

RESEARCH ARTICLE

Ground Substrate Affects Activity Budgets and Hair Loss in Outdoor Captive Groups of Rhesus Macaques (*Macaca mulatta*)

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How the captive environment influences the behavior of animals is relevant to the well-being of captive animals. Captivity diverges from the natural environment in many ways, and one goal of enrichment practices is to encourage species-typical behavior in these unnatural environments. This study investigated the influence of grass vs. gravel substrate on activity budgets and degree of hair loss in seven groups of captive rhesus macaques housed in outdoor enclosures at the California National Primate Research Center. Groups having grass substrate spent a greater proportion of their time foraging and a smaller proportion of time grooming compared with groups having gravel substrate. Increased time spent grooming in gravel enclosures may have contributed to significantly greater hair loss in those enclosures. A causal relationship between ground substrate on foraging and grooming, and therefore hair loss, is strengthened by similar changes in activity budgets and hair loss in a single group that was moved from gravel to grass substrate halfway through the study. These results add to growing evidence that substrate type in captivity is important to consider because it affects animal well-being. In particular, these results reveal that grass substrate is more effective than gravel in stimulating foraging and reducing allo-grooming to levels that are comparable to wild populations, and enable animals to maintain healthier coats. *Am. J. Primatol.* 70:1160–1168, 2008. © 2008 Wiley-Liss, Inc.

Key words: primates; captive environment; foraging; grooming; colony management; welfare

INTRODUCTION

In the wild, an animal's environment affects its behavior. Abundance and distribution of food can affect group size [Janson & Goldsmith, 1995], dispersal [Isbell, 2004; Packer, 1979], and agonistic interactions [Pruetz & Isbell, 2000; van Schaik, 1989]. Similarly, the captive environment influences the behavior of captive animals. The manner in which behavior is changed by captivity, relative to the wild condition, is important for the welfare of the animals. Furthermore, the quality and external validity of the research on captive animals is contingent upon the well-being of the captive animals [Olsson et al., 2003; Sherwin, 2004].

Foraging Enrichment

Foraging for food is a primary occupation for wild, free-ranging primates, and may take up 40–60% of the day [Altmann & Muruthi, 1988; Goldstein & Richard, 1989]. As a result, foraging enrichment is often used to keep captive animals busy and to encourage foraging behavior. Effective foraging enrichments for primates range from artificial substrates or feeding devices that contain food [Bayne et al., 1992; Novak et al., 1998] to floor litters (e.g., woodchips) and beddings (e.g., straw)

[Blois-Heulin & Jubin, 2004; Byrne & Suomi, 1991]. For example, woodchips increase foraging behavior among captive groups of several primate species, including rhesus macaques (*Macaca mulatta*), a species commonly kept in captivity for scientific study [Chamove et al., 1982]. Similarly, peat floor litter increases time spent foraging in capuchin monkeys (*Cebus capucinus*), but ground corn cob floor litter does not [Ludes & Anderson, 1996].

Foraging enrichments may also improve captive primate welfare by reducing aggression [Boccia, 1989; Chamove et al., 1982], inactivity [Blois-Heulin & Jubin, 2004], and abnormal behavior [Watson, 1992]. Foraging enrichment may also decrease the time primates spend in affiliative social interaction [Byrne & Suomi, 1991]. Imposed foraging tasks may,

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however, have some negative effects. When bonnet macaque (*M. radiata*) mothers experienced variable foraging demand, their infants showed less secure attachment than infants whose mothers experienced a stable, predictable foraging demand [Rosenblum & Andrews, 1991].

When foraging opportunities are unavailable, many captive animals appear to redirect that behavior, sometimes with negative consequences. Increasing foraging opportunities can reduce harmful behaviors. Thus, providing puzzle feeders and grooming boards to captive rhesus macaques reduced hair-pulling among singly housed individuals [Tully et al., 2002; Watson, 1992]. Providing sunflower seeds in woodchip bedding stopped hair-pulling almost entirely in social groups of captive rhesus macaques [Boccia & Hijazi, 1998]. In some studies, removal of foraging enrichment resulted in animals resuming levels of self-directed (i.e., self-groom, hair-pulling) and affiliative (i.e., social contact, allogroom) behaviors they exhibited before receiving enrichment [Blois-Heulin & Jubin, 2004; Byrne & Suomi, 1991; Watson, 1992].

Primates: Wild vs. Captive

A key difference between wild and captive primates is the nature of their food resources. Captive primates are fed large amounts of monkey chow every day, typically in predictable locations, whereas wild primates must search for foods that vary in distribution, abundance, size, time, and visibility. Captive primates are thus expected to spend less time foraging.

Time budgets of wild animals strike a balance among all activities, trading off less important activities in favor of more important ones. A reduction in time spent foraging frees up time to engage in other behaviors such as resting or affiliation. Indeed, time spent foraging may be a limiting factor of female primates' social time [Dunbar, 1992]. Thus, wild macaques that spend more time foraging appear to spend less time grooming than macaques that forage less [Chopra et al., 1992; Kurup & Kumar, 1993; Seth & Seth, 1986; Teas et al., 1980].

Similarly, the time that is freed up from foraging effort in captivity may be taken up by affiliative interactions. Indeed, primates in captivity with extensive leisure time may spend so much time grooming that hair loss results. While there are many factors that may contribute to prevalent hair loss among captive animals (e.g., hormonal variation, skin disease), hair loss owing to over-grooming and hair-pulling have been reported in some captive primate populations [Crockett et al., 2007; Reinhardt et al., 1986].

Grooming and hair-plucking in particular might be expected to increase when foraging opportunities

are lacking because frustrated motivation to forage can be redirected toward inappropriate stimuli, such as the fur of cagemates. Although there is little evidence yet of redirected foraging toward grooming and hair-plucking among primates [Boccia & Hijazi, 1998], several examples exist for birds and other mammals [Beyen et al., 1992; Huber-Eicher & Wechsler, 1998; Meehan et al., 2003].

At the California National Primate Research Center (CNPRC), rhesus macaques living in outdoor enclosures have ground substrate consisting either entirely of gravel and dirt or grass to varying degrees. Grass substrate may enhance the ecological complexity of the captive environment by providing extra foraging opportunities. In particular, grass substrate may serve as foraging enrichment in the same way as floor litters [Blois-Heulin & Jubin, 2004], and may supplement the monkey chow diet because wild macaques feed on grasses [Goldstein & Richard, 1989], and grass habitats are more favorable to arthropods, which are also often eaten by primates.

The focus of this study was to determine how ground substrate affects the activities of rhesus macaques. We predicted that grass substrate would constitute foraging enrichment such that groups with grass substrate would spend more time foraging and less time grooming compared with groups with gravel substrate. We also predicted that hair loss would be more extensive in gravel enclosures because of the increased time spent grooming in those enclosures. Data on activity budgets and hair loss were collected to test these hypotheses.

METHODS

Study Groups

The study was conducted at the CNPRC in Davis, CA, over 171 days (1,557 total hours of observation) during a 14-month period from September 2006 to October 2007. The protocol for this study was approved by the Institutional Animal Care and Use Committee of the University of California, Davis. The subjects of this study were individuals in seven groups (Groups 1, 2, 5, 8, 14, 16, and 18) of rhesus macaques housed in 0.2 ha enclosures (Table I).

Four groups had naturally growing grass in their enclosure (at least 30% grass of the 0.2 ha area) and two groups had gravel/dirt substrate with no grass. Another group (Group 2) began the study in a gravel enclosure and was moved to a grass enclosure (30% grass coverage) after seven months (Table I). This group provides an additional opportunity to compare activity budgets and degree of hair loss in the same animals facing both conditions.

All enclosures were otherwise similar in having ten A-frame houses, multiple suspended barrels and swings, and several perches. Monkey chow was

TABLE I. Characteristics of Study Groups

Group	Group size range	Ground substrate
1	129–156	Grass
2	141–180	Both ^a
5	160–187	Grass
8	156–180	Gravel
14	78–102	Grass
16	122–146	Grass
18	123–158	Gravel

^aGroup 2 was moved from an enclosure with gravel to an enclosure with grass after seven months.

provided to each group at approximately 0700 hr every morning, and again between 1430 and 1530 hr in the afternoon by pouring monkey chow into food hoppers at a cement feeding pad. Monkey chow was typically available throughout the day because groups usually do not eat all of the chow that is given.

Rhesus macaques in this outdoor colony were managed with a minimal level of disturbance, and individuals of each enclosure were free to interact with one another as they chose. Disturbances were usually limited to daily health checks, quarterly health examinations on all animals, and occasionally, removal of injured or ill animals.

Rhesus macaques at the CNPRC lived year-round in stable social groups that are comparable in size to wild rhesus groups (wild group size range: 10–180) [Chopra et al., 1992; Teas et al., 1980]. As the enclosures were outside, the macaques were exposed to natural weather conditions (32–43°C summer high temperatures, –7 to 0°C winter low temperatures, and rain) and local fauna (e.g., ground squirrels, starlings, magpies, crows, and gopher snakes).

Behavioral Observations

Systematic sampling of activities was conducted on animals in all seven enclosures using instantaneous scan samples. Scan samples were collected on all animals two years and older for the following activities: allo-groom, huddle, feed, forage, rest, locomotion, play, and aggression (Table II). For grooming and aggression, both the actor and the recipient of a behavior were noted as participating in that behavior. Auto-grooming was observed very rarely (<1% time budget) and was therefore counted as rest. Occasionally, individuals were engaged in feeding and another activity simultaneously, usually grooming or huddling. In these cases, B. A. B. (who conducted all observations) recorded the behavior as feeding when individuals were at the feeding pad and recorded the other behavior (usually groom or

TABLE II. Operational Definitions for Behaviors

Behavior	Operational definition
Huddle	Sitting in social contact with another animal
Groom	Picking or manipulating another animal's fur or skin with the hands or mouth
Feed	Eating or manipulating monkey chow; drinking water
Forage	Picking through the ground substrate with hands
Rest	Sitting alone; not engaging in the other activity categories
Locomotion	Walking or running along the ground or over suspended surfaces
Play	Rough and tumble wrestling and chasing; play face displayed
Aggression	Bared teeth display, lunge, stare, aggressive scream, slap, bite, push, hit, attack, and chase

huddle) when individuals were greater than 10 m from the feeding pad.

Scan samples were collected every hour, on the hour, from 0800 to 1600 hr in Winter, and from 0800 to 1700 hr in other months. Scan duration varied between 2 and 10 min. Individuals were not identified during scans owing to large group sizes. To reduce the possibility of double-counting individuals, groups were scanned systematically from left to right, and individuals were not counted if it was unclear whether or not they had been counted already. Greater than 70% of all individuals intended for sampling (animals 2 years and older) were counted in all scans.

Each group was observed for one day (0800–1700 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.

Hair Loss

The degree of hair loss of 425 adult and immature females (3 years and older) and 77 adult and immature males (4 years and older) was recorded on a 5-point categorical scale modified from Honess et al. [2005]. The hair loss scale consisted of nine levels: 1–5, including half-scores, where 1 represented perfect coat condition and 5 represented bald or nearly bald condition (Table III).

Hair loss was scored at seven time points, spaced every 45 days, over a 12-month period. All adult and subadult animals were assigned a hair loss score at each of the seven time points, except individuals that were not found during observation hours. Hair loss was scored for an additional month in Fall 2007 for Group 2 in order to compare hair loss scores for the

TABLE III. Definitions of Hair Loss Categories

Hair loss score	Definition
1	Perfect coat condition
1.5	1–2 small patches of fur missing
2	3–4 small patches of fur missing, totaling 2–5 cm ²
2.5	Multiple patches or one large patch of fur missing, involving <25% of body
3	Multiple patches or one large patch of fur missing, involving 25–50% of body
3.5	Generalized alopecia involving 50% of body
4	Generalized alopecia involving >50% of body
4.5	Alopecia involving 75% of body
5	Bald or nearly bald

same animals during the same season (Fall 2006 vs. Fall 2007) on the two different substrates.

Statistical Analyses

Analyses of activity budgets were based on 1,535 scan samples taken over 171 days. For each group, the overall mean proportion of individuals engaged in each activity was calculated by averaging the hourly scan samples over all days observed. Hourly values were weighted equally to control for daily variation in activities. Because hourly scan samples from the same day are not necessarily independent, monthly average proportions were calculated for all activities for each group to reduce the influence of nonindependence on statistical analyses. For each group, the monthly average proportion of individuals engaged in an activity was calculated by averaging all per-scan proportions of the same month for that activity. The monthly average proportion is the unit of analysis for all analyses of variance.

The standard errors for the overall mean proportion of animals engaged in each activity category were calculated using the total number of individuals counted (summed over days and hours of the day) per group as the sample size. Standard errors could also be calculated for the proportion of animals engaged in each activity, rather than using counts of individuals engaged in each activity. Therefore, we also calculated standard errors using a second method that uses the total number of scans (summed over days and hours of the day) per group as the sample size. The two different methods returned standard error values that were nearly identical.

Statistical analyses for Group 2 differed owing to their change in substrate. Group 2 lived in a gravel enclosure from September 2006 through March 2007, was moved to a grass enclosure in April 2007, and remained there until the end of the study in October 2007. Seasonal variation could account for

differences in activity budgets, so monthly average proportions for each activity were calculated for September and October, 2006 and 2007, the only months in the two calendar years that overlapped.

A multiple analysis of variance (MANOVA) test was used to test for overall differences due to substrate. Monthly average proportions of individuals engaged in each activity were treated as the unit of analysis (grass: $n = 63$ months, gravel: $n = 38$ months). For this analysis, the monthly average proportions of individuals engaged in each activity were pooled for all groups having the same substrate. It was necessary to exclude one of the eight behavior categories in the analyses because there are only seven dimensions to a data set with eight linearly dependent categories (i.e., add up to 100%). Play was excluded because we had no specific hypotheses regarding the influence of substrate on play. This MANOVA models the effect of ground substrate on seven of the eight activity categories.

The MANOVA result indicates only when a difference exists among the activity categories between grass and gravel substrates. Additional analyses are required to determine the nature of the effect. Consequently, post hoc univariate analyses of variance (ANOVAs) were carried out on each of the seven activity categories. Finally, 95% confidence intervals were calculated for all mean proportions for each group and activity category to directly observe the effect size. Confidence intervals can detect differences without formal hypothesis testing and were used to compare activity budgets for Group 2 during Fall 2006 and Fall 2007 due to small sample size (grass: $n = 2$ months, gravel: $n = 2$ months).

For the four groups in grass and the two groups in gravel, a Mann–Whitney U -test was used to test for differences in hair loss between substrates using the median hair loss score for each female ($n = 365$) and male ($n = 77$). Group 2 was analyzed separately. A Wilcoxon matched-pairs test was used to test for differences in median hair loss score among animals in Group 2 between grass and gravel substrates (Fall 2006: $n = 60$; Fall 2007: $n = 60$).

RESULTS

Activity Budgets

The overall mean proportion of individuals engaged in foraging in grass cages was more than twice that of individuals in gravel cages, whereas the overall mean proportion of individuals engaged in grooming in grass cages was about half that of individuals in gravel cages (Fig. 1).

The MANOVA result for the effect of substrate on the seven activity categories indicates that significant differences exist between the substrates ($F = 56.75$, $P < 0.0001$). Post hoc univariate ANOVAs revealed that, compared to groups with gravel, a

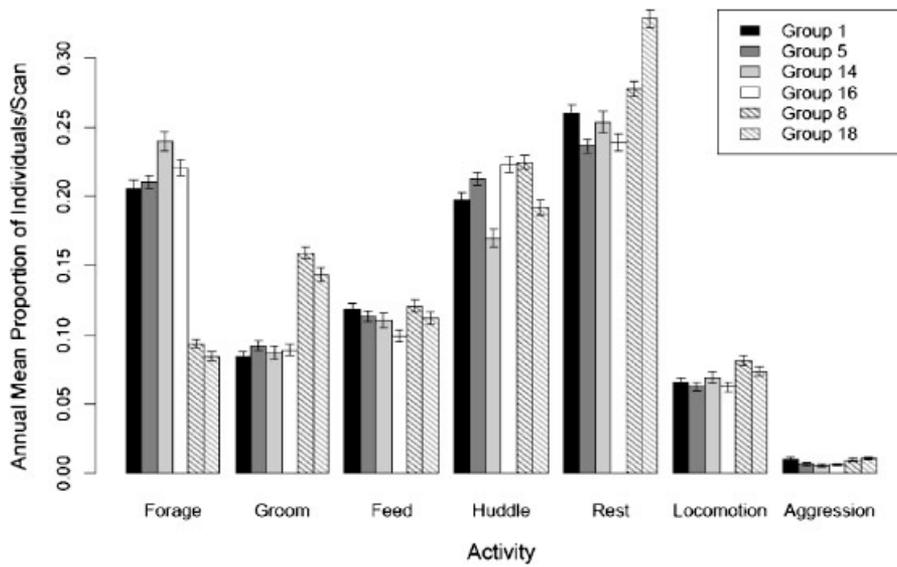


Fig. 1. The mean proportion of individuals engaged in each activity over the 14-month study period is plotted for four grass enclosures (1, 5, 14, and 16, solid bars) and for two gravel enclosures (8, 18, hatched bars). Error bars indicate 95% confidence intervals for each estimate.

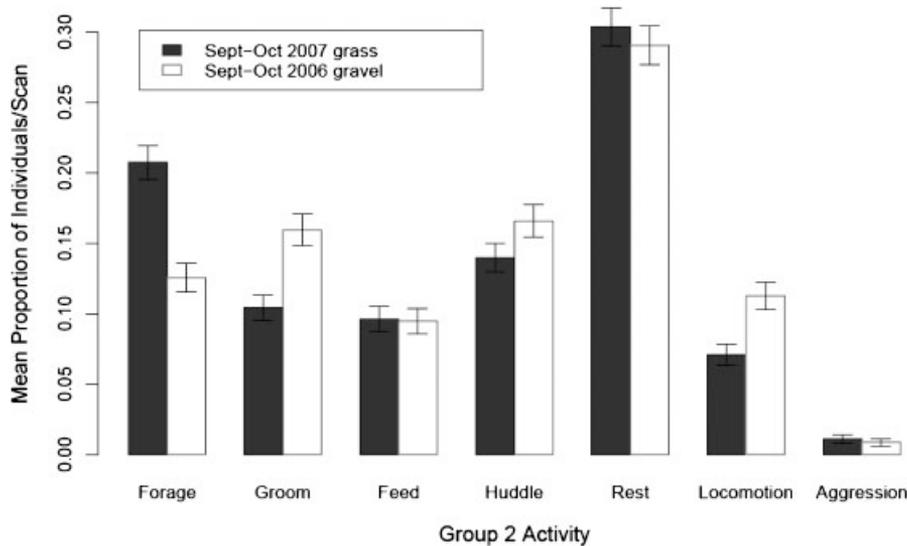


Fig. 2. Group 2 represents a within-group comparison of the influence of grass and gravel substrates on activity budgets. The mean proportion of individuals engaged in each activity is plotted for two time periods: September and October 2006 (gravel), and September and October 2007 (grass). Error bars indicate 95% confidence intervals for each estimate.

greater proportion of individuals foraged in groups with grass ($F = 238.2, P < 0.0001$), but a smaller proportion of individuals groomed ($F = 100.5, P < 0.0001$), rested ($F = 10.6, P = < 0.002$), and moved ($F = 7.36, P = 0.008$). No significant differences were observed between grass and gravel substrate in huddling ($F = 1.73, P = 0.19$), feeding ($F = 0.26, P = 0.61$), or aggression ($F = 0.041, P = 0.84$) (Fig. 1).

The effect sizes for proportion of time spent moving and resting are more equivocal than the clear

separation observed between grass and gravel substrates for proportion of time spent grooming and foraging. The 95% confidence interval of grass Group 14 (6.6–7.3%) overlaps that of gravel Group 18 (7.0–7.7%; Fig. 1). For resting, the 95% confidence interval for gravel Group 8 (27.6–28.4%) is closer to those of grass Groups 1 and 14 (25.4–26.6%) than it is to the other gravel group (32.4–33.6%; Fig. 1).

Animals in Group 2 spent more time foraging and less time grooming and moving after they were moved from an enclosure with gravel to an enclosure

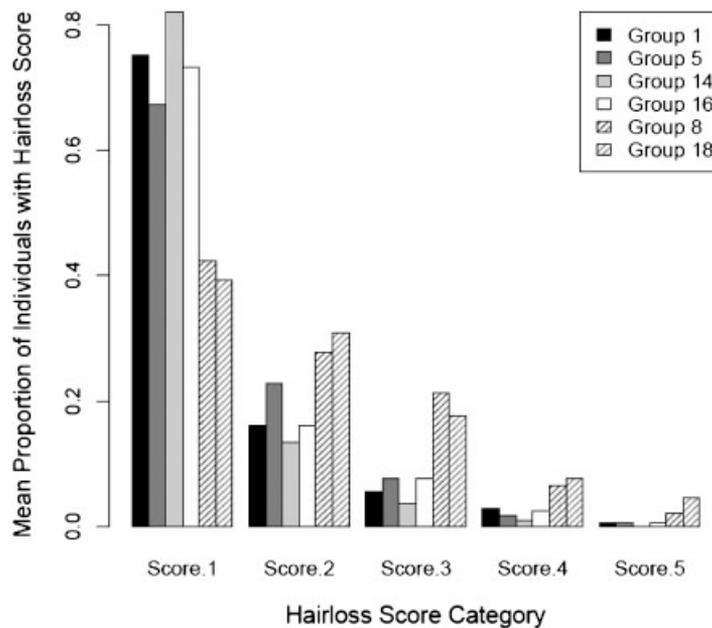


Fig. 3. The mean proportion of individuals having each hair loss score over the 12-month study period for four grass groups (solid bars: 1, 5, 14, 16) and two gravel groups (hatched bars: 8, 18).

with grass. The 95% confidence intervals for proportion of time spent foraging, grooming, and moving show clear separation between Fall 2006 (gravel) and Fall 2007 (grass). However, there was no substantive difference in proportion of time they spent resting, feeding, huddling, or engaged in aggression between Fall 2006 and Fall 2007, as 95% confidence intervals overlap one another (Fig. 2).

Hair Loss

Animals in enclosures with gravel substrate exhibited significantly worse hair loss than those in enclosures with grass among both males and females (females: $n = 365$, $U = 7,045.5$, $P < 0.0001$; males: $n = 77$, $U = 292.5$, $P < 0.0001$; Fig. 3). All four grass groups exhibited better coat condition (mean hair loss score: Group 1 = 1.5, Group 5 = 1.6, Group 14 = 1.3, Group 16 = 1.5) compared with the two gravel groups (Group 8 = 2.1, Group 18 = 2.2). Individuals in Group 2, the group that moved from gravel to grass substrate halfway through the study, also exhibited better coat condition in grass than in gravel (Fall 2006 vs. Fall 2007: $W = 783.5$, $n = 60$ animals, $P = 0.008$).

DISCUSSION

This study investigated the effects of ground substrate on activity budgets among seven captive groups of rhesus macaques. We found a uniform pattern across all groups: macaques living in enclosures with grass spend more time foraging, less

time grooming, and a little less time moving than macaques living in enclosures with gravel.

Captive vs. Wild Activity Budgets

Foraging is a complex behavior that consists of appetitive (goal-seeking) and consummatory (goal-satisfying) phases [Lindburg, 1998], and studies of captive animals suggest that foraging is a highly motivated behavior that is distinct from feeding [Neuringer, 1969; Rushen et al., 1993]. For example, callitrichids chose unshelled over shelled peanuts 80% of the time [Chamove, 1989]. Rhesus macaques preferred to retrieve monkey biscuits from a food puzzle even when the same food was freely available [Reinhardt, 1994]. Foraging is a major activity among wild primates that may be severely reduced in captivity when food is provided ad libitum in easily found locations. This study shows that grass substrate in outdoor enclosures constitutes foraging enrichment similar to artificial foraging devices and floor litters [Blois-Heulin & Jubin, 2004; Lutz & Novak, 1995].

The difference in foraging behavior between grass and gravel substrates suggests that groups with grass substrate exhibit behavior closer to that of wild rhesus groups. Most studies of wild macaques combine feeding and foraging behaviors into the same category (we limit comparisons to studies that used instantaneous scan sampling techniques, the methods employed in this study). Under this definition, wild rhesus monkeys living in forests spend

30–45% of the day feeding or foraging for food, whereas rhesus monkeys living in more urban areas with access to human foods spend about 16–29% of their time feeding or foraging for food [Chopra et al., 1992; Goldstein & Richard, 1989; Malik & Southwick, 1988; Seth & Seth, 1986].

Among captive groups at the CNPRC, groups with grass substrate spent 20–24% of the day foraging plus 9–11% of the day feeding (on monkey chow). Therefore, approximately 30% of the day is spent feeding/foraging, which is at the low end of the range of variation for forest rhesus monkeys and higher than that for urban rhesus monkeys. Groups with gravel substrate spent approximately 20% (9–11% feeding, 8–12% foraging) of the day feeding or foraging, approximately the same as urban rhesus monkeys.

Wild groups typically increase locomotion when they increase foraging effort, as increased daily travel is required to encounter more food patches. This relationship did not hold for these study groups. Groups with grass foraged more and tended to move less, and the reverse was true for groups with gravel. Two factors likely contribute to the observed pattern. First, captive animals cannot travel long distances because the dimensions of the enclosures limit movement. Second, monkeys engaged in foraging behavior often moved short distances while foraging, such that during scan samples, foraging behavior was more likely to be recorded than the brief movement between foraging bouts.

The clear pattern of greater foraging and less grooming on grass compared with gravel substrate suggests that captive rhesus macaques may in part replace grooming with foraging when they live in a foraging enriched environment. This is consistent with previous findings that captive primates with increased foraging demand showed a decrease in social activity [Byrne & Suomi, 1991; Plimpton et al., 1981].

The difference in time spent foraging and grooming between substrates does not appear to be a one-to-one trade-off, however. In spending more time foraging, macaques in grass enclosures also spent less time moving and resting. Nonetheless, the effect size of the difference in locomotion between grass and gravel substrates was small compared with the large difference in grooming, and the effect size of the difference in resting was variable. Although gravel Groups 8 and 18 spent a greater proportion of time resting than the grass groups, no difference in time spent resting was observed between substrates among animals in Group 2, which moved from gravel to grass substrate. Therefore, rhesus groups that forage less appear to replace much of that time with grooming, and some groups may spend additional time resting.

Wild rhesus monkeys also appear to substitute grooming for foraging. Urban rhesus monkeys with

access to human food tend to spend more time grooming (about 9–15% of their time) while forest-dwelling rhesus groups spend about 2–10% of their time grooming [Chopra et al., 1992; Malik & Southwick, 1988; Seth & Seth, 1986]. Captive groups with grass substrate spent approximately 8–9% of the day grooming, at the high end of forest groups and the low end of the range for urban groups, whereas captive groups with gravel substrate spent approximately 14–16% of the day grooming, similar to that of urban groups.

Foraging, Grooming, and Hair Loss in Captivity

Individuals living in enclosures with gravel substrate had significantly poorer coats than individuals living in enclosures with grass, among both males and females. This was also the case for the animals in Group 2 that switched from an enclosure with gravel to one with grass. We suggest that poorer coat condition was partly because of greater time spent grooming by animals in gravel enclosures. Two additional observations support a causal relationship between grooming and hair loss. First, hair-plucking was regularly observed during normal allo-grooming bouts, although no monkey was ever observed to pluck its own fur. Second, animals frequently exhibited bald spots amid an otherwise thick fur coat, a pattern suggestive of hair loss because of directed hair-pulling to localized areas of the body. Better coat condition on grass suggests that greater foraging opportunities allow more appropriate foraging behavior, which leads to less effort spent on grooming and hair-plucking, and therefore, less hair loss. Both foraging and grooming involve similar hand-eye motor skills, and it suggests that fine finger manipulation of objects is a goal-satisfying behavior requiring a certain percentage of their time to simulate the conditions they have faced over evolutionary time.

These results have obvious scientific, management, and welfare implications. Because rhesus macaques are kept in large numbers in captivity for scientific and biomedical research, adding grass substrate to outdoor enclosures may be a relatively simple way to encourage species-typical behavior. Improving the fit between animals and their captive environment will serve three important functions. First, the validity of scientific studies that use rhesus macaques will improve because the animals will live and behave more normally. Second, by increasing the opportunities for rhesus macaques to forage in grass, grooming should decrease and hair loss should be reduced, thus greatly improving their coat condition. Finally, given that foraging takes up a large percentage of time among wild populations, our finding that captive primates benefit in multiple ways from increased foraging opportunities in grass

is likely to be broadly applicable to other captive animals, particularly for other terrestrial and semi-terrestrial primates, i.e., those that often forage on the ground under natural conditions.

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