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RESEARCH ARTICLE

Factors Affecting Aggression Among Females in Captive Groups of Rhesus Macaques (*Macaca mulatta*)

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Captive groups of primates often exhibit higher rates of aggression than wild, free-ranging groups. It is important to determine which factors influence aggression in captivity because aggression, particularly intense aggression, can be harmful to animal health and well-being. In this study, we investigated the effect of ground substrate as well as season, rank, age, and group size on rates of agonistic interactions per female in seven captive groups of rhesus macaques ($n = 70$ females, 1,723 focal samples) at the California National Primate Research Center. Agonistic interactions were divided into three categories: displacements, mild aggression, and intense aggression. Females living in enclosures with gravel substrate were 1.7 times more likely to be involved in intense aggression (e.g. chases and physical contact) than females living in enclosures with grass (Poisson regression model: $P<0.001$). High-ranking females were at least 1.3 times more likely to be involved in mild (e.g. threats and lunges) aggression than lower-ranking females (low rank: $P = 0.03$; mid rank: $P = 0.001$). Females of all ranks were 1.5–1.9 times more likely to be involved in both intense and mild aggression during the breeding season than other seasons. Age and group size did not affect rates of mild or intense aggression. These findings indicate that although some aggression appears to be natural and unavoidable, i.e. aggression during the breeding season, the well-being of captive macaques can be improved by developing grass substrate in outdoor enclosures. Am. J. Primatol. 73:1152–1159, 2011.

Key words: aggression; dominance rank; ground substrate; colony management; welfare

INTRODUCTION

Captive groups of primates often exhibit higher rates of aggression than wild, free-ranging groups [Marriott, 1988; Rowell, 1967; Southwick, 1969]. Such increases in aggressive behavior may have deleterious effects on animal health, such as increased stress [Honess & Marin, 2006a; Kalin, 1999], injury, social overthrow, or even death [McCowan et al., 2008; Oates-O'Brien et al., 2010]. Indeed, one of the main challenges of captive management is how to reduce aggression, because it can negatively affect the physical and psychological health of animals in captivity [Honess & Marin, 2006b].

In the wild, availability and distribution of food influences agonistic interactions and thus dominance relationships among females [Barton & Whiten, 1993; Koenig et al., 1998; Pruetz & Isbell, 2000; van Schaik, 1989; Wrangham, 1980]. Because female reproductive success is, in part, limited by access to food resources [Trivers, 1972], the nature of food resources is particularly important in female agonistic relationships—favoring contest competition when foods are worth usurping from others [Chancellor & Isbell, 2009; Isbell et al., 1998; Koenig, 2000; Saj & Sicotte, 2007]. Captive primates are traditionally fed once or twice per day, and their primary food, monkey chow, is given all at once, and often in a single location, creating an extraordinarily spatially clumped resource that likely rarely occurs under natural conditions. As a high-quality resource that is slowly consumed, monkey chow is a potentially usurpable resource, which may encourage agonistic competition.

To reduce aggression in captivity, one approach has been to modify foraging conditions. Floor litters (i.e. woodchips), beddings (i.e. straw), and other natural foraging materials added to enclosures encourage foraging behavior in captive primates [Blois-Heulin & Jubin, 2004; Chamove et al., 1982; Ludes & Anderson, 1996] and, in some cases, also reduce aggression [Chamove et al., 1982]. Agonistic interactions may decrease when animals feed on foods that are small and quickly eaten because such

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foods can be consumed before they can be taken away by others [Isbell & Pruetz, 1998; Isbell et al., 1998]. Thus, for example, in experiments with captive rhesus macaques (*Macaca mulatta*), the frequency of agonistic interactions for apple pieces declined as the pieces became smaller, regardless of the interfood distance [Chancellor & Isbell, 2008; Mathy & Isbell, 2001].

The presence of certain kinds of vegetation in outdoor enclosures may have a similar effect. For instance, rhesus macaques living in enclosures with grass as ground cover spent more time foraging (20–24% in grass vs. 8–12% in gravel) [Beisner & Isbell, 2008] and increased the tortuosity of their travel paths [Beisner & Isbell, 2009] relative to animals in enclosures with gravel substrate. Given that grass is a food that is small and quickly eaten, and that it creates a habitat suitable for arthropods which are also small and quickly eaten, grass ground cover is expected to reduce both the frequency and intensity of aggression relative to groups living in enclosures with gravel as the ground cover.

Rhesus macaques are classified as the most despotic of the macaques. They are characterized by severe aggression and highly asymmetrical dominance interactions, even in the wild [Thierry, 2004]. Their naturally high levels of aggression are often exacerbated in captivity because animals cannot readily escape threatening situations, creating a challenge for facility managers who strive to promote health and well-being in their captive charges. At the California National Primate Research Center (CNPRC), rhesus groups live in enclosures that include grass or are restricted to gravel. We predict that (1) animals in enclosures with grass ground cover express less frequent and less intense aggression. Furthermore, we anticipate, based on earlier studies [Bernstein & Ehardt, 1985; Erwin & Erwin, 1976; Judge & DeWaal, 1997; Ram et al., 2003; Wilson & Boelkins, 1970], that additional factors influence the expression of aggression. In particular, we expect (2) higher ranking animals to be more involved in aggressive interactions than lower ranking animals, perhaps because higher ranking animals have more individuals below them with whom to fight, have more aggressive and bold personalities that have allowed them to maintain high rank, or have more at stake in the preservation of their rank [Ram et al., 2003]; (3) older animals to be more involved in aggressive interactions than younger animals [Bernstein & Ehardt, 1985]; (4) larger groups (and thus higher animal density) to have higher rates of aggression than smaller groups [Erwin & Erwin, 1976; Judge & DeWaal, 1997]; and (5) rates of aggression to be higher during the breeding season than during other seasons because of increased levels of competition for mates [Wilson & Boelkins, 1970]. In this study, we test these predictions in a population of captive, outdoor-housed groups of rhesus macaques.

METHODS

Study Site and Groups

The study was conducted at the CNPRC in Davis, CA from September 2006 to November 2007. All research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates as well as all laws of the United States government. This research was approved by the University of California, Davis Institutional Animal Care and Use Committee, protocol ♯12063. At the CNPRC, social groups of rhesus macaques are housed in 0.2 ha (60 m $\times$ 30 m) outdoor enclosures that are identical in nearly every respect except for ground substrate. Grass substrate consisted of grass patches that varied over the study period as a result of seasonal changes in temperature and rainfall as well as macaque foraging behavior. Grass ranged in height from very short to approximately 15 cm. Gravel substrate consisted of small, gray pebbles spread over most of the enclosure. Enclosures were otherwise similar in having ten A-frame houses, multiple suspended barrels, swings, and several perches. Monkey chow was given to each group at approximately 07:00 hr every morning and again between 14:30 and 15:30 hr in the afternoon, always in the same location. Monkey chow was typically available throughout the day because groups usually do not eat all the chow that is given. Additionally, either fresh fruits/vegetables or a seed mixture (supplemental food resources) were scattered throughout the enclosures every morning.

Seven groups were studied, four of which had naturally growing grass in their enclosures (at least 30% grass of the 0.2 ha area) and three of which had gravel/dirt substrate with no grass (Table I). One group (Group 2) began the study in a gravel enclosure and was moved to a grass enclosure (30% grass coverage) after 7 months for colony space management reasons. The new enclosure for Group 2 was identical to the previous one in its dimensions and the location and orientation of feeding hoppers, shaded areas, and A-frame houses. The animals were

TABLE I. Characteristics of Study Groups

Group	Group size range	Group age[a] (years)	Ground substrate
1	129–156	11	Grass
2	141–180	30	Both[b]
5	160–187	20	Grass
8	156–180	15	Gravel
14	78–102	24	Grass
16	122–146	30	Grass
18	123–158	16	Gravel

[a]Group age is measured from the year of group formation to 2006, the beginning of the study period.
[b]Group 2 was moved from an enclosure with gravel to an enclosure with grass after 7 months.

given 1 week to adjust to their new environment before resuming observations. Group 2 therefore provided an experimental component to the study, allowing comparison of the same animals in both grass and gravel substrates.

Rhesus macaques in this outdoor colony were managed with a minimal level of disturbance, and individuals of each group were free to interact with one another as they chose. Disturbances within the enclosure were typically limited to daily morning health checks, four round-ups per year to conduct health examinations on all animals and removal of injured or sick animals for medical treatment.

Ten adult females, all 3 years or older, were selected as focal subjects from each group ($n = 70$ females). Focal animals were chosen randomly from three rank categories: high (three per group), middle (four per group), and low (three per group). Females in the top third of the dominance hierarchy were assigned a rank of high, those in the middle third, a rank of middle, and those in the bottom third, a rank of low. For Group 2, the same focal animals were observed in both grass and gravel substrate conditions. Relative dominance ranks were obtained from records of weekly behavioral observations of displacements and aggressive interactions conducted by the behavioral management staff.

The study period was divided into four seasons, the boundaries of which were defined by changes in macaque behavior and weather. Autumn (September–November) was defined by the breeding season. Winter (December–February) was defined by cold temperatures (20–30°F) and frequent rainfall. Spring (March–May) was defined by the birth season. Summer (June–August) was defined by hot (90–110°F) and dry weather.

Behavioral Observations

B.A. Beisner observed each group for 1 day (08:00–17:00 hr) on a rotating schedule, such that each group was observed once every 2 weeks. Once all groups had been observed, the cycle began anew. Each group was observed for a total of 24–26 days during the study period. Each focal animal within a given group was observed once per day, and the order of focal animals was randomly chosen for each day of observation. Focal samples were 20 min in duration, and all occurrences of agonistic interactions involving the focal animal, regardless of whether the focal animal was the initiator or recipient, were recorded and placed into one of three categories: displacements (nonaggressive approach by one animal followed by the other animal moving away), mild aggression (threats and lunges), and intense aggression (chases, bites, and attacks). Agonistic events were considered distinct if they were separated by at least 10 sec of nonaggression or if the focal animal's opponent was different. A total of 1,723 focal samples were completed (grass samples = 1,113, gravel samples = 610). The unit of analysis was the frequency of agonistic interactions per focal sample, which was converted into a rate of frequency per hour.

Statistical Analyses

We analyzed the frequency of agonistic interactions per hour using mixed-effects Poisson regression models [McCullagh & Nelder, 1989]. Models were fit to the data on the following dependent variables: frequency of displacements per hour, frequency of mild aggression per hour, and frequency of intense aggression per hour. Fixed effects included substrate type, female rank and age, season, and group size (a measure of animal density since all groups live in 0.2-ha enclosures). We included random effects for female and group (female nested within group) as well as date of observation in all models to account for potential nonindependence of data from the same focal animal, the same group, or observations from the same day. We ran a series of models for each dependent variable using a stepwise procedure where a single predictor or interaction term was added to the model at each step until all possible models were fit. Akaike's Information Criterion (AIC) scores were used to select the best fit model, i.e. the model with the lowest AIC score. Following the recommendation of Burnham and Anderson [2002], nested models having a difference in AIC score less than or equal to two ($\Delta AIC \leq 2$) were considered equivalent. All analyses were performed using the R statistical computing program [R Development Core Team, 2008].

RESULTS

Displacements

Mean and standard errors of rate of displacements are presented in Table II. For frequency of displacements per hour, the best fit model included fixed effects for substrate, female rank, female age, and group size (compared with the second best fit model: $\Delta AIC = 2$). The rate of displacements was more frequent in enclosures with grass substrate compared with gravel substrate ($\beta = -0.23$, $P = 0.04$), among high-ranking females relative to mid-ranking ($\beta = -0.29$, $P = 0.0009$) but not relative to low-ranking females ($\beta = -0.05$, $P = 0.55$), among younger females ($\beta = -0.034$, $P = 0.0009$), and in larger groups compared with smaller groups ($\beta = 0.006$, $P = 0.002$).

Females in enclosures with grass substrate were 1.5 times more likely to be involved in a displacement than females in enclosures with gravel substrate. The model prediction of rate of displacements was 2.1 and 1.4 for grass and gravel substrates, respectively.

High-ranking females were 1.3 times more likely to be involved in a displacement than mid-ranking females. The model prediction of rate of displacements

TABLE II. Mean (±SE) Rates of Agonistic Interactions Per Hour

Variable	Condition	Mean displace	Mean mild aggression	Mean intense aggression
Substrate	Grass	2.10±0.09	1.37±0.07	0.354±0.038
	Gravel	1.86±0.11	1.25±0.09	0.546±0.056
Season	Autumn[a]	1.99±0.11	1.54±0.10	0.570±0.059
	Winter	2.10±0.17	1.02±0.10	0.366±0.063
	Spring	1.87±0.15	1.02±0.10	0.299±0.058
	Summer	2.14±0.17	1.65±0.15	0.300±0.059
Rank	High	2.23±0.14	1.60±0.11	0.419±0.055
	Mid	1.76±0.11	1.14±0.09	0.399±0.054
	Low	2.07±0.13	1.25±0.09	0.447±0.056
Age	3–5.9 years	2.24±0.17	1.26±0.11	0.500±0.075
	6–10.9 years	2.01±0.10	1.37±0.09	0.433±0.046
	11+ years	1.86±0.12	1.33±0.09	0.353±0.052
Group size	Small (<100)	1.56±0.17	1.58±0.16	0.261±0.062
	Medium (100–150)	1.96±0.11	1.14±0.08	0.504±0.057
	Large (>150)	2.20±0.11	1.42±0.09	0.400±0.043

[a]Breeding season.

was 2.1, 1.6, and 1.7 per hour for high-, mid-, and low-ranking females.

Additionally, displacements were more frequent among younger females than among older females; females were 1.2 times more likely to be involved in a displacement for every 5-year decrease in age.

Finally, displacements were more frequent in larger groups than in smaller groups; females were 1.4 times more likely to be involved in a displacement with every 50-animal increase in group size.

Mild Aggression

Mean and standard errors of rate of mild aggression are presented in Table II. The best fit model for mild aggression included fixed effects for rank, substrate, season, and the interaction term substrate × season (compared with the second best fit model: $\Delta AIC = 4$). Rates of mild aggression per female per hour were significantly higher among high-ranking females compared with mid- and low-ranking females (mid-rank $\beta = -0.34$, $P = 0.001$; low-rank $\beta = -0.23$, $P = 0.03$). High-ranking females were 1.4 and 1.3 times more likely to be involved in mild aggression than were mid- and low-ranking females, respectively (Fig. 1).

Rates of mild aggression per female per hour were significantly higher in gravel substrate compared with grass, but only during spring and summer (main effects: gravel substrate $\beta = -0.28$, $P = 0.04$; spring $\beta = -0.64$, $P < 0.0001$; summer $\beta = -0.09$, $P = 0.55$; winter $\beta = -0.40$, $P = 0.007$; interaction terms: substrate × spring $\beta = 0.66$, $P = 0.009$; substrate × summer $\beta = 0.48$, $P = 0.05$) (Fig. 1). Females in enclosures with gravel were 1.4 and 1.2 times more likely to be involved in mild aggression compared with females in enclosures with grass during spring and summer, respectively. Conversely, females in enclosures with grass were

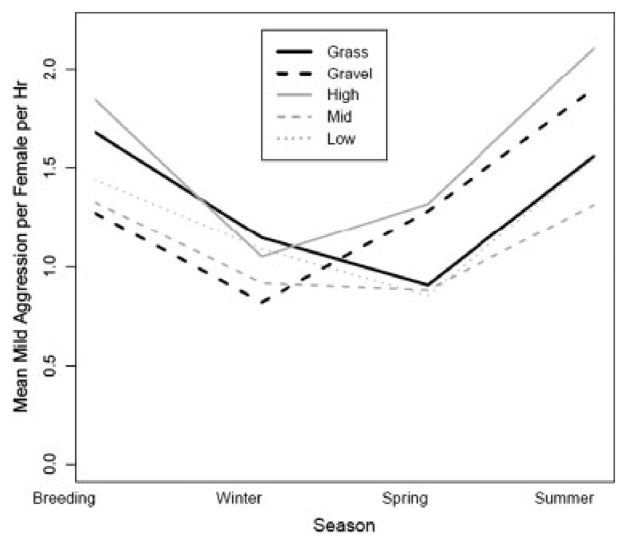

Fig. 1. Mean frequencies of mild aggression per female per hour for grass and gravel substrate as well as high-, middle-, and low-ranking females of all seven groups across all four seasons. During winter and the autumn breeding season, females in grass enclosures were involved in significantly more mild aggression than those in gravel. However, during spring and summer, females in gravel enclosures were involved in significantly more mild aggression than those in grass. High-ranking females were involved in significantly more mild aggression than mid- and low-ranking females. There was no significant difference between mid- and low-ranking females in their rates of mild aggression.

1.3 and 1.4 times more likely to be involved in mild aggression compared with females in enclosures with gravel during the autumn breeding season and winter, respectively.

Intense Aggression

Mean and standard errors of rate of intense aggression are presented in Table II. The best fit model for rates of intense aggression included fixed effects for substrate and season (compared with the second best fit model: $\Delta AIC = 4$). Rates of intense

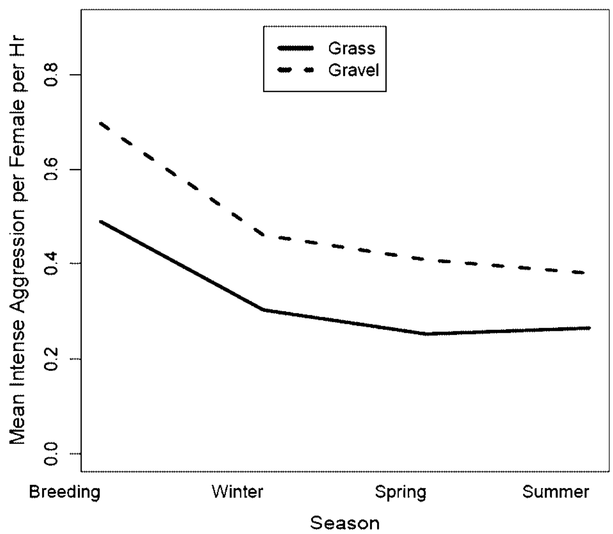

Fig. 2. Mean frequencies of intense aggression per female per hour for grass and gravel substrate enclosures across all four seasons. Females in gravel substrate were involved in more intense aggression than those in grass during all seasons of the year. Intense aggression was significantly more frequent during the autumn breeding season than in all other seasons; there was no significant difference in rate of intense aggression among winter, spring, and summer.

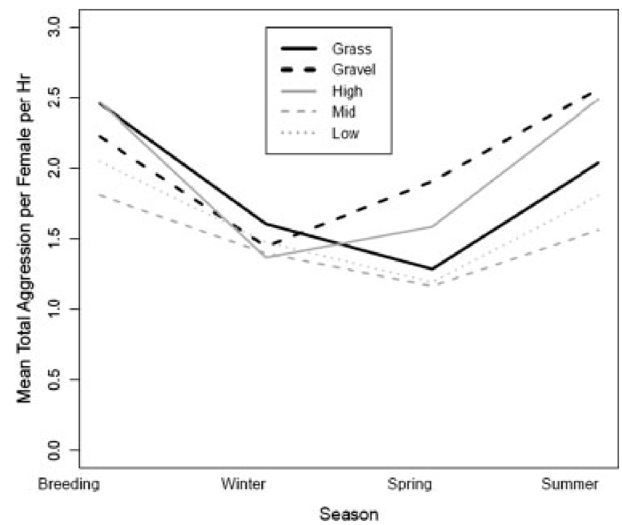

Fig. 3. Mean frequencies of total aggression (mild+intense) per female per hour for grass and gravel substrates as well as high-, middle-, and low-ranking females of all seven groups across all four seasons. Females in gravel substrate were involved in significantly more total aggression during spring and summer, but there was no significant difference in rate of total aggression between the substrates during autumn and winter. High-ranking females were involved in significantly more total aggression than mid-ranking females; this effect is driven by rank differences in mild aggression, as there was no rank affect on intense aggression.

aggression per female per hour were significantly influenced by substrate ($\beta = 0.51$, $P = 0.01$) and season (spring $\beta = -0.63$, $P = 0.002$; summer $\beta = -0.62$, $P = 0.007$; winter $\beta = -0.48$, $P = 0.01$) (Fig. 2). Intense aggression was more common in enclosures with gravel substrate than in enclosures with grass substrate. Females in gravel enclosures were 1.7 times more likely to be involved in intense aggression than females in grass enclosures. Intense aggression was most common during the autumn breeding season. Females were 1.6, 1.8, and 1.9 times more likely to be involved in intense aggression during the breeding season than during winter, summer, and spring, respectively.

Total Aggression

For total aggression, the sum of mild and intense aggression, the best fit model included fixed effects for rank, season, substrate, and the interaction term substrate × season (compared with the second best fit model: $\Delta AIC = 2$). Rates of total aggression per female per hour were significantly higher among high-ranking females compared with mid-ranking females ($\beta = -0.27$, $P = 0.009$) but not with low-ranking females ($\beta = -0.17$, $P = 0.10$) (Fig. 3). Rates of total aggression per female per hour were significantly higher in autumn relative to spring and winter (spring $\beta = -0.66$, $P < 0.0001$; summer $\beta = -0.19$, $P = 0.18$; winter $\beta = -0.43$, $P = 0.0002$) (Fig. 3). Additionally, rates of total aggression per female per hour were significantly higher in gravel substrate only during spring (substrate $\beta = -0.09$, $P = 0.50$; substrate × winter $\beta = 0.01$, $P = 0.95$; substrate × spring $\beta = 0.50$, $P = 0.03$; substrate × summer $\beta = 0.32$, $P = 0.18$).

Experimental Group 2

Group 2 moved from an enclosure with gravel substrate into one with grass substrate half-way through the study. Because seasonality has an effect on agonistic interactions, we limited the analysis to autumn, the only season when Group 2 was observed in both gravel and grass substrate. The influence of ground substrate on agonistic interactions is similar to the overall pattern across groups. Poisson regression models indicate that females in Group 2 were involved in a higher rate of displacements ($\beta = 1.02$, $P = 0.0002$) and a lower rate of intense aggression ($\beta = 1.32$, $P = 0.016$) when in grass substrate (Fig. 4). However, unlike the other groups, there was no significant difference in mild aggression between grass and gravel conditions during the autumn breeding season nor was there a significant rank effect.

DISCUSSION

Rhesus macaques are included in the most despotic grade of macaques [Thierry, 2004]. Among ‘‘despotic’’ macaques, aggression is normal and even necessary for the successful maintenance of the group's social hierarchy as aggression is used by both sexes to establish and reinforce social relationships [Lindburg, 1971]. The frequency or intensity of

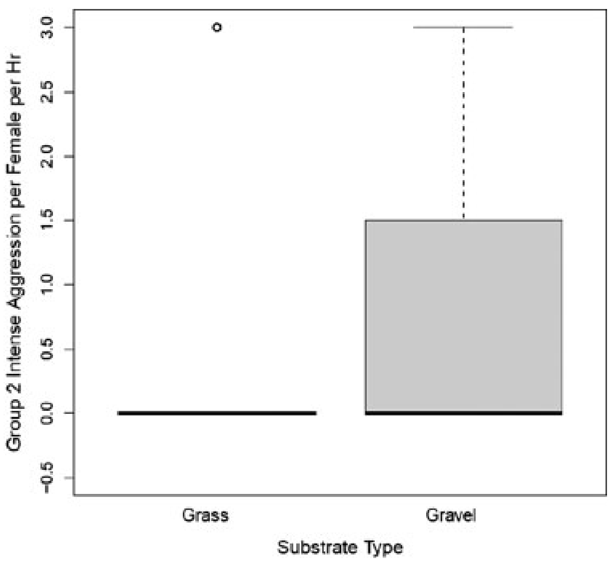

Fig. 4. Frequency of intense aggression per female per hour in Group 2 during two consecutive autumn breeding seasons (2006 and 2007) in gravel substrate and grass substrate, respectively. The black line represents the median, and boxes represent the inter-quartile range. The upper (and lower) whiskers are drawn to the largest (or smallest) data point not lying above the 75th percentile (or below the 25th percentile)+1.5*IQR.

aggression in captivity is often higher than that of wild groups of rhesus macaques [Southwick, 1969]. Intense aggression in captive groups of rhesus is often associated with more wounding and the potential for social overthrow [McCowan et al., 2008; Oates-O'Brien et al., 2010]. In this study, we found that high-ranking females were more likely to be involved in displacements and mild aggression than lower ranking females, which is consistent with the view that high-ranking individuals often act to assert or maintain their high positions. However, intense aggression in our study did not come from high-ranking females asserting their power to maintain their positions in the hierarchy because they were not more involved in intense aggression than other females. Dissociation between rank and more intense aggression is consistent with the view that captivity generates unusually stressful conditions for group-living macaques. Identification of factors that increase intense aggression is thus essential for managers seeking to promote animal health and social stability.

In this study, we found that living in enclosures with gravel ground cover significantly increased intense aggression. Fortunately, this is a factor that can be corrected by managers of captive groups. Reduced rates of intense aggression is one of several interrelated effects that grass substrate has on rhesus behavior. Rhesus macaques in this population have previously been found to spend more time foraging and less time grooming, and to move along more tortuous pathways associated with their foraging efforts when living in enclosures with grass substrate [Beisner & Isbell, 2008, 2009]. Animals living in grass enclosures may have reduced rates of intense aggression because they spend more time foraging [Beisner & Isbell, 2008]. More time spent in other activities suggests that less time will be spent engaged in aggression, but we suggest that this is more than an issue of time budgets. Female competitive behavior in general is thought to be the product of selection favoring agonistic interactions over food as the limiting factor in reproduction [Trivers, 1972; Wrangham, 1980]. Therefore, when conditions favor competition over food, females should engage in agonistic interactions whether they live in the wild or in captivity. Such conditions include certain characteristics of foods, including limited abundance and usurpability. Abundance is more of an issue in wild conditions than in captivity but slower consumption time has been shown in both wild and captive conditions to increase contest competition [Beisner & Isbell, 2008; Chancellor & Isbell, 2008; Gemmill & Gould, 2008; Hanya, 2009; Isbell et al., 1998; Mathy & Isbell, 2001]. In contrast, grass and the arthropods living in grassy environments tend to be nonusurpable resources because they are consumed quickly [Beisner & Isbell, 2008], and foods that are difficult to usurp reduce opportunities for contest competition. We suggest that intense aggression was reduced in groups of rhesus macaques living in enclosures with grass ground cover because grass increases the time animals spend foraging, particularly on smaller food items that provide fewer opportunities for aggressive interactions.

Another factor found to increase the rate of intense aggression significantly in this study was the breeding season. Grass substrate also appears to alleviate the intensity of aggression during this time. A reduction in intense aggression during the breeding season was seen even when the same individuals were moved from an enclosure with gravel to one with grass. Compared with females in gravel enclosures, females in grass enclosures were more likely to use mild aggression than intense aggression during the fall breeding season and winter. Grass substrate also reduced the absolute frequency of both mild and intense aggression during spring and summer, thereby reducing the rate of total aggression during these seasons. We suggest that this reduction occurred because females are occupied more often with new infants, new grass, or both, beginning in the springtime. Although some aggression during the breeding season may be unavoidable, grass substrate can improve the health and well-being of captive groups by reducing the intensity of aggression during the breeding season and the frequency of aggression during other seasons of the year.

The maintenance of grass substrate in outdoor enclosures at the CNPRC is rather straightforward. The grass is watered regularly during the spring, summer, and autumn months of the year (watering during the winter is unnecessary due to sufficient rainfall). Although over-foraging may reduce the grass cover in very large groups, greater than 50% grass coverage has been successfully maintained for many years in enclosures of up to 160 animals. Personal observation suggests that significant reduction or complete loss of grass ground cover occurs when the grass is not watered sufficiently during the summer months and when groups are maintained at a very large group size (160+ animals) for several years, which results in over-foraging.

The potential negative impact of intense aggression on captive social groups of macaques is multifaceted. From a welfare perspective, frequent severe aggression can lead to serious injury, group instability, and social overthrow [Flack et al., 2005; McCowan et al., 2008; Oates-O'Brien et al., 2010], which may increase psychological stress via increased unpredictability [Sapolsky, 1994]. From a management perspective, frequent severe aggression, particularly those events that result in injury, require more frequent implementation of management actions, such as veterinary care, temporary or permanent removal of individuals from the social group, and relocation of these individuals, which demand significant time and resources.

Finally, we found that higher group density did not increase either mild or intense aggression, which contrasts with findings in other captive conditions [Erwin & Erwin, 1976; Judge & DeWaal, 1997]. However, evidence regarding the impact of crowding on aggressive behavior in captive primates is mixed. As our seven study groups were formed between 11 and 30 years before this study, our results are most consistent with the hypothesis that crowding is not problematic for long-standing, stable groups of captive primates, which have had sufficient time to adjust to the crowded conditions [De Waal, 1989]. On the other hand, higher densities did increase the rate of displacements. Although not as dramatic as intense aggression, if displacements occur at rates that are substantially higher than in the wild, they may affect the psychological health, and by extension, eventually the physical health of captive primates. Future research will address this by more directly examining stress in these captive groups.

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