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Risk factors for stereotypic behavior and self-biting in rhesus macaques (*Macaca mulatta*): animal's history, current environment, and personality

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Abstract

Captive rhesus macaques sometimes exhibit undesirable abnormal behaviors, such as motor stereotypic behavior (MSB) and self-abuse. Many risk factors for these behaviors have been identified but the list is far from comprehensive, and large individual differences in rate of behavior expression remain. The goal of the current study was to determine which experiences predict expression of MSB and self-biting, and if individual differences in personality can account for additional variation in MSB expression. A risk factor analysis was performed utilizing data from over 4,000 rhesus monkeys at the California National Primate Research Center. Data were analyzed using model selection, with the best fitting models evaluated using Akaike Information Criterion. Results confirmed previous research that males exhibit more MSB and self-biting than females, MSB decreases with age, and indoor reared animals exhibit more MSB and self-biting than outdoor reared animals. Additionally, results indicated that animals exhibited less MSB and self-biting for each year spent outdoors; frequency of room moves and number of projects positively predicted MSB; pair separations positively predicted MSB and self-biting; pair housed animals expressed less MSB than single housed and grate paired animals; and that animals expressed more MSB and self-biting when in bottom rack cages, or cages near the room entrance. Based on these results we recommend limiting exposure to these risk factors when possible. Our results also demonstrated a relationship between personality and MSB expression, with animals low on gentle temperament, active in response to a human intruder, and high on novel object contact expressing more MSB. From these results we propose that an animal's MSB is related to its predisposition for an active personality, with active animals expressing higher rates of MSB.

Keywords

Stereotypy; self-abuse; personality; rhesus; risk-factor; management

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Introduction

Rhesus macaques (*Macaca mulatta)* are one of the most commonly used primate species in bio-medical research [Carlsson et al. 2004]. In captivity rhesus can develop "abnormal" behaviors that are statistically rare in wild populations, cause harm to the animal, or are the result of past damage or illness [Mench and Mason 1997]. Stereotypic behaviors, defined as repetitive behaviors caused by central nervous system dysfunction, frustration, or repeated attempts to cope [Mason 2006], are the most commonly seen abnormal behaviors in rhesus macaques [Lutz et al. 2003; Lutz et al. 2011]. Motor stereotypic behavior (MSB) is the most common, and has been reported to occur in 18.4–48.4% of indoor-housed rhesus, and in as much as 83% of singly housed populations [Lutz et al. 2003; Lutz et al. 2011]. MSB may include repetitive full body behaviors such as pacing, bouncing, swaying, circling, rocking, and somersaulting [Coleman and Maier 2010; Lutz et al. 2003; Rommeck et al. 2009].

Stereotypic behaviors are generally thought to develop out of chronic frustration, unavoidable stress or fear, a need to cope with an abnormal environment, or developmental dysfunction of the central nervous system [Mason 1991; Mason and Latham 2004]. Environments conducive to high rates of stereotypic behavior are therefore often considered suboptimal, and conducive to poor welfare [Mason 1991; Mench and Mason 1997]. Indeed, in a meta analysis of studies that compared environments or treatments, stereotypic behavior was usually highest in conditions linked with poor welfare (i.e. environments associated with signs of stress, fear, depression, or demonstrated to be poor through additional measures) [Mason and Latham 2004]. However, this analysis also found that *within* an environment, individuals that displayed the most stereotypic behavior often had the highest *individual* measures of welfare, with non-stereotyping or low-stereotyping individuals having the lowest measures of welfare [Mason and Latham 2004]. Therefore one must use caution when utilizing stereotypic behavior as an indicator of animal well-being; although certain (perhaps sub-optimal) environments may lead to undesired increases in overall stereotypic behaviors in a population, individual behavior expression cannot necessarily be used to assess welfare between subjects. For example, some individuals may express stereotypic behavior at high rates because they are frustrated, while others may do so because the behavior helps cope with a suboptimal environment [Mason and Latham 2004]. Furthermore, underlying physical problems that prevent activity may inhibit individuals that would otherwise engage in stereotypic behavior.

Self-abusive abnormal behaviors, such as self-biting, self-hitting, and head-banging, are an even greater concern for captive primates than MSB. Self-biting is particularly concerning because it can potentially result in injury severe enough to require heavy sedatives or humane euthanasia [Lutz et al. 2003; Novak 2003]. Self-biting is not as common as MSB, and has only been reported in 0.2–3.1% of indoor housed rhesus. Singly housed populations are at much higher risk however, with reports of self-biting in as many as 16–25% of animals [Lutz et al. 2003; Novak 2003].

Past research has found many risk factors for the development and expression of both MSB and self-biting in rhesus macaques. Rearing condition has been a common predictor for both behaviors, with individuals more likely to develop abnormal behaviors when raised in total or partial isolation, without a mother, or simply without a social group [Fittinghoff et al. 1974; Lutz et al. 2007; Novak et al. 2006; Rommeck et al. 2009]. Individual housing has consistently been a major predictor for MSB and self-biting, with risk for developing both behaviors increasing with each year spent in individual housing [Lutz et al. 2003], risk for developing self-biting highest when individual housing occurs at an early age [Lutz et al. 2003; Novak 2003], and abnormal behaviors expression most frequent when animals are individually housed [Baker et al. 2012a; Schapiro et al. 1996]. Stressful events such as

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relocations and veterinary procedures have been shown to positively predict development of self-biting [Novak 2003; Rommeck et al. 2009], while number of blood draws has been shown to positively predict development of MSB [Lutz et al. 2003]. Finally, males are more likely than females to develop either behavior [Lutz et al. 2003; Novak 2003; Rommeck et al. 2009], and, in a cross-sectional study, rate of MSB has been shown to decrease with age [Lutz et al. 2003].

Despite the many predictors of MSB and self-biting on a population level, the development of these behaviors on an individual level is still somewhat unpredictable. The inability of environmental factors to fully predict which animals will display abnormal behavior is possibly due in part to individual differences in the animals [Lewis et al. 2006; Novak et al. 2006]. Personality, broadly defined as patterns of behavior that are consistent over time, represents a significant source of individual variation that can influence well-being [Capitanio 2008]. In humans, personality has been shown to influence depression [Kendler et al. 2006; Kendler et al. 2004], disease [Capitanio 2008], and subjective well-being [Steel et al. 2008]. Similarly, personality in rhesus macaques has been shown to predict individual differences in a variety of outcomes, including disease progression [Capitanio et al. 2008; Capitanio et al. 1999], subjective well-being [Weiss et al. 2011], and HPA activity [Capitanio et al. 2004].

The first goal of the current study was to determine which environments and experiences predict expression of MSB and self-biting in captive rhesus macaques. Based upon previous research, we expected rearing condition [Fittinghoff et al. 1974; Lutz et al. 2007; Novak et al. 2006; Rommeck et al. 2009], sex [Lutz et al. 2003; Novak 2003; Rommeck et al. 2009], and age of individual [Lutz et al. 2003] to predict both MSB and self-biting. In addition, we hypothesized that time spent in outdoor groups prior to living indoors would provide crucial social and environmental stimulation to promote proper development and protect animals against the expression of abnormal behaviors. Conversely, one may predict that exposure to outdoor stimulation and enrichment may increase frustration caused by a lack of stimulation indoors, and exacerbate abnormal behaviors [Latham and Mason 2010]. Stressful experiences have predicted MSB and self-biting in the past, and we expected the experiences of room relocations, pair separations, and number of projects to which the animals had been assigned to also positively predict both abnormal behaviors. In addition to predictors of the behaviors from the history of the animal, we were also interested in *current* environmental predictors of the behaviors. We expected current pairing status to influence expression of MSB and self-biting as has been similarly demonstrated with previous research.

Another current predictor of interest was cage location, specifically cage level and position of cage relative to the entrance of the room. The majority of indoor rooms housing rhesus monkeys at many primate facilities have two rows of stacked cages, such that animals are either in top or bottom level cages. The two rows of cages are facing each other, such that animals can see individuals across from them. We hypothesized that animals would be more stressed in cages in close proximity to the door and in cages on the bottom level, and therefore expected these cages to have higher rates of both MSB and self-biting. Proximity to the entrance of a room has been shown to predict abnormal feather pecking in parrots, indicating that proximity to the door is a stressor for the animals [Garner et al. 2006]. Cage level may be important to welfare because animals in lower level cages are only a few inches off the ground, and have restricted upward movement. Rhesus macaques are predisposed to retreat upwards when faced with a predator, and bottom level animals are unable to perform this when faced with a human caretaker [Reinhardt and Reinhardt 2000]. Bottom level cages also may be conducive to poor welfare because they receive overall lower levels of ambient light [Schapiro and Bloomsmith 2001]. Increased rates of MSB in

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bottom level cages have been demonstrated in vervet monkeys [Seier et al. 2011], however this relationship was not found in rhesus [Schapiro and Bloomsmith 2001]. It is important to note however that this research was only done on singly housed juvenile males, and does not necessarily represent the entire population of captive rhesus.

The second goal of this study was to determine if individual differences in personality can account for differences in MSB expression, and which individuals are most at risk for expressing this behavior. Previous research has demonstrated that temperament can significantly predict the odds of an animal developing MSB [Vandeleest et al. 2011]. In the current research we aimed to evaluate if temperament, as well as multiple other measures of responsiveness (e.g. response to a threatening intruder) can be predictive of the rate of expression of MSB, conditional on an animal's past environmental experiences. Unfortunately, we had too few cases of personality-assessed animals that displayed self-biting to conduct a similar analysis on this outcome measure.

As the review above indicates, some of these hypotheses have been tested in previous research; our large sample size (more than 4000 subjects), however, enables us to test hypotheses about multiple (including new) risk factors in the same data set, and from a larger demographic of animals.

Methods

Subjects

Subject animals were rhesus macaques housed indoors at the California National Primate Research Center (CNPRC). Indoor cages at the CNPRC have a floor space of 4.3–8.0 square feet and a height of 30–36 inches. At the time of observation subjects were either pair housed, grate-pair housed, or singly housed. Pair housed animals share two adjacent cages. Grate-pair housed animals have limited physical contact with their neighboring animal through a small metal mesh divider between the two cages; although they do not have full physical contact, and cannot access each other's cage, they have the ability to see and groom each other. Singly housed animals are given visual access to at least one other monkey at all times. All subjects were cared for in compliance with protocols approved by the Institutional Animal Care and Use Committee at the University of California Davis, adhered to the requirements of the Animal Welfare Act and US Department of Agriculture regulations [Animal Welfare Act 1985], and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates.

Subjects were raised in one of four conditions: field cage, corn crib, indoors with mother, or in the nursery. Field cages are large ½ acre outdoor enclosures that house approximately 50–200 animals, while corn cribs are roughly 400 square foot outdoor enclosures that house approximately 15–30 animals. Field cage and corn crib reared animals were raised in their respective outdoor enclosure with their biological or foster mother. Indoor mother reared and nursery reared animals were raised indoors with no social group. Indoor mother reared animals were housed in a cage with their biological or foster mother, and at most with one additional adult and infant pair. Nursery reared animals were separated from their mother at birth and individually housed until 3 weeks of age, at which time they were given visual access to an infant of the same age, with whom they were eventually paired at 5 weeks of age.

Three analyses were performed: MSB environmental risk factor analysis, self-bite environmental risk factor analysis, and MSB and personality analysis. Analyses were limited to animals that were over one year of age, born at the CNPRC, and not involved in research projects at the time of observation. The MSB and personality analysis was limited to animals

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that had taken part in the BioBehavioral Assessment (BBA) (see below); a similar analysis could not be performed for self-biting, inasmuch as too few BBA-assessed animals had been recorded exhibiting this behavior. The self-bite environmental risk factor analysis was limited to animals between one and ten years of age in order to exclude any age groups that were never recorded biting (subjects that do not respond to remediation efforts to decrease self-biting are often put on terminal projects, or in rare cases euthanized according to the CNPRC IACUC-approved SIB humane endpoint policy).

The MSB risk factor analysis comprised 61,744 observations from 4,013 subjects (1498 males, 2515 females), with an average age of 9.21 years. The MSB and personality analysis comprised 13,820 observations from 1,145 subjects (453 males, 692 females), with an average age of 5.52 years. The self-bite risk factor analysis comprised 38,630 observations from 3,286 subjects (1301 males, 1985 females), with an average age of 5.71 years.

Data Collection

MSB and self-bite data were collected from "abnormal behaviors scans" performed between September 2006 and May 2011. In an abnormal behavior scan, a trained behavioral observer would watch and record 4–16 animals at a time for 5 minutes. Each animal was monitored for multiple abnormal behaviors, including MSB and self-bite (for ethogram definitions of behaviors used in the analyses see table 1). Behaviors were recorded using 1–0 sampling with one-minute intervals, such that each individual could receive a score of 0–5 for any behavior (a score of five was given if the animal showed the behavior at least once in each one minute interval, a score of four meant the animal showed the behavior in four of the one minute intervals, etc.). Trained observers were required to reach a joint probability of agreement inter-observer reliability of > 85% before recording data. All observers were trained to avoid eye contact with the animals and to be as unobtrusive as possible to the animals during observations. Abnormal behavior scans were systematically performed on all animals housed indoors between 9–24 times a year (over the 104 months that this study spans, abnormal behavior scans were sometimes performed once every month and a half, and sometimes multiple times a month). Because abnormal behavior scans have taken place at the CNPRC since September 2005, most animals in the data-set had previously taken part in multiple behavior scans, and were habituated to the observers.

A subset of the animals recorded in abnormal behavior scans also took part in the BBA [Capitanio et al. 2006b; Golub et al. 2009]. Each year since 2001 the majority of rhesus macaques born at the CNPRC that are available for testing take part in the 25-hour BBA program. Infants between the ages of approximately 90 and 120 days were temporarily separated from their mothers or social partners at 9 AM and relocated to individual indoor cages for the 25-hour testing period, during which they experienced multiple behavioral and physiological assessments, followed by return to their original housing.

Each individual received a holding cage "activity" and "emotionality" score for Day 1 and Day 2 of the testing period. Scores were created based on 5-minute focal observations performed by a single live observer at the beginning (Day 1) and end (Day 2) of the 25-hour period. The observer recorded multiple behaviors, including both activity states and events, and exploratory and confirmatory factor analyses yielded a two-factor solution, reflecting "activity" and "emotionality" [Golub et al. 2009].

Subjects took part in a 4-minute human intruder (HI) test during the 25-hour period. During this test the subject was placed in a testing cage where an unfamiliar human positioned herself in various positions relative to the caged subject, while multiple behavioral responses were recorded. Exploratory and confirmatory factor analyses found that these responses

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could best be explained using a four factor model including “activity,” “emotionality,” “aggression,” and “displacement.” [Gottlieb and Capitanio 2013].

A novel object score was created for each individual by placing a small plastic object in the cage for the entire 25-hour testing period. Inside the plastic object was an accelerometer that recorded any movement of the object during the 25-hour period. Novel object use was recorded as the mean number of 15-second intervals in which the subject touched the object during an average 5-minute period (scores could theoretically range from a minimum of 0 to a maximum of 20). Scores were further broken down into two categories: mean score during the daytime (9:45AM – 4:20PM) and mean score overnight (4:50PM – 6:30 AM).

At the end of the 25-hour period the technician who performed the tests and handled the infants scored each individual on a 7-point Likert scale for multiple behavioral measures of temperament. Exploratory and confirmatory factor analysis found that these behavioral measures could be simplified into a four-factor model of temperament: “gentle,” “vigilant,” “confident,” and “nervous” [Golub et al. 2009].

Analysis

Risk factors for abnormal behaviors were determined using generalized mixed effects modeling with hierarchical model selection in R computational software [Team 2011]. MSB analyses were performed using a Poisson distribution, where count of MSB in a single observation was the outcome, while self-bite analyses were performed using a binomial distribution, where presence/absence of self-bite in a single observation was the outcome. Multiple observations were performed on the same individuals, and individual was included in all models as a random effect. Age was included as a covariate in self-bite models, as it is a factor that may influence other variables, however due to non-random attrition the significance and influence of age on self-bite was not evaluated. All reported beta coefficients are conditional values, meaning they are determined with all other coefficients held constant.

Hierarchical model selection was performed through comparison of multiple models, starting with the simplest possible model that included only the intercept and a random effect for animal. Additional models were then compared in a stepwise fashion that included either a single new variable or different clusters of variables. Comparison of models continued such that each step compared new models to the best fitting model from the previous step. The variable selection process was predetermined based on biological significance and increasing complexity of the variables. At each step, Akaike Information Criterion (AIC) was used to evaluate whether the addition of variables improved the final model. AIC is a popular information criterion used to compare candidate models, in which models are rewarded for goodness of fit and penalized for increased number of predictors in the model [Akaike 1987]. At each step analyses would continue with the model with the lowest AIC, which is considered to be the optimal model. If two models were within 2 AIC of each other, these models were considered to fit the data equally, and both models were kept in consideration as plausible models [Burnham and Anderson 2002]. Predictors were then added to both plausible models in the same stepwise fashion, until there were multiple final plausible models. The model with the lowest AIC, as well as any models within 2 AIC of this model, were selected from the final models as “candidate models.” To avoid type 1 errors with such a large data set, if presented with multiple “candidate models” the most parsimonious model (the model with the least number of predictors) was selected as the final best fitting model. Contrasts were performed between all levels of categorical variables with more than two levels (for example, there are four types of rearing condition), and 95% confidence intervals were used to evaluate which levels of the variable were functionally distinct. Correlations existed between many predictors in the personality analysis (both

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temperament and human intruder factor analyses were performed with an oblique rotation), and model diagnoses were performed at each step to insure collinearity did not occur.

Finally, to determine co-morbidity between MSB and self-biting, a final analysis was performed to determine if MSB significantly predicted self-biting. To control for the many overlapping risk factors for these behaviors only two models were compared; the first model included every environmental risk factor from the final models for MSB and self-biting, while the second model additionally including MSB as a predictor for self-biting.

Results

Motor Stereotypic Behavior Environmental Risk Factors

For all steps in the MSB environmental risk factor model selection process, there was always a clear best fitting model at least 2 AIC below all other models. As a result, the model selection process concluded with a single candidate model that best predicted MSB expression given the different environmental risk factors. In the final model animals reared in a corn crib, indoors with a mother, or in a nursery expressed 4.44, 9.68, and 11.02 times as much MSB as animals raised in a field cage, respectively. Nursery reared and indoor mother reared animals expressed 2.48 and 2.18 times as much MSB as corn crib reared, respectively. Males expressed 1.07 times as much MSB as females. Expression of MSB decreased exponentially with age. MSB increased by 3% for each relocation to a new room. MSB decreased by 20% for every year that an animal spent outdoors. MSB increased by 10% every time an animal was permanently separated from its social partner. MSB increased by 5% for each additional project to which an animal was assigned. Singly housed animals and grate pair housed animals expressed 1.34 and 1.32 times as much MSB as pair housed animals, respectively. Animals housed on the bottom rack of a cage exhibited 1.27 times as much MSB as animals on the top rack. And finally, MSB expression was lower in cages further away from the front of the room, with MSB expression decreasing by 1% for every cage between a subject animal and the door. See table 2 for a list of the beta coefficients, standard error, 95% confidence intervals, and contrasts for each variable in the model. In the online supplementary table we have provided the AICs of a few other models with different environmental risk factors for MSB. Note that none of these models fit as well as the final model, they are simply included for comparison.

Self-Bite Environmental Risk Factors

The self-bite environmental risk factor analysis yielded four candidate models. Two of the self-bite risk factor models are equally parsimonious, each having five predictors for self-bite, and both of these models are presented in full detail as equally fitting final models of self-bite. All four candidate models are presented with their corresponding AICs in the online supplementary table. For comparison, the AICs of other non-candidate models have been included in the online supplementary table as well. In the first model, animals reared in a nursery were 4.95 times as likely to self-bite as animals reared in a field cage. Males were 2.27 times as likely to self-bite as females. Self-biting decreased by 46% for every year that an animal spent outdoors. Animals housed on the bottom rack of a cage were 1.4 times as likely to self-bite as animals on the top rack. And finally, self-biting was more rare in cages further away from the front of the room, with likelihood of self-biting decreasing by 4% for every cage between a subject animal and the door. In the second model animals reared in a nursery were 5.42 times as likely to self-bite as animals reared in a field cage. Males were 2.27 times as likely to self-bite as females. Self-biting decreased by 42% for every year that an animal spent outdoors. Self-biting increased by 16% for every time an animal was permanently separated from its social partner. And finally, the likelihood of self-biting decreased by 5% for every cage between a subject animal and the door. See table 3 for a

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detailed description of the beta coefficients, standard error, 95% confidence intervals and contrasts for each variable in the models.

Motor Stereotypic Behavior and Personality

The MSB and personality analysis was performed on a subset of the data from the MSB environmental risk factor analysis. All risk factors from the previous analysis remained predictors of MSB in this subset of data and were kept in the personality model as covariates, except for number of projects. It is likely that number of projects no longer had strong predictive power because this new subset of data included a younger set of animals; these animals had been assigned to fewer projects, and so this variable displayed less variation.

The MSB and personality analysis yielded four candidate models. The final model is presented in full detail, however all four candidate models are still presented with their corresponding AICs in the online supplementary table. For comparison, the AICs of a few other non-candidate models with different personality measures are included in the supplementary table as well. In the final model, in addition to environmental risk factors, animals exhibited higher rates of MSB if they were low on the temperament trait "gentle," had more daytime novel object contact, or scored high on HI-activity. See table 4 for a detailed description of the beta coefficients, standard error, and 95% confidence intervals for each variable in this model.

Comorbidity of Motor Stereotypic Behavior and Self-Bite

MSB positively predicted self-bite, with expected self-biting increasing by 26% for each observed MSB (see table 3 for beta coefficients, standard error, and 95% confidence intervals, see the online supplementary table for comparison of AICs)

Discussion

Abnormal Behavior Environmental Risk Factors

The final model of environmental risk factors for expression of MSB included every risk factor that was evaluated as a significant predictor of MSB, including rearing condition, sex, age, room moves, years outdoors, pair separations, project count, current pairing, cage level, and cage position. The self-bite environmental risk factor analysis yielded two final models. Both final models included rearing condition, animal sex, number of years outdoors, and cage position as risk factors for expression of self-bite. In addition, one of the two models included cage level and the other model included pair separations.

Demographically males expressed higher rates of MSB and self-biting, and expression of MSB decreased with age. These results are consistent with previous research on sex [Lutz et al. 2003; Novak 2003; Rommeck et al. 2009] and age [Lutz et al. 2003]. Lutz and colleagues proposed in their 2003 risk factor analysis that MSB may be related to an animal's activity level, and the decrease in MSB with age may be related to a decrease in general activity of the animal. This is consistent with our results on these variables as well as with our results on personality and MSB, as will be discussed below.

Past Housing Risk Factors

Rearing condition was a significant predictor of MSB and self-bite, however the effect of rearing condition was slightly different for each behavior. MSB expression was highest in animals reared in a nursery or indoors with a mother, and lowest in animals reared in a field cage. Field cages are larger and more complex than corn cribs, with more social relationships and space to explore. The field cage has long been considered the "gold

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standard” of captive primate rearing, and these results support this idea. Surprisingly our data did not show a difference in MSB between nursery rearing and indoor mother rearing conditions. It should be noted that although there is support that nursery rearing leads to a higher rate of some abnormal behaviors compared to indoor mother rearing [Lutz et al. 2003; Rommeck et al. 2009], Lutz et al. [2003] similarly did not find a difference between the two conditions with regards to MSB. Therefore, early age cage size and complexity may be the most salient predictors of MSB, as even the stimulation and support of a mother does not appear to decrease or prevent the development of the behavior. Overall these results show a hierarchy of rearing condition, with field cage rearing leading to the lowest expression of MSB, followed by corn crib rearing, and with indoor rearing being the most problematic.

Unlike the MSB risk factor results, the only rearing condition found to be a significant predictor of self-biting was nursery rearing, relative to field cage rearing [Rommeck et al. 2009]. While it is surprising that the analysis did not find statistical differences between any other rearing conditions, it is important to note that the beta coefficients showed a similar trend to the MSB analysis; nursery reared individuals showed the most self-biting, indoor mother reared individuals showed more self-biting than outdoor reared, and corn crib reared individuals showed more self-biting than field cage reared. These trends are consistent with previous research which has shown nursery reared rhesus to be at higher risk for developing self-biting than indoor mother reared, and indoor mother reared to be at higher risk than outdoor reared.

In addition to the problems associated with indoor rearing, we found that animals expressed 20% less MSB and between 42–46% less self-abuse for each year spent outdoors in field cage or corn crib social housing. These results support our hypothesis that outdoor socialization has a protective effect on developmental trajectories in rhesus macaques, and can decrease abnormal behavior expression. As already demonstrated, animals reared indoors are at much higher risk of developing abnormal behaviors, and our results indicate that an intervention as simple as housing animals outdoors for one year later in life may drastically improve chances of normal development. That being said it is important to note that this model is based on retrospective data, and experimental data is necessary to demonstrate a causal relationship. Furthermore, we cannot determine if the beneficial effects of outdoor social housing were a result of socialization, or simply increased stimulation outdoors. Further research is needed to separate these confounding variables, and to determine if similar benefits can be found with indoor social housing alone. In addition, further research is needed to determine if the timing of outdoor socialization is important, as it may be particularly beneficial for this outdoor social experience to occur early in development.

Past Experience Risk Factors

It is generally believed that exposure to unavoidable stressful events can lead to higher rates of stereotypic behavior development and expression [Mason 1991], and previous research has demonstrated that events such as blood draws and veterinary procedures are predictive of MSB and self-biting [Lutz et al. 2003; Novak 2003]. We predicted that room moves and pair separations would positively predict the expression of both behaviors, because these experiences are potentially stressful forms of social disruptions. Permanent separation of a pair is an obvious form of social disruption, where two animals that share a cage are separated and prevented from having social access to each other (note that only permanent and not temporary separations were included in this analysis). An indoor monkey’s social environment however does not only consist of conspecifics in a shared cage; indoor housed rhesus have visual access to multiple other animals in a room, and develop social relationships (e.g., dominance) despite having no physical contact. Moving an animal to a

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new room removes familiar conspecifics and introduces unfamiliar animals, challenging the animal with new social stressors. An even more extreme form of social disruption occurs when animals housed in outdoor social groups are moved indoors to a room with new individuals. Our results demonstrated that animals that experienced a high number of pair separations were at higher risk for both MSB and self-biting, and animals that had a high number of room moves exhibited higher rates of MSB, supporting our hypothesis that these social disruptions can be stressful for rhesus macaques (it is important to recognize that pair separations as a predictor was not included in both final models of self-biting, and therefore we can be less confident in its functional relevance and predictive ability). It should be noted that although the effect size of room moves was relatively small (animals were expected to exhibit only 3.4% more MSB with each room move), the average animal in our sample moved 13.88 times before their observation, with a standard deviation of 7.8. An animal with 8 room moves more than another animal is expected to exhibit 1.31 times as much MSB, showing that in practice there is potential for a large effect of room moves given how often such moves occur.

The number of projects to which animals were assigned was also a significant predictor of MSB, however the effect size of project count was relatively small (animals exhibited only 4.6% more MSB with each additional project), and the average subject had been in only 2.26 projects, with a standard deviation of 2.54. Thus while project count positively correlated with MSB, it was a weak predictor. We currently do not know exactly what aspects of projects increase rates of MSB, however blood draws and veterinary procedures have previously independently been established as significant predictors of abnormal behaviors. If experiences such as these are perceived as stressful to the animals, it may be that projects with a high number of similarly invasive and potentially stressful procedures are particularly conducive to MSB. Alternatively, it may be that animals that have been on a high number of projects have frequently been administered ketamine, an NMDA receptor antagonist commonly used to anesthetize nonhuman primates. Ketamine has been demonstrated to lead to short term increases in stereotypic behavior in rats [Hunt et al. 2005; Ishmael et al. 1998], and therefore ketamine may be responsible for the correlation between project count and MSB expression. Further research is needed to determine specifically what aspects of a project lead to the observed increase in MSB, and why.

Current Housing Risk Factors

Results demonstrated that animals show higher rates of MSB when singly housed or grate pair housed, and are at higher risk for both MSB and self-abuse when housed closer to the door in a room, or on the bottom rack of cages (however because it was not in both final models we are less confident about the effect of cage level on self-biting). Given that past research has shown high-risk for development of abnormal behaviors with single housing, we expected animals currently singly housed to express higher rates of MSB than animals currently paired or grate paired. Interestingly, there was no statistical evidence for a difference in MSB between singly housed and grate pair housed animals, and grate pair housed individuals expressed more MSB than paired individuals. Grate pair housing has been touted as an alternative means of socialization for animals that cannot be pair housed, either for behavioral or research related reasons. These results however indicate that grate pair housing leads to expression of MSB at a rate closer to single housing than pair housing, and are consistent with recent findings that partial contact housing is associated with higher levels of abnormal and tension-related behaviors than full contact housing in female rhesus macaques [Baker et al. 2012b]. With the recent increased emphasis on the importance of socially housing primates [Committee 2011] it is important to recognize that partial contact pair housing may not necessarily be an appropriate form of socialization equivalent to pair housing for rhesus macaques.

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The markedly higher expected rate of MSB and self-abuse in animals housed in the bottom cage level demonstrates that the lower level may be a particularly problematic environment for rhesus monkeys. This may be due to restricted upward movement in bottom cages that prevents animals from climbing above human caretakers, or the lower level of ambient light, although further research is needed to determine which aspects are most salient to the animals. Our results are in contrast to those of Schapiro and Bloomsmith [2001], who did not find a significant relationship between abnormal behaviors and cage level. Unlike their study, which was conducted on singly housed juvenile males, our study was conducted on all age/sex classes. It is possible that the effects that we found were driven by bottom-tier housing's negative effects for animals with different demographic characteristics (females, pair housed, etc.); future research is needed to determine which individuals are most at risk in lower levels.

The increase in MSB and self-abuse found in animals housed closer to the entrance of a room may be due in part to their close proximity to outside noise and activity. Previous research has demonstrated that rhesus in cages close to the door that are able to see activity in neighboring preparation rooms have higher rates of the stress hormone cortisol [Capitanio et al. 1996]. Although most rooms at the CNPRC now have closed windows that prevent animals from observing outside room activity, animals close to the entrance are still able to hear adjacent activity. Noises heard from outside the room may become associated with certain husbandry procedures. If these noises are only intermittently paired with husbandry procedures it can lead to high levels of frustration [Bassett and Buchanan-Smith 2007], and may explain the higher rates of MSB in these animals. While the results on cage position are promising, and can inform management decisions of where to position high-risk animals, future research is needed to determine what aspects of being housed near a room entrance or on the bottom rack are particularly problematic for the animals.

The results on current housing environment are particularly exciting because they may provide a means to decrease rate of abnormal behaviors once they have developed. The previously explained past housing and experience predictors of abnormal behaviors were risk factors derived from the history of the animal. The current housing risk factors, pairing status and cage position, are conditional on these past risk factors, and represent current risk at the time of observation. With this in mind, these results are informative that given an animal's history, they are expected to show higher rates of both MSB and self-biting if housed in bottom level cages, and cages closer to the door. Therefore, moving an animal that is currently self-biting to a top level cage away from the door may be an effective means of decreasing the behavior. While promising, we emphasize that our results only demonstrate correlational relationships, and further research is needed to determine causation.

Motor Stereotypic Behavior and Personality

The final model of MSB and personality included three measures of personality obtained when the animals were 3–4 months old: gentle temperament, human intruder activity, and contact with novel objects. These predictors of MSB are conditional on the environmental predictors of MSB determined in the first analysis. In other words, given an animal's rearing condition, number of room moves, years outdoors, etc., these personality measures are predictive of MSB. This informs us that individual differences in temperament can help explain why only some individuals in captivity develop high rates of MSB: animals can be at high-risk for development of MSB based on known environmental risk factors and yet express low rates of the behavior, or never develop the behavior at all. These results show that when housed indoors, individuals scoring low on gentle temperament, high on activity during a human intruder challenge, and showing high contact with novel objects expressed the highest rates of the behavior.

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The question then arises of why animals with these personality traits express higher rates of MSB, and what these measures have in common. The first measurement, gentle temperament, is a factor score comprised positively of gentle, calm, flexible, and curious. Animals that scored low on this temperament rating expressed higher rates of MSB, and can be broadly viewed as agitated, restless, and inflexible. The second measurement, human intruder activity, is a factor score representing an animal's activity during the human intruder test. Animals that scored high on this factor were more active when faced with a threatening stimulus, and expressed higher rates of MSB. The final measure, contact of novel objects, is a direct count of how often an animal contacted a novel object when in the BBA holding cage. Animals that contacted the novel object frequently during the BBA test period were either confident, curious, or simply contacted the object frequently as a result of being highly active in the cage. Animals that contacted the novel object frequently expressed higher rates of MSB.

While these three domains may represent different aspects of an individual's personality, they are linked through an animal's tendency for movement and activity. A highly active individual is likely to score low on gentle, high on human intruder activity, and high on contact of novel object. With this in mind, these results suggest that inherently active animals express higher rates of MSB in captivity. MSB is a full body behavior that involves high amounts of movement and activity. The most common form of MSB in rhesus is pacing, where animals pace in circles in their cages. MSB has been hypothesized to function as a replacement behavior for species-typical locomotor activity, and has been shown to decrease in rhesus monkeys that are provided larger cages with increased opportunity for movement [Draper and Bernstein 1963; Paulk et al. 1977]. MSB has also been hypothesized to be related to an animal's general activity levels or desire to move [Clubb and Vickery 2006] and has been shown to correlate with other measures of normal activity [Bildsøe et al. 1991]. The current research lends further support to these ideas, demonstrating that rhesus high on measures related to inherent activity are expected to express higher rates of full body active MSB when housed indoors later in life.

It is important to note however that although some individuals are expected to express higher rates of MSB in captivity, we cannot conclude that these individuals particularly have difficulty coping, or experience compromised welfare compared to their non-active non-stereotyping counterparts. As Mason and Latham demonstrated in their 2004 meta analysis, environments conducive to high rates of MSB are associated with compromised welfare, but given an environment, those individual within the environment that develop MSB often demonstrate the highest individual measures of welfare. Because the personality analysis was conducted conditionally on environment, these results demonstrate that given the environmental history of the animal, active animals express the most MSB. Although speculative, active animals may actually be better suited to cope with the environmental stressors of captivity. MSB should by no means be considered a “positive' behavior, but inactivity and unresponsiveness to the environment may be less preferable from a welfare perspective. We currently do not have data on animal activities when not engaging in MSB, so further research is needed to determine the general activity budget and relative welfare of individuals who do or do not engage in high levels of MSB. Research on the coping abilities of these animals, as well as individual measures of welfare, will help illuminate the implications of active personalities developing higher rates of MSB.

From a practical standpoint these results can help investigators decide which animals to utilize for research projects. Stereotypic behavior can be a confound in some specific areas of research [Garner 2005], and in these cases selecting subject animals with lower general activity may minimize the expression of MSB over the course of a long-term study. Of course, such selection of subjects will also limit the generalizability of the study's research results [Capitanio et al. 2006a].

These results differ from previous research on MSB utilizing BBA data, which found indoor-reared animals high on nervous and gentle temperaments significantly more likely to develop MSB [Vandeleest et al. 2011]. The differences between the current and previous study are likely due to differences between the demographics of the individuals used in the studies, and major differences in data analysis and variables modeled. Demographically, the previous study was performed on individuals ranging from 0.43–4.70 years old, while the current analysis includes individuals ranging from 1.00–10.29 years old. In modeling the effect of personality on MSB, the previous analysis utilized a logistic regression, using only presence/absence of MSB as the modeled outcome. The current analysis utilizes a count outcome, and models of expected count of MSB using a Poisson regression and repeated observations on the same individuals. These different methods of analyses answer different questions, as the previous study modeled the risk of displaying MSB at all, while the current study models the expected rate of expressing the behavior. The current analysis also differs in the variables chosen for analysis. Unlike the previous study, the current analysis includes additional covariates of environmental risk factors for MSB as determined in the first section of this paper, as well as additional measures of personality such as human intruder response, activity and emotionality scores, and contact of novel objects.

Comorbidity of Motor Stereotypic Behavior and Self-Bite

Our results found individuals that displayed MSB more likely to self-bite than non-MSB individuals, supporting previous researching showing comorbidity between the two abnormal behaviors [Rommeck et al. 2009]. Unlike previous research however, our analysis controlled for environmental risk factors for both abnormal behaviors, demonstrating that the comorbidity of MSB and self-biting is not simply a result of shared environments. Rather, the type of monkey that is likely to develop MSB in captivity is also more likely to develop self-biting in captivity. Although we do not know the "type" of monkey most likely to self-bite, our study found that the type of monkey who displays an active personality most likely to exhibit high rates of MSB. Further research is needed to determine if active monkeys are also most likely to self-bite, or if there are different distinguishing features of a monkey who develops both MSB and self-abusive behaviors.

Conclusions and Recommendations

Environments conducive to a high rate of development of stereotypic behavior are considered to have relatively poor welfare compared to those with in which stereotypic behaviors are rare. The risk factors for MSB determined in this study are important because they inform us of which environments and experiences may be particularly stressful or difficult for rhesus macaques. In contrast, the risk factors for self-biting are important because self-biting in itself is a welfare concern, and should be minimized and avoided at all costs. Based on our results we recommend that nursery rearing should be utilized only when other options are not available, and that animals should be reared in large outdoor social groups when possible. We recognize that it is not always possible to raise rhesus in outdoor social groups, and that many facilities do not have outdoor housing available. In these higher risk rearing environments we strongly recommend providing opportunities for group socialization both early and later in development. When group socialization is not available, we emphasize the importance of full contact socialization. Socialization through a partial contact grate divider is likely preferable to single housing for some outcomes, however our results demonstrate that such housing is not a suitable replacement for full contact pair housing with regard to MSB. Once animals have been established in full contact pairs, long-term maintenance of these pairs is important; separation from a social partner is presumably

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stressful and should be avoided unless absolutely necessary. Similarly, relocating animals into new rooms should be limited when possible, as this event appears to be stressful for the animals.

From our results we can infer that bottom level cages and cages close to the room entrance worsen an animal's well-being; however given the current structure of most primate facilities these caging options are unavoidable. While research is needed to find ways to improve the quality of life in these cages, as well as a need for development/implementation of a caging system that prevents lower level confinement, for now we recommend avoiding bottom level and front of room cages for animals that are high-risk or have a history of self-abuse. If an indoor-housed animal begins to self-bite, or appears to have trouble coping with their environment, we recommend relocation within the same room to a top row cage away from the door. We note, however, that all suggestions are all based upon a correlational analysis, and further research is needed to determine whether the measures we have identified are causal.

In addition to environmental risk factors for abnormal behaviors, this research demonstrated a direct relationship between animal personality and rate of expression of MSB. Animals which, during a brief separation/relocation in infancy, were rated lower on gentle temperament (i.e., were rated less calm, gentle, curious, and flexible), displayed more activity in response to a human intruder, and showed a higher rate of contact with novel objects, were demonstrated to express higher rates of MSB. Taken together, these results may indicate that an animal's rate of expression of MSB is related to their predisposition for an active personality, with active animals expressing higher rates of MSB. Management strategies aimed at lowering overall colony levels of MSB therefore might benefit from prioritizing the protection of active animals. For example, active animals might best be housed in upper level cages, or toward the rear of a room. That being said, from a welfare perspective it is still unclear whether active animals actually have the most trouble coping with sub-optimal environments, or if they are simply more likely to utilize MSB as a mechanism for coping with a lack of space for active movement.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Table 1

Abnormal Behavior Ethogram

Behaviors scored as motor stereotypic behaviors	Pacing	Walking in the exact same pattern—either back and forth or in a circle—3 or more repetitions.
	Swinging	Grasping a part of the cage with one or more hands or feet while moving in the exact same pattern—either back and forth or in a circular pattern—for 3 or more repetitions.
	Flipping	3 or more repeated forward or backwards somersaults.
	Twirling	3 or more repeated horizontal turns of the body.
	Rocking	Rhythmic movement either side-to-side or forward and backward for at least 3 repetitions.
	Bouncing	Jumping up and down for 3 or more repetitions using a rigid posture. This behavior should not be confused with bouncing with a less rigid posture, which appears to serve only to make noise or shake the cage.
	Head Twist	Moving, lifting, or twisting the head in an exaggerated way 3 or more times.
Behaviors scored as self-abuse	Self Bite	Biting of the monkey’s own body.

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Table 2

Variables included in final model for MSB environmental risk factor analysis. Variables with positive beta (ß) estimates positively predict MSB, variables with negative beta estimates negatively predict MSB. Categorical variables all have a "referent" variable, the variable to which other levels of the variable are compared. For categorical variables all variables compared to the referent are indented. Referent variables do not have beta estimates.

Variable	ß Estimate (SE)	Lower 95% CI	Upper 95% CI
Final Model: Motor stereotypic behavior (MSB) ~ rearing, sex, age, room moves, years outdoors, pair separations, project count, current pair, cage level, cage position			
Rearing – Field Cage	–	–	–
Rearing – Corn Crib	1.49 (0.15)	1.20	1.78
Rearing – Indoor Mother	2.27 (0.14)	2.00	2.54
Rearing – Nursery	2.40 (0.11)	2.18	2.62
Sex – Female	–	–	–
Sex – Male	0.07 (0.09)	−0.12	0.25
Age in years (linear predictor)	−0.18 (0.02)	−0.22	−0.14
Age in years (quadratic predictor)	−0.004 (.001)	−0.01	−0.003
Room Moves	0.03 (0.01)	0.02	0.05
Years Outdoors	−0.22 (0.02)	−0.26	−0.18
Pair Separations	0.10 (0.02)	0.07	0.13
Project Count	0.05 (0.01)	0.02	0.07
Current Pair –Paired	–	–	–
Current Pair – Grate Paired	0.28 (0.08)	0.13	0.43
Current Pair – Single	0.29 (0.03)	0.24	0.34
Cage Level - Bottom	–	–	–
Cage Level – Top	−0.24 (0.02)	−0.28	−0.20
Cage Position	−0.01 (0.002)	−0.02	−0.01
Contrasts			
Corn Crib– Field Cage	1.49	1.20	1.78
Indoor Mother– Field Cage	2.27	2.00	2.54
Nursery– Field Cage	2.40	2.18	2.62
Indoor Mother– Corn Crib	0.78	0.44	1.12
Nursery–Corn Crib	0.91	0.60	1.23
Nursery– Indoor Mother	0.13	−0.13	0.40
Grate Paired –Paired	0.28	0.13	0.43
Single – Paired	0.29	0.24	0.34

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Table 3

Variables included in the final models for self-bite environmental risk factor analysis. Variables with positive beta (ß) estimates positively predict self-bite, variables with negative beta estimates negatively predict self-bite. Categorical variables all have a “referent” variable, the variable to which other levels of the variable are compared. Referent variables do not have beta estimates. For categorical variables all variables compared to the referent are indented. A linear covariate is included in the model for age, however since it is intended to be a covariate and not a predictor it is not reported.

Variable	ß Estimate (SE)	Lower 95% CI	Upper 95% CI
Model 1: Self-bite ~ rearing, sex, years outdoors, cage level, cage position			
Rearing – Field Cage	–	–	–
Rearing – Corn Crib	0.08 (1.20)	−2.27	2.43
Rearing – Indoor Mother	1.05 (0.78)	−0.48	2.58
Rearing – Nursery	1.60 (0.63)	0.37	2.83
Sex – Female	–	–	–
Sex – Male	0.82 (0.44)	−0.042	1.68
Years Outdoors	−0.61 (0.16)	−0.92	−0.30
Cage Level - Bottom	–	–	–
Cage Level – Top	−0.34 (0.23)	−0.79	0.11
Cage Position	−0.04 (0.02)	−0.09	0.001
Model 2: Self-bite ~ rearing, sex, years outdoors, pair separations, cage position			
Rearing – Field Cage	–	–	–
Rearing – Corn Crib	0.08 (1.18)	−2.24	2.39
Rearing – Indoor Mother	1.11 (0.78)	−0.42	2.64
Rearing – Nursery	1.69 (0.63)	0.46	2.92
Sex – Female	–	–	–
Sex – Male	0.82 (0.44)	−0.04	1.68
Years Outdoors	−0.55 (0.16)	−0.86	−0.24
Pair Separations	0.15 (0.12)	−0.09	0.38
Cage Position	−0.05 (0.02)	−0.09	−0.004
Contrasts			
Corn Crib– Field Cage	0.08	−2.27	2.43
Indoor Mother– Field Cage	1.05	−0.48	2.58
Nursery– Field Cage	1.60	0.37	2.83
Indoor Mother– Corn Crib	0.97	−1.45	3.39
Nursery–Corn Crib	1.52	−0.74	3.77
Nursery– Indoor Mother	0.55	−0.60	1.69
Motor stereotypic behavior (MSB) and Self-bite			
MSB	0.23 (0.05)	0.13	0.33

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Table 4

Variables included in the final model for MSB and personality. Variables with positive beta (β) estimates positively predict MSB, variables with negative beta estimates negatively predict stereotypy.

Variable	β Estimate (SE)	Lower 95% CI	Upper 95% CI
Final Model: Motor Stereotypic Behavior (MSB) ~ rearing, sex, age, room moves, years outdoors, pair separations, current pair, cage level, cage position, gentle score, daytime novel object contact, HI-activity score			
Gentle Score	−0.22 (0.10)	−0.41	−0.03
Daytime Novel Object Contact	0.11 (0.05)	0.01	0.26
HI-Activity Score	0.19 (0.10)	0.004	0.38