the breeding season is defined as September through February, and the birthing season is defined as March through August in North America.[6,7]

In the present study, retrospective data from 20 overthrow events and 20 control situations were collected from our institutional database over a 10-y period. Here we report the results of a retrospective study assessing the role of biologically plausible variables, alone or in combination, in the occurrence of matrilineal overthrow events.

Materials and Methods

Study population. All animals in this study were maintained on protocols approved by the University of California–Davis IACUC. The California National Primate Research Center maintains large rhesus macaque breeding groups (80 to 120 animals) in half-acre (0.2 ha) outdoor enclosures (field cages) as previously described.[15] These enclosures have variable demographic composition and population density among cages and have diverse histories with some populations having been divided to establish new field cage breeding groups. Management and husbandry practices are consistent among all cages.

Selection of overthrow events (cases) and controls. Inclusion criteria for overthrow events (cases) required severe aggression resulting in the death or removal of the alpha female or her matriline from a field cage. In addition, an interval of 6 mo or more since any previous overthrow event was required to qualify as a unique event. Inclusion criteria for controls required no previous history of overthrow in that field cage at the time it was to be matched with a case. Each control was matched to a case by date of the overthrow event to control for possible confounding of seasonality and for ease of data capture. Twenty overthrow events occurring from January 1996 through January 2007 met inclusion criteria and were selected as cases. For each case, a control was selected randomly from the pool of available controls. If the selected control met the inclusion criteria then it was chosen; otherwise another random selection was performed.

Variables. All data were collected from either the institutional database or behavioral observation logs. The behavioral management staff at the California National Primate Research Center is highly experienced in animal observation and maintains extensive data on the rank of animals and any changes that occur over time. Cage density at the time of the matrilineal overthrow and at 6 and 12 mo prior to the overthrow event was determined. Demographics were collected by using sex and the following ages for breakdown: infants (younger than 1 y), juveniles (1 to 2 y old), adolescent females (2 to 3.5 y of age), and adult females (older than 3.5 y).[16] Males typically are considered adults after canine eruption, therefore the remaining demographic groups were adolescent males (older than 2 to 6 y of age) and adult males (older than 6 y). Sex ratio was defined as the ratio of the number of males to the number of females. The 2 top-ranking male and female (alpha and beta) animals were identified from behavior observation logs, and the ages of the 2 top-ranking males and females were obtained from the database.

Absence of the alpha and beta males and females was determined by using animal relocation histories maintained as part of the database. Pregnancy status of alpha and beta females was determined from the reproductive history portion of the database. Review of the database and behavior observation logs also allowed for determination of the total number of adult females in the alpha matriline. A recent change in the male hierarchy was defined as change in rank of either of the 2 top-ranking males over the 6 wk prior to the overthrow event and was determined by using the behavior observation logs. Time since group formation was defined as the time interval between establishment of the breeding group and the overthrow event and was determined from the database. The numbers of adult females and adolescent males in each alpha matriline was determined by using combined data from behavior logs and the database.

Statistical analysis. The Fisher exact test (STATA v.6, StataCorp, College Station, TX) was used to assess seasonality. Continuous variables were dichotomized by using the median of the cases as the basis for the dichotomization. Categorical and converted continuous data were placed into 2×2 contingency tables to determine frequency of case and matched control pairs by exposure status. The data for each variable were analyzed univariately by using the McNemar test for association (Stata version 10, StataCorp, College Station, TX). Stepwise conditional logistic regression (SPSS version 16.0, SPSS, Chicago, IL) was used to generate a multivariate prediction model by using as the pool of predictors all variables with a univariate McNemar P value less than 0.3. In doing the conditional logistic regression analysis, the maximum likelihood based procedure failed to converge when including 'absence of alpha females.' To circumvent this problem, exact logistic regression (StatXact version 10, Cytel, Cambridge, MA, and Stata version 10.1, StataCorp) was used to obtain the results.

Principal component analysis. The data reduction feature of principal component analysis (SPSS version 16.0, SSPS) was used as an alternative method of responding analytically to the situation of having a large number of predictor variables (25) relative to the sample size (20 cases and 20 controls). The principal components that emerged from the analysis were rotated with an orthogonal rotation to increase their interpretability. The principal component scores were computed for each case and control by using the factor weights of the corresponding principal components. The principal component scores were used as independent variables in a multivariate conditional logistic regression to evaluate their predictive value of the log odds of matrilineal overthrow events.

Results

Twenty overthrows occurred in the 11 y from January 1996 to January 2007 among 16 field cages, yielding an average of 1.8 overthrows per year. Whereas 60% of the overthrow events occurred during the breeding season, the remaining 40% occurred during the birthing season (Fisher exact $P = 0.75$). The data and results of the categorical predictor variable assessments for cases and controls are presented in Table 1. A statistically significant association was found for the variable 'absence of alpha females' and the occurrence of overthrow events. In 7 cases and only 1 control, the alpha female had been relocated to the hospital at the time of the overthrow ($P = 0.031$). For 2 overthrow events, the beta females were in the hospital at the time of the overthrow, whereas no beta females were absent in the controls. In 2 overthrow cases, both the alpha and beta females were absent from the group. Alpha and beta females were relocated to the hospital for health conditions such as pregnancy complications or trauma.

The results of the dichotomized continuous variables are summarized for the cases and controls in Table 2. The 'cage density at overthrow' variable was not found to be statistically significant ($P = 0.11$); however, there does appear to be a trend toward a lower median cage density among the cases as compared with the controls. Two other predictor variables were marginally nonsignificant: 'number of juvenile males' ($P = 0.11$) and 'number of adolescent males' ($P = 0.11$). All other dichotomized continuous predictor variables showed no significant lack of homogeneity between cases and controls. The median ages of the alpha and beta male and female, demographic breakdown, and time since group formation were found to be quite similar between cases and controls. The median sex ratio was 1 male:3.5 females in the cases compared with 1 male:4.9 females among the controls ($P = 0.29$).

Stepwise logistic regression using conditional maximum likelihood estimation was used in an attempt to evaluate the multivariate predictive value of the predictors on matrilineal overthrow events. All predictors with McNemar P values less than 0.3 were available for entry into the conditional logistic regression. Due to the observed slope of infinity for the variable 'absence of alpha females,' all regressions that included this variable demonstrated lack of convergence in the process of estimation of the regression coefficients. Excluding the variable 'absence of alpha females,' the most promising model included 2 predictors: 'number of juvenile males' ($P = 0.068$) and 'number of adolescent males' ($P = 0.068$).

Exact logistic regression then was used to evaluate the predictive value of 'number of juvenile males', 'number of adolescent males', and 'beta females pregnant' (the most promising predictors) and 'absence of alpha females' on matrilineal overthrows. Table 3 summarizes the results of the several fitted models. The table shows that 'number of juvenile males' and 'number of adolescent males' were statistically significant predictors ($P = 0.031$ and $P = 0.035$, respectively), when included together without other predictors (trial 1), supporting their predictive value identified by the stepwise conditional logistic regression. In trial 2, 'number of juvenile males' and 'number of adolescent males' remained significant ($P = 0.047$ and $P = 0.044$, respectively) in the equation that also included 'beta females pregnant' ($P = 0.54$). The 'number of juvenile males' and 'number of adolescent males' were borderline nonsignificant ($P = 0.12$ and $P = 0.097$, respectively) in the model that also included 'absence of alpha females' ($P = 0.34$; trial 3). When all 4 promising variables were in the exact logistic regression (trial 4), the 'number of juvenile males' and 'number of adolescent males' were the closest to being significant ($P = 0.14$ and $P = 0.11$, respectively); the other 2 predictors were 'absence of alpha females' ($P = 0.30$) and 'beta females pregnant' ($P = 0.46$).

Principal component analysis resulted in a substantial reduction of the predictor space with 8 principal components emerging that had eigenvalues greater than 1 (range, 6.193 to 1.171) accounting for 76.9% of the total variability in the original 25 predictor variables. Table 4 gives the highest factor loadings for the 8 rotated principal components. The interpretation of these factors was as follows:

Factor 1. The 6 most important variables were 'cage density at overthrow,' 'cage density 6 mo prior to overthrow,' 'cage density 1 y prior to overthrow,' 'number of infant males,' 'number of juvenile females,' 'number of adult females.' This was called the Density Factor.

Factor 2. The 2 most important variables were the 'number of adult males' and 'sex ratio.' This was called the Male Factor.

Factor 3. The 3 most important variables were the 'alpha female pregnant,' 'beta female pregnant,' and 'number of adolescent females.' This was called the Reproductive Factor.

Table 1. Number of cases and matched controls exposed and not exposed for categorical predictor variables in rhesus macaque colonies for matrilineal overthrows occurring 1996 to 2007

Categorical predictor variable	No. of cases	No. of matched controls	No. of cases and matched controls exposed	No. of cases exposed and matched controls not exposed	No. of cases not exposed and matched controls exposed	No. of cases and matched controls not exposed	P
Absence of alpha females	7	1	1	6	0	13	0.031
Absence of beta females	2	0	0	2	0	18	0.50
Absence of alpha and beta males	0	0	0	0	0	20	1.00
Recent changes in male hierarchy	2	1	0	2	1	17	1.00
Alpha females pregnant	4	6	2	2	4	12	0.69
Beta females pregnant	4	8	3	1	5	11	0.22

Table 2. Number of cases and matched controls exposed and not exposed for continuous predictor variables using dichotomized set points in rhesus macaque colonies for matrilineal overthrows occurring 1996 to 2007

	Basis of dichotomization						
Continuous predictor variable	Median of cases	Median of controls	No. of cases and matched controls above dichotomized set point	No. of cases above and matched controls below dichotomized set point	No. of cases below and matched controls above dichotomized set point	No. of cases and matched controls below dichotomized set point	*P*
Cage density at overthrow	93.5	113	8	2	8	2	0.11
Cage density 6 mo prior	97.5	104	6	4	7	3	0.54
Cage density 1 y prior	94.5	106	8	2	7	3	0.18
Age of alpha female (y)	12.7	13.3	6	4	5	5	1.00
Age of beta female (y)	6.9	6.4	3	7	5	5	0.77
Age of alpha male (y)	12.2	12.1	5	5	5	5	1.00
Age of beta male (y)	10.2	9.9	5	5	5	5	1.00
No. of infant males	7.5	8	7	3	4	6	1.00
No. of infant females	10.5	10.5	6	4	4	6	1.00
No. of juvenile males	4.5	8.5	8	2	8	2	0.11
No. of juvenile females	7	9	5	4	9	2	0.27
No. of adolescent males	13	14	4	2	8	6	0.11
No. of adolescent females	9	10	9	1	4	6	0.38
No. of adult males	9	8.5	5	6	5	4	1.00
No. of adult females	33.5	41.5	6	4	7	3	0.55
No. of adolescent males in alpha matriline	0	0.5	5	2	5	8	0.45
No. of adult females in alpha matriline	3	3.5	4	3	6	7	0.51
Sex ratio (male: female)	1:3.5	1:4.9	4	6	2	8	0.29
Time since group formation (y)	12	12.5	6	4	4	6	1.00

Table 3. Exact logistic regression results for select variables in rhesus macaque colonies for matrilineal overthrows occurring 1996 to 2007

Variable	Estimated odds ratio	95% Confidence interval	*P*
Trial 1			
No. of juvenile males	0.139	0.012–0.871	0.031
No. of adolescent males	0.157	0.014–0.907	0.035
Trial 2			
Beta females pregnant	0.466	0.069–2.730	0.54
No. of juvenile males	0.155	0.013–0.980	0.047
No. of adolescent males	0.167	0.015–0.967	0.045
Trial 3			
Absence of alpha females	4.518	0.413–237.560	0.34
No. of juvenile males	0.193	0.016–1.349	0.12
No. of adolescent males	0.202	0.018–1.239	0.097
Trial 4			
Absence of alpha females	4.844	0.443–255.355	0.30
Beta females pregnant	0.407	0.051–2.529	0.46
No. of juvenile males	0.214	0.018–1.494	0.15
No. of adolescent males	0.210	0.019–1.281	0.11

Factor 4. The 3 most important variables were the 'absence of alpha female,' 'age of the alpha male,' and 'number of juvenile males.' This was called the Alpha Factor.

Factor 5. The 2 most important variables were the 'age of the beta female' and the 'number of adolescent males in the alpha matriline.' This was called the Alpha-in-Waiting Factor.

Factor 6. The 3 most important variables were the 'absence of alpha female,' 'recent changes in male hierarchy,' and 'beta male age.' This was called the Hierarchy Factor.

Factor 7. The most important variables were the 'number of adolescent males' and 'time since group formation.' This was called the Number of Adolescent Males Factor.

Factor 8. The most important variable was the 'age of the alpha female.' This was called the Alpha Female Age Factor.

Multivariate conditional logistic regression on the 8 principal components or factors is summarized in Table 5. The table shows that factors 1 and 4 were marginally nonsignificant predictors ($P = 0.087$ and 0.072, respectively) of matrilineal overthrow events. The remaining 6 principal components had decidedly nonsignificant predictive values ($P \geq 0.185$).

The first principal component (the Density Factor) was inversely related to the log odds of a matrilineal overthrow. Because all 6 highest-loading variables had positive factor weights, the log odds of a matrilineal overthrow increased as the density (at overthrow, 6 mo prior to the overthrow, and 1 y prior to the overthrow) decreased, as the number of adult and juvenile females decreased, and as the number of infant males decreased.

The fourth principal component (the Alpha Factor) was positively related to the log odds of a matrilineal overthrow. The age of the alpha male and the absence of the alpha female variables had positive factor weights, indicating that the log odds of a matrilineal overthrow increased as the age of the alpha male increased and when the alpha female was absent. The 'number of juvenile males' variable had a negative factor weight, indicating that the log odds of a matrilineal overthrow increased as the number of juvenile males decreased.

Table 4. Rotated component matrix generated from 21 variables in matrilineal overthrows in rhesus macaque colonies from 1996 to 2007

	Principal Components							
Predictor variable	1	2	3	4	5	6	7	8
Cage density at overthrow	0.962							
Cage density at 6 mo prior	0.938							
Cage density 1 y prior	0.896							
No. of adult females	0.864							
No. of juvenile females	0.721							
No. of infant males	0.696							
No. of adult males		0.927						
Sex ratio		0.915						
Beta female pregnant			0.874					
Alpha female pregnant			0.625					
No. of adolescent females			–0.593					
Age of alpha male (y)				0.736				
No. of juvenile males (y)				–0.663				
Absence of alpha female (y)				0.584		0.509		
No. of adolescent males in alpha matriline					0.768			
Age of beta female (y)					0.709			
Age of beta male (y)						0.674		
Recent changes in male hierarchy						–0.631		
No. of adolescent males							0.810	
Time since group formation							–0.633	
Age of alpha female (y)								0.913
No. of infant females								
No. of adult females in alpha matriline								
Absence of beta female								
Absence of alpha or beta male								

Table 5. Conditional logistic regression results for 8 factors of matrilineal overthrows in rhesus macaque colonies occurring at the CNPRC 1996 to 2007.

	Odds ratio	95% Confidence interval	*P*
Factor 1	0.175	0.024–1.289	0.087
Factor 2	2.920	0.599–14.230	0.19
Factor 3	0.838	0.051–13.877	0.90
Factor 4	6.530	0.845–50.480	0.072
Factor 5	0.529	0.085–3.284	0.494
Factor 6	1.034	0.310–3.453	0.957
Factor 7	0.445	0.090–2.194	0.320
Factor 8	2.051	0.274–15.353	0.484

Discussion

Our univariate analysis indicates a strong and significant association between absence of the alpha female and the occurrence of a matrilineal overthrow event. In 7 cases, the alpha female was absent, and in 2 of these cases both the alpha and beta females were absent at the time of the overthrow. This prevalence reflects the importance of the alpha and beta females in maintaining social stability. Interestingly, no top-ranking males were absent at the time of an overthrow, and there were very few changes in the male hierarchy in both the cases and controls. The presence and stable social rankings of males, however, did not prevent the overthrows from occurring. The median sex ratio was 1 male:3.5 females in the cases, which is very close to that observed in the wild (1 male:2.4 females).[18] These findings are consistent with previous observations of overthrows, which report that during the overthrow event the top-ranking males often attempt to stop the mob attack but are ineffective and eventually allow the attack to continue with no further intervention.[7]

The strength of the absence of the alpha female and occurrence of a matrilineal overthrow event was not as convincing in the multivariate analysis. The association became nonsignificant when adjusted simultaneously for 'number of juvenile males,' 'number of adolescent males,' and 'beta females pregnant.' In addition, principal component analysis followed by multivariate analysis revealed marginally nonsignificant log odds of a matrilineal overthrow increasing as the age of the alpha male increased and when the alpha female was absent.

Although not statistically significant, median cage density was consistently lower in the cases as compared with the controls at the time of the overthrow as well as at 6 mo and 1 y prior to the overthrow event. Principal component analysis and multivariate analysis revealed the log odds of a matrilineal overthrow increased as the density (at overthrow, 6 mo prior to the overthrow, and 1 y prior to the overthrow) decreased, as the number of adult and juvenile females decreased, and as the number of infant males decreased.

Pregnancy status was not a significant contributing factor in the 20 overthrows we assessed. The median ages of the alpha and beta males were similar between case and control groups, and differences were not significant. Median time since cage formation also was similar between the cases and controls and not a significant determinant. Demographics between the 2 groups were similar for most groups considered, and no increased number of adolescent females was observed in overthrow events in this study, in contrast to earlier overthrow studies at our institution.[16] The numbers of juvenile males and adolescent males were lower in cases than controls. How smaller numbers in these age groups would contribute to an overthrow is unclear, and this finding is contrary to recent observations that juvenile males frequently are instigators of aggression, particularly those from high-ranking matrilines with few daughters.[12] Median number of adult females in the matriline was the same between the 2 groups, as was the number of adolescent males in the alpha matriline. The demographic similarity between the cases and controls suggests that population structure was not a significant determinant for the occurrence of overthrows in this series of events.

Rhesus macaque social structure is very complex, with diverse interactions among many individuals with different temperaments and personalities. Therefore, the multiple factors leading to social instability and overthrows may be somewhat unique to each group. Alternatively, a focus on monitoring and tracking social relationships on multiple levels (individual to entire social network measures) by using a longitudinal approach might provide us with insight into the more subtle types of social structures and dynamics that lead to problematic aggression and overthrows in rhesus groups.[13] At our institution, careful, regular observations are performed on all field cages to monitor for any changes in rank of animals or increased aggression. Decisions to remove overly aggressive animals temporarily or permanently from these groups are made as deemed necessary by colony management. In addition, when top-ranking animals are removed for health purposes, every attempt is made to return them to their cage as soon as possible. In some circumstances, top-ranking females are unable to remain reproductive due to health concerns. These females receive tubal ligation and are returned to their group to perform their important role as alpha or beta in the maintenance of social stability. Further assessment of cage density needs to be made to determine the reasons for the decreased density in some groups and not others. Careful evaluation is required prior to removing animals from rhesus macaque breeding colonies, to avoid the removal of socially influential animals and decreased cage density, both of which effects may contribute to social destabilization in the cage.

Failure to obtain a definitive result in the present study is due in part to the small sample size. However, despite the small sample size, cage density and the presence of the alpha female appear to be important factors to consider when managing captive breeding groups of rhesus macaques. Future studies involving larger sample sizes would be valuable in confirming or diminishing the importance of these relationships.

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