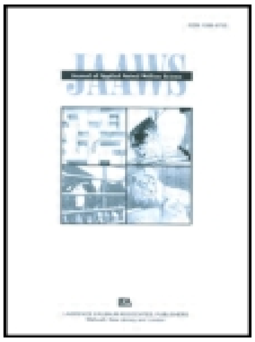

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Primate Location Preference in a Double-Tier Cage: The Effects of Illumination and Cage Height

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Nonhuman primates are frequently housed in double-tier arrangements with significant differences between the environments of the upper and lower-row cages. Although several studies have investigated whether this arrangement alters monkeys' behavior, no studies have addressed the two most notable differences, light and height, individually to determine their relative importance. This experiment examined how rhesus and long-tailed macaques allocated their time between the upper and lower-row cages of a 1-over-1 apartment module under different lighting conditions. In Condition A, monkeys' baseline degree of preference for the upper- and lower-row was tested. In Condition B, the lighting environment was reversed by limiting illumination in the upper-row cage and increasing illumination in the lower-row cage. In both conditions, monkeys spent more time in the upper-row cage, thus indicating a strong preference for elevation regardless of illumination. The amount of time that monkeys spent in the lower-row cage increased by 7% under reversed lighting, but this trend was not significant. These results corroborate the importance of providing captive primates with access to elevated areas.

Due to financial, spatial, and other practical demands, traditional housing for nonhuman primates comprises double-tier arrangements. Despite the prevalence

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of this system, there is considerable debate regarding whether the double-tier cage system compromises the psychological well being of primates housed in the lower row cages. Some researchers have criticized double-tier arrangements because primates housed in lower row cages are unable to perform species-typical vertical escape responses when confronted with threatening situations (Reinhardt & Reinhardt, 1999). In essence, confining primates to the lower row forces them to adopt an exclusively terrestrial lifestyle to which they may not be biologically adapted. Although the upper row of a laboratory cage does not closely mimic an arboreal environment, it does provide nonhuman animals with a resting place above the ground that may accommodate several species-specific behaviors. Studies of the two species investigated here have shown that both species rely on elevated locations for sleeping and refuge from terrestrial predators (Seth, Chopra, & Seth, 2001; Wheatley, 1980). Providing these species access to elevated space in captivity accommodates their natural tendency to utilize their environment's vertical dimension during times of potential danger.

In addition, lighting conditions in lower row cages are considerably darker than those in the upper row. A recent study on the lighting environment of standard double-tier cages confirmed that each of nine sampled locations in the lower row was significantly darker than the same location in the upper row (Schapiro, Stavisky, & Hook, 2000). Because most nonhuman primates are diurnal nonhuman animals, adapted for life in the daylight, it is important to provide them with a well-illuminated environment. Indeed, the few studies that have investigated the effect of illumination on primates suggest that insufficient illumination can have a detrimental effect on monkeys' neuroendocrine systems (Reinhardt, 1997).

These notable differences between the environment of the upper and lower row raise a number of concerns regarding both the psychological well being of animals housed in such an arrangement and the reliability of research conducted using these animals. Although several studies have addressed these concerns, the effects of double-tier housing remain unclear. In some studies on the behavior of captive primates, animals confined to the ground level exhibited more stereotypical behavior than animals with access to elevated space (Draper & Bernstein, 1963; Watson & Shively, 1996). However, other recent investigations of this issue have found no behavioral differences (positive or stereotypical) between animals housed in the upper versus the lower row of double-tier cages (Schapiro & Bloomsmith, 2001; Schapiro et al., 2000). Nevertheless, it is important to note that reports indicating that primates housed in the lower row are not affected behaviorally do not imply that these animals are not adversely affected by their environment in other less apparent ways. For instance, if primates housed in the lower row "perceive the presence of humans above them as particularly threatening" (National Research Council, 1998), they are more likely to have elevated levels of stress hormones than animals in the upper row (Van der Kar, Richardson-Morton, & Rittenhouse, 1991). Similarly, if monkeys housed in the lower row do not receive sufficient illumination, they may develop hormonal irregularities. For example, during a 1-year period in which the illumination of a marmoset colony room was unintentionally maintained at lower than normal levels, subjects showed a pronounced reduction in fecundity. When the lighting levels were corrected, all animals rebounded to normal rates of reproduction (Heger, Merker, & Neubert, 1986). As Reinhardt and Reinhardt (2000) have noted, the uncontrolled physiological variability resulting from differences in illumination could reduce the validity of experimental data across a range of contexts.

The United States Department of Agriculture (1999), the National Research Council (1998), and the European Commission (2002) have all recognized these inadequacies of the double-tier system and have recommended that primates not be restricted to the lower row of double-tier cages. However, this solution is not easily implemented in most research facilities because abandoning the lower row of double-tier cages doubles the space required to house the animals. In addition to increasing space requirements, relocating animals housed in the lower row requires the purchase of costly new cages. Although a shift away from double-tier housing may be a worthwhile enterprise in the long run, it is critical to consider less costly and more easily implemented options that can immediately improve the living conditions for animals in the lower row and help assure reliable data from animals housed in double-tier cages.

In a recent investigation of this issue, Clarence, Scott, Dorris, and Paré (2006) proposed a unique solution for improving the double-tier housing system by incorporating new structures designed for maximal animal welfare (greater access to vertical space), with the extant double-tier system that remained in use for the daily separation and transfer of animals to and from a research laboratory. By implementing such housing refinements that easily interlace with traditional double-tier housing systems, institutions can move toward improved housing arrangements gradually without facing the high costs associated with a complete restructuring of the traditional housing environment. Still, for many institutions the additional space and cost required for this refinement is prohibitive; thus, it remains important to consider other inexpensive alternatives that can improve the double-tier system and bring current housing systems into accord with United States Department of Agriculture (2002) guidelines, which mandate that lighting be uniformly diffused throughout the animal environment.

The aim of this research was to determine how rhesus (*Macaca mulatta)* and long-tailed (*Macaca fascicularis*) macaques respond to the environmental differences between the upper and lower rows of double-tier cages while examining the effect of increasing illumination in the lower row with wall-mounted lighting. Although several studies have investigated whether the overall differences between the upper and lower row cages affect monkeys' behavior

(Schapiro & Bloomsmith, 2001; Schapiro et al., 2000; Watson & Shively, 1996), no studies have addressed the two most notable differences of light and height individually. In this experiment, we pitted the variables of illumination and cage height directly against one another to determine the relative importance of each. By revealing the independent influences of light and height, we hope to inform decisions regarding how best to improve housing practices for laboratory primates.

Across two conditions, rhesus and long-tailed macaques were given simultaneous access to both an upper and lower row cage connected by a transfer tunnel. In Condition A, we measured monkeys' baseline level of preference for the upper and lower row cage of the apparatus. In Condition B, we reversed the lighting environment by limiting illumination in the upper row cage and increasing illumination in the lower row cage. Preference for the upper and lower row of the apparatus was compared between these conditions in order to isolate the influences of illumination and cage height.

We believe that by using location preference as our dependent measure, our data reveal the environmental conditions in which monkeys feel most comfortable. Compared with focusing on the presence or absence of stereotypical behaviors, which may only emerge after significant psychological disturbance, examining preference affords a more sensitive measure of an animal's well being (Clarence et al., 2006; Reinhardt, 1992).

MATERIALS AND METHODS

Subjects and Housing

Ten male rhesus macaques (*Macaca mulatta*), and 4 male long-tailed macaques (*Macaca fascicularis*)—mean ± standard error: 7.14 ± 0.66 years—were tested. All animals were pair-housed in the upper or lower row of double-tier cages (Primate Products, Inc.) and maintained on a 14 hr light–10 hr dark cycle. The number of subjects from each cage level was equal. Subjects were provisioned with Monkey Diet (LabDiet®) and fresh fruit twice daily, and access to water was limited to increase motivation for juice reward in an unrelated study. All procedures were carried out in accordance with an Institutional Animal Care and Use Committee protocol at Duke University.

Procedure

Each subject was tested individually under normal (A) and reversed (B) lighting conditions. The order of conditions was counterbalanced across subjects. In both conditions, monkeys were given simultaneous access, via a stainless steel transfer tunnel, to the top and bottom cages of a 1-over-1 apartment module (Primate Products, Inc., SKU: 1C-A29A). The transfer tunnel was constructed specifically for this experiment and designed such that subjects could pass through the tunnel but not rest comfortably inside it.

In Condition A, the lighting environment of the apartment module was unaltered That is, the upper row cage was better illuminated than the lower row cage. In Condition B, the lighting environment was reversed. Illumination was decreased in the upper row by placing a stainless steel bedding pan on top of the apartment module, thus blocking light from entering through the top of the cage. Illumination was increased in the lower row by mounting a fluorescent lightbulb behind the cage. This bulb was identical to those used for overhead illumination of the testing room. A translucent barrier was placed in front of the bulb to diffuse light evenly in the lower row cage.

To ensure the accuracy of lighting manipulations, illumination measurements were taken using a digital light meter (Center Technology Corp., Item #Q3370) at nine different points within each cage and matched to an array of previously recorded averages for those locations (under normal lighting conditions). Mean illumination levels for each condition are shown in Table 1. A repeated measures ANOVA for Condition (normal illumination, reversed illumination) X Location (top cage, bottom cage) on illumination levels revealed no main effects but yielded a significant interaction indicating that lighting manipulations were successfully matched across experimental conditions, $F_{1,16} = 37.96$, $p < .0001$.

Each subject was tested in each condition for 60 min. Monkeys were habituated to the apparatus for 30 min prior to each session to minimize the influence of preferences for, or aversions to, novelty. The duration of the habitation period was determined after pilot observations that macaques became accustomed to the apparatus within 30 min. Experimental sessions were recorded with a video camera that was positioned on a tripod on the floor approximately 3 m in front of the apparatus. Experimenters remained outside the testing room and were out of the subjects' visual and auditory range during periods of data

TABLE 1
Mean Light Levels at Nine Positions Within the Apparatus (Foot Candles[a])

Condition	*Cage*	*Front Left Top*	*Front Left Bottom*	*Front Right Top*	*Front Right Bottom*	*Back Left Top*	*Back Left Bottom*	*Back Right Top*	*Back Right Bottom*	*Middle*	*Mean*
A	Upper row	16.77	12.22	14.13	11.48	22.5	36.63	35.22	3.16	2.86	17.22
	Lower row	0.32	1.89	0.39	2.55	2.73	1.77	0.9	0.86	1.94	1.48
B	Upper row	0.48	1.35	0.44	1.56	2.46	1.11	1.08	0.79	1.75	1.22
	Lower row	21.00	5.71	21.19	6.87	27.92	21.07	19.4	8.78	9.11	15.67

[a]In Condition A (normal lighting), the upper row cage was better illuminated than the lower row cage at each of nine sampled positions. In Condition B, the normal lighting environment was reversed and the lower row cage was better illuminated than the upper row cage at all nine positions.

collection. To prevent social factors from influencing behavior, subjects were tested individually, and the normally transparent side doors of the experimental apparatus were covered with opaque paper. In order to minimize the influence of other extraneous variables, all food, water, and enrichment devices were removed from the apparatus prior to testing. All test sessions were conducted on weekend afternoons when the colony room was used exclusively for this experiment.

RESULTS

Video recordings were scored for the percentage of time that animals spent at each level of the apparatus. A repeated measures ANOVA for Condition (normal illumination, reversed illumination) X Location (top cage, bottom cage) revealed a main effect of location, $F_{1,26} = 19.01$, $p < .001$ (Figure 1). Specifically, monkeys exhibited a strong preference for the upper row, spending an average of 68% of their time in the top cage across conditions. Although the average amount of time spent in the lower row of the apparatus was 7% greater when the lower row had supplemental illumination, the interaction was not significant $F_{1,26} = 0.75$, $p = .39$.

A monkey's normal housing location did not influence his location preference during the experiment. A factorial ANOVA with the factors of Normal Housing Location (top cage, bottom cage) X Condition (normal illumination, reversed

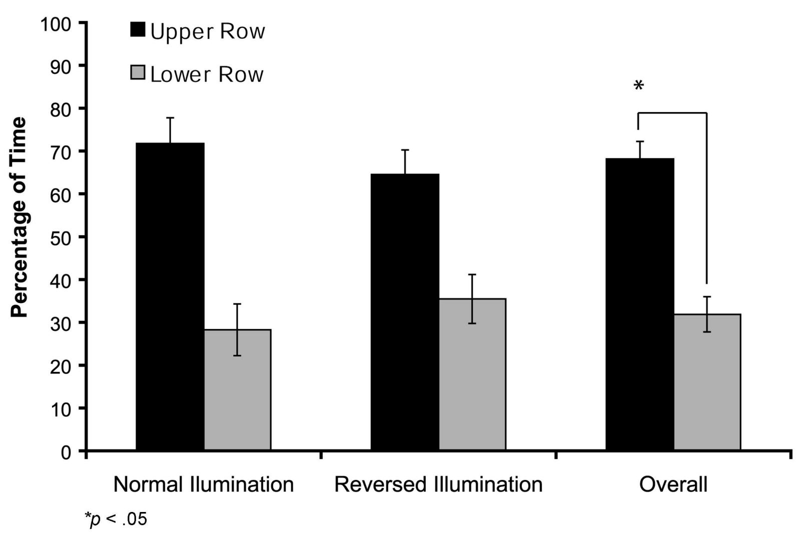

FIGURE 1 Mean percentage of time in the upper and lower row of apparatus.

illumination) on the percentage of time at each level of the apparatus revealed no main effects or interaction ($ps > .05$), indicating that previous housing location did not influence location preference. Finally, a factorial ANOVA with the factors of Species (rhesus, long-tailed) X Condition (normal illumination, reversed illumination) on the percentage of time at each level of the apparatus revealed no main effects or interaction ($ps > .05$), indicating no differences between the two species tested.

DISCUSSION

Across conditions, monkeys showed a strong preference for the upper row of a standard double-tier cage. This result is consistent with several other studies that have documented macaques' preference for elevation in other contexts (Bernstein & Draper, 1964; Clarence et al., 2006; Reinhardt, 1992; Rosenblum, Kaufman, & Stynes, 1964). Preference for the upper row cage decreased only marginally when this area was darkened and better illumination was available in the lower row. When pitted against one another, macaques found access to elevated space far more important than access to light. Because rhesus and long-tailed macaques both utilize the arboreal dimension of their environment for sleep, rest, and protection from terrestrial predators (Seth, Chopra, & Seth, 2001; Wheatley, 1980), it is not surprising that these animals prefer to occupy elevated space in captive environments. By providing these animals with cages that afford access to high-resting surfaces, researchers can promote healthy species-typical behavior.

Our results corroborate the importance of housing macaques in the upper row of double-tier cages whenever possible. If financial or spatial constraints require that some animals be housed in the lower row of double-tier cages, we suggest providing these animals with regular access to a multilevel activity module. In our colony room, one activity module is often shared by two pairs of macaques. Every afternoon we rotate which monkeys have access to the activity module such that each monkey has access to the unit for 12 hr daily. This arrangement requires only half the space that would be needed to house all macaques in the upper row yet still provides each animal with daily access to elevated areas.

Although monkeys did not spend significantly more time in the lower row cage during periods of reversed lighting, we cannot conclude that well-illuminated cages are not important to captive macaques. All animals in this experiment were tested without access to social partners, food, or enrichment devices; this may have eliminated many opportunities to exploit the benefits of a well-illuminated cage. We suspect that illumination is most likely to be important to macaques during grooming, foraging, and visual inspection of manipulanda. This hypothesis is supported by previous research indicating that macaque location preference is often guided by the time of day and the activities typically performed at that time (e.g., grooming; Reinhardt, 1992). It is also possible that access to vertical space is so important to macaques that it overshadows secondary preferences for illumination. Future research could examine these possibilities by investigating how macaques allocate their time when tested with social partners, manipulanda, or horizontally adjacent cages that differ in illumination.

CONCLUSION

The results of this study demonstrate the importance of providing captive macaques with access to elevated space. Our data also indicate that the illumination of lower row cages can easily be increased to match that of upper row cages with the installation of wall-mounted lights that illuminate lower row cages from behind. This housing refinement exemplifies a practical and inexpensive solution for ensuring uniform illumination as mandated by the United States Department of Agriculture (2002). In addition to potentially increasing the quality of life for animals housed in the lower row, increasing illumination in the lower row reduces variability in the research environment that, in turn, may reduce the number of animals required for research.

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