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Response to novel housing in two groups of captive tufted capuchin monkeys (*Cebus apella*)

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Abstract The influence of age, maternal status, and the presence of a group male on use of space was assessed in two groups of captive tufted capuchin monkeys that underwent a move from indoor housing to a larger outdoor facility. Both groups originally contained two adult males, but only one group retained a male after the move. Following the move, mothers spent less time on the ground when carrying their infants than they did when not carrying their infants. In the group with no male (1) individuals decreased time spent on the ground relative to pre-move levels, whereas no such difference was noted in the group with the male; (2) females spent more time carrying their infants than did females in the group with a male. In the group with the adult male, juveniles spent less time on the ground than did non-mother adult females, whereas no difference had existed prior to the move. Grooming rates dropped from pre-move to post-move, but the mean number of partners with which each animal was in contact increased. Measures of social behavior varied across post-move observation periods inversely to time spent on the ground. These results are consistent with the view that an individual's relative vulnerability influences behavioral conservatism in novel environments, and suggests a relatively profound role for males in promoting exploration of new space in this species.

Keywords Use of space · *Cebus apella* · Novel environment · Stress · Predation

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Captive primates often face moves to novel housing when new facilities are built or individuals are transferred for breeding purposes. Experimental data indicate that exposure to novel environments can be a powerful stressor, producing marked increases in blood cortisol and signs of behavioral agitation (e.g., Hennessy 1984; Jordan et al. 1985). However, wild primates also move into novel environments, such as when an animal emigrates from his or her natal group or a group splinters. This suggests that neophobia does not completely inhibit exploration of new environments, and raises the question of what factors influence reactions to new environments. An understanding of these factors may be beneficial in easing transitions for captive primates during moves.

Age might be a factor influencing response to novel housing. Juvenile capuchins are found on the ground less frequently and generally appear more risk-aversive in their use of space than other age–sex classes (Fragaszy 1990; Rose 1994). This might reflect an anti-predation adaptation given juveniles' relative vulnerability, and we might therefore predict greater neophobia early in life. However, other studies have indicated that attraction to novel foods and objects peaks during the juvenile years (Menzel and Menzel 1979 for marmosets, *Saguinus fuscicollis*; Kummer and Goodall 1985; Visalberghi 1988, for tufted capuchins, *Cebus apella*). It is not clear whether this attraction to novelty generalizes to novel environments, and if juveniles should therefore be more or less exploratory in a novel environment than other age–sex classes.

Maternal status might also affect responses to novel housing. Fragaszy (1990) reported that capuchin mothers carrying infants tend, like juveniles, to avoid the ground and behave in a risk-avoidant fashion. Risk-avoidant behavior by mothers may be related to the physiological states associated with lactation, in which case we would expect mothers to move cautiously whether or not they are carrying their infant. An alternative, though not mutually exclusive, suggestion is that females carrying infants are compromised if they must move rapidly, such as when escaping from a predator. Infants represent a significant weight burden for the carrier: a capuchin infant weighs approximately 10% of the mother's non-pregnant weight at birth and grows rapidly thereafter (Fragaszy and Adams-Curtis 1998). If perception of compromised mobility motivates caution, we would specifically expect individuals carrying an infant to be more cautious about moving in unfamiliar spaces.

The presence or absence of adult males might also affect group members' responses to novel environments. Capuchin males spend more time vigilant (looking outward and upward) than do females in natural settings (van Schaik and van Noordwijk 1989; Fragaszy 1990; Rose and Fedigan 1995), and have been reported to be the first to detect a model predator (Van Schaik and van Noordwijk 1989). Thus, it may be that the presence of an adult male lends a sense of security to other group members, and they will be more at ease in a novel environment with a male present than without a male present.

The current study took advantage of a planned move of two groups of tufted capuchin monkeys (*C. apella*) to new housing. At the time of the move, most of the adult males were removed from the groups as part of a breeding transfer with another facility. For the first several weeks at the new facility, one group had no adult males and the other had only one adult male. We examined the influence of age, maternal status, and the presence of a group male on the monkeys' response to the new environment.

Time spent on the ground constituted our primary dependent measure. Capuchins, like many primates, avoid moving on the ground in less familiar areas or when conditions are uncertain (Fragaszy 1990). When faced with threats in captivity (e.g., capture for husbandry purposes), capuchins tend to climb to the highest possible point of their enclosure (personal observation). Thus, capuchins' tendency to move about on the ground would seem to be a good indicator of their comfort in their surroundings. Corroborating the validity of this measure, Vitale et al. (1991) reported that tufted capuchins that were exposed to a snake model increased their use of the floor (where the model was placed) across the exposures, and their alarm vocalizations and other behavioral indicators of fear decreased during this time.

We also performed exploratory analyses on the percent of time animals spent on the ground as a function of time in the novel enclosure, and the percent of time animals spent in close proximity or body contact and grooming prior to and following the move. Individuals from various species of monkey have been demonstrated to show increased affiliative behavior when exposed to stressors such as novel environments (e.g., Jordan et al. 1985); alternatively, in a new environment, increased vigilance may preclude engaging in normal amounts of social activities. These social behavior measures, then, may provide some insights into the animals' adjustment to their new surroundings.

Methods

Subjects

Subjects comprised two groups of tufted capuchin monkeys (*C. apella*). One group (hereafter the "MG" for "male's group") contained one adult male (aged approximately 35 years), 12 adult females (aged 6 years and older), four juvenile females (age range: 34–69 months),[1] and seven dependent infants (less than 1 year old). The other group (hereafter the "AFG" for "all-female group") contained ten adult females, five juvenile females (age range: 23–53 months), and seven dependent infants. Adult females with dependent infants were classed as "mothers" (MG: $n=7$; AFG: $n=7$); mothers included primarily multiparous females, although two mothers in the AFG and one in the MG were primiparous. Non-mothers (MG: $n=5$; AFG: $n=3$) included both nulliparous females (two of three non-mothers in the AFG, none in the MG) and mothers of juvenile or adult offspring.

Prior to the move, the MG had contained one additional adult male, and the AFG had contained two adult males. These additional males were removed from the groups during the move as part of an exchange of breeding males with another facility. Data were collected for the current study before new males were introduced to the groups. Prior to the move, the groups had been intact, save for births and culling, for a period of 5 years. All individuals were born in captivity with the exception of the one adult male, who was wild caught as a young adult.

Housing/apparatus

For the 5 years prior to the move to novel housing the groups had been housed in exclusively indoor enclosures on the campus of the University of Georgia in Athens, GA. Each group's enclosure consisted of two rooms, each measuring 4.8×2.33×2.25 m, connected by a small opening (0.5×0.5 m). The rooms were furnished with perches, Prima-hedrons (Primate Products), and bedding material.

In November 1996 the groups were released into adjacent enclosures at LABS of Virginia in Yemmassee, SC. Each enclosure consisted of a large outdoor corral (18.3×12.2 m) with a smaller indoor area attached. Indoor and outdoor areas were divided by a guillotine door located close to ground level. Outdoor enclosures contained four multi-platformed (one to three levels) wooden structures. The structures were connected by a series of double wooden beams, with the highest beam approximately 1.5 m off the ground, and the lowest

[1] Due to an oversight during pre-move data collection, pre-move data were not collected for the youngest juvenile in the MG. This juvenile's data were thus excluded from all analyses.

approximately 0.5 m off the ground. The ground of the outdoor enclosures was grass, and there was no cover on the enclosures.

At both the University of Georgia and the LABS sites animals were fed twice daily on a diet of commercial monkey chow and had access to water ad libitum. While at the University of Georgia the animals were additionally fed fresh fruit once daily. The food at LABS was placed in large feeding bins found on the first level of one or two (depending on the group) of the structures in each group's enclosure. The food at the University of Georgia was placed on the floor of each group's enclosure.

Procedure

The data reported here were collected using a scan sampling technique. Pre-move data were collected according to the following protocol. Each adult and juvenile[1] in a given group was located in a set order, and data on that animal were recorded. When each animal was located the observer recorded its location in the enclosure, whether this was on or off the ground, the identities of any grooming partners, and the identities of animals in body contact or close proximity (touching distance). Subjects were listed as having five partners if they were in a large huddle of animals, based on an estimate of how many partners an animal could have in close proximity or body contact, and scored as having two partners if in proximity to or contact with an animal carrying an infant. If every animal in a group was located within 5 min, the observer waited until 5 min had passed from the start of the current scan before beginning the next scan. This rule was to ensure that samples of each animal's behavior were at least 5 min apart and thus relatively independent. During data collection a continuous record of aggression (reported elsewhere) was also kept.

Post-move data were collected according to a protocol identical to that just described for the pre-move data, with the exception that carrying of infants was added to the list of behaviors recorded during each scan. Because each group now had access to both an indoor and an outdoor enclosure, we also followed the rule that if less than 50% of a group was visible outside, data collection for that group was suspended until more animals entered the outdoor area. This relatively arbitrary rule was set to maximize the data collected; 100% subject visibility was too high a criterion, as some animals inevitably spent time in their indoor enclosure. Data collection was suspended based on this rule on five occasions (once per group during the second data collection period, and three times in the AFG during the final data collection period; see below for dates of data collection), during which data were collected on the other group. On the first day of data collection only, animals in the AFG were locked out of the indoor enclosure. This was done because animals in this group were initially hesitant to remain in the outdoor area, and thus data could not have otherwise been collected.

Pre-move data were collected during three time periods: on 10 days between May 9 and June 6, on seven days between June 26 and July 23, and on 6 days in September 1996. Between 7 and 12 scans were collected per group per day, and total observation times for each period were 400, 300, and 300 min for the MG and 370, 330, and 300 min for the AFG. The groups arrived at the LABS site on 22 November 1996 and were released into the indoor portion of their new enclosures. On 23 November each group was given free access to either its indoor or outdoor enclosure for approximately 1 h before being locked into the indoor enclosure for the night. Post-move data were then collected according to the current protocol during three periods, each lasting two to three days: 24–26 November, 30 November–1 December, and 14–15 December 1996. Data collection was aborted early during the second post-move period due to rain on 1 December. The attempt was made to obtain a total of 16 scan samples on each group during each day of post-move data collection, alternating eight scans on one group, then eight on the other. Alternating observations minimized a time confound in comparing the two groups. Actual number of scans obtained varied per individual, as all animals were not visible during all scans. Total observation time varied per observation period due to the differing length of time it took to obtain the desired number of scans, and due to the early termination of data collection during the second observation period. Observation times for the first, second, and third sampling periods, respectively, were 314, 85, and 209 min for the MG, and 210, 95, and 156 min for the AFG. All data collection sessions (pre-move and post-move) commenced between 9:30 a.m. and 12 p.m.

Pre-move data were collected by Matheson; post-move data were collected by Matheson and Fragaszy during the first post-move period and by Matheson thereafter. Interobserver reliabilities (percent agreement) were calculated based on the first period's data; reliabilities were 94% for animal location, 96% for carrying, and 98% for close proximity/body contact and grooming.

The number of scans in which each individual was found on the ground was converted to a percentage of scans in which that individual was visible. Parametric statistical analyses were used when possible; nonparametric statistical analyses were used when sample sizes for the specific comparisons were lower than ten, as this compromises the normality assumption of parametric statistics.

Results

Age as a factor

Following the move, juveniles in the MG, but not the AFG, spent a significantly lower percent of their time on the ground than did non-mother adult females (MG: 17.2% for juveniles vs. 36.3% for non-mother adults, Mann-Whitney U test: $U=0$, $n_1=3$, $n_2=5$, $P<0.02$; AFG: 8.7% for juveniles vs. 14.8% for non-mother adults, $U=6$, $n_1=5$, $n_2=3$, NS). Prior to the move to novel housing, no significant differences had been found between juveniles and non-mother adults in percent of time spent on the ground (MG: 27.9% for juveniles vs. 23.5% for non-mother adults, $U=5$, $n_1=3$, $n_2=5$, NS; AFG: 24.3% for juveniles vs. 40.7% for non-mother adults, $U=1$, $n_1=5$, $n_2=3$, NS). We compared juveniles to adult females with no dependent infants because maternal status was one of the factors expected to influence females' behavior.

No significant correlation was found between juveniles' age in months and the percent of time that they spent on the ground following the move (Spearman $\rho=0.699$, $n=8$, NS), or prior to the move (Spearman $\rho=0.565$, $n=8$, NS). Juveniles from both groups were combined for the purposes of these analyses because keeping the groups separate would have resulted in sample sizes that were too small to analyze statistically.

Maternal status

Following the move, no significant differences were noted between mothers and non-mothers in time spent on the ground, although all mothers spent less time on the ground than did non-mothers (MG: 29.0% for mothers vs. 36.3% for non-mothers, $U=7$, $n_1=7$, $n_2=5$, NS; AFG: 10.3% for mothers vs. 14.8% for non-mothers, $U=6$, $n_1=7$, $n_2=3$, NS). Prior to the move, mothers in the MG spent *more* time on the ground than did non-mother adult females, although the difference was not significant (MG: 38.6% for mothers vs. 23.5% for non-mothers, $U=6$, $n_1=7$, $n_2=5$, NS; AFG: 29.8% for mothers vs. 40.7% for non-mothers, $U=4$, $n_1=7$, $n_2=3$, NS).

Following the move, mothers spent a greater percent of their time on the ground when they were not carrying their infants, as compared to when they were carrying infants (MG: 32.8% when not carrying vs. 8.1% when carrying, Wilcoxon t-test: $T=1$, $n=7$, $P<0.05$; AFG: 13.1% when not carrying vs. 2.1% when carrying, $T=0$, ties = 1, $n=6$, $P<0.05$). Eight out of the 14 mothers (four in each group) in fact spent 0% of their time on the ground while carrying, whereas only one mother spent 0% of her time on the ground when not carrying. Furthermore, mothers in the AFG spent more time carrying infants than did mothers in the MG (52.6 vs. 19.9%, $U=4$, $n_1=7$, $n_2=7$, $P<0.01$). Carrying was not recorded during pre-move data collection.

Effect of the male

The MG did not show a significant decrease in time spent on the ground when they moved to the new enclosure, whereas the AFG (the group without the male) did. There was a significant main effect of move condition (pre-move versus post-move) and a significant interaction between move condition and group (MG or AFG) on the time animals spent on the ground (two-way ANOVA: $F_{(1, 28)}=13.882$, $P=0.001$, $\eta^2=0.331$ and $F_{(1,28)}=8.757$, $P=0.006$, $\eta^2=0.238$, respectively). Examination of confidence intervals revealed that it was the AFG's post-move mean that was significantly lower than the other three, which did not differ from each other.

Exploratory analyses

A significant quadratic trend was evident for both groups' time spent on the ground across post-move periods (trend analyzes: MG: $F_{(1,14)}=15.461$, $P=0.002$, $\eta^2=0.525$; AFG: $F_{(1,14)}=7.545$, $P=0.016$, $\eta^2=0.350$). Pre-move data did not differ significantly across time periods, and were thus pooled for the purposes of comparison with post-move time periods. Pairwise comparisons using the Bonferroni correction revealed that the AFG spent significantly less time on the ground during all three post-move periods than during the pre-move period ($P=0.000$, 0.013, and 0.001, respectively), and significantly more time on the ground during the second post-move observation period than during the first ($P=0.017$). The only significant contrast in the MG indicated that they spent significantly more time on the ground during the second post-move period than during the first ($P=0.001$) (see Fig. 1).

The MG, but not the AFG, showed significant variability in grooming across pre-move observation periods (chi-square test: MG: $\chi^2=6.16$, d.f. = 2, $P<0.05$; AFG: $\chi^2=0.8104$, d.f. = 2, NS), as well as post-move observation periods (MG: $\chi^2=9.4062$, d.f. = 2, $P<0.01$; AFG frequencies were too low to analyze by period). However, rates of grooming were lower for both groups across all post-move periods compared with all pre-move periods (see Fig. 2), and comparisons of pooled pre-move and post-move frequencies were significant (MG: $\chi^2=27.62$, d.f. = 1, $P<0.005$; AFG: $\chi^2=19.54$, d.f. = 1, $P<0.005$). For these analyses, frequency of grooming for each condition was compared to expected frequencies based on the relative number of scans taken

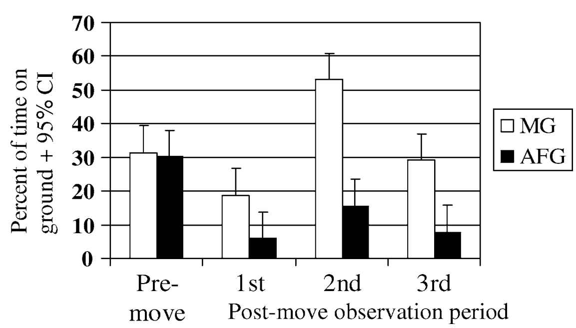

Fig. 1 The all-female group (*AFG*) spent significantly less time on the ground than the male's group (*MG*) following the move to novel housing

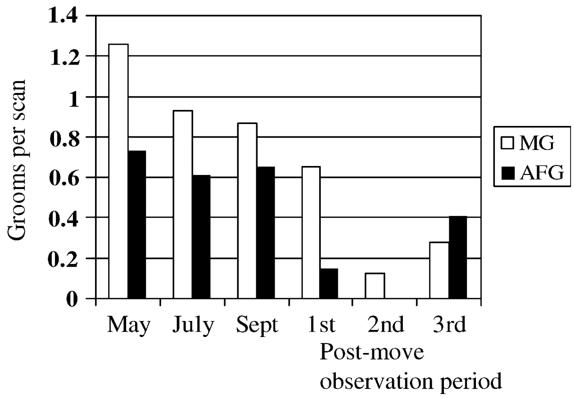

Fig. 2 The number of grooming bouts per scan was significantly lower following the move to novel housing (*AFG* all-female group, *MG* male's group)

during each observation period; we display the data descriptively as grooming bouts per scan for ease of comparison. Grooming bouts that continued across consecutive scans were only counted as one bout.

The mean number of partners each animal had in close proximity or contact did not vary significantly across pre-move observation periods, but did differ across post-move observation periods. Pre-move data were thus pooled, and there was a significant main effect of move condition (pre-move, first, second, third post-move) but no interaction between move condition and group ($F_{(3,84)} = 31.772$, $P < 0.001$, $\eta^2 = 0.528$, and $F_{(3,84)} < 1$, respectively). Pairwise comparisons using the Bonferroni correction indicated that animals had a significantly greater mean number of partners in close proximity or contact during the first and third post-move observation periods than during the pre-move condition or the second post-move observation period (all $P = 0.000$; see Fig. 3).

Discussion

Our current data indicate that age may impact use of novel space: in both groups, juveniles spent less time on the ground compared with non-mother adult females.

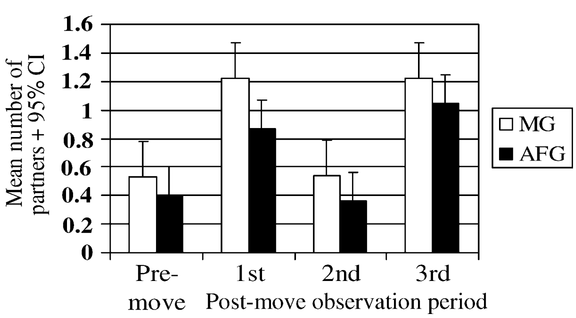

Fig. 3 Mean number of partners in close proximity or body contact increased significantly in the 1st and 3rd sampling periods following the move to novel housing (*AFG* all-female group, *MG* male's group)

Although the difference was not significant in the AFG, this can perhaps be accounted for by the relatively low amount of time spent on the ground by this group as a whole; the direction of the difference is at least consistent with the MG. It appears that juveniles do not have the same tendency to explore novel spaces as they do to explore novel objects and foods as reported by other authors (Menzel and Menzel 1979; Kummer and Goodall 1985; Visalberghi 1988). Our data instead suggest that juveniles might be more cautious in novel spaces, as would be predicted based on their relative vulnerability to predation.

Our data also suggest an influence of maternal status on response to novel housing, at least in terms of the presence of an infant. Following the move, mothers were less likely to be on the ground while they carried their infants than when they were not carrying them. Infant capuchins routinely ride on animals other than the mother (Fragaszy et al. 1991); it would be an easy matter for a mother to wait to go to the ground until after her infant had dismounted or moved to another carrier. Mothers of young infants did not spend less time on the ground in general than other females, suggesting that an infant's presence may be the main factor that deters mothers from going to the ground, although a contribution of mothers' physiological state cannot be ruled out from these data.

The AFG spent consistently less time on the ground during all post-move observation periods, both compared to the MG and to AFG's own pre-move data. Females in the group seemed considerably more hesitant to leave the indoor enclosure and also spent a significantly greater amount of time carrying their infants than did mothers in the MG. These findings are at least consistent with the idea that the females in the AFG perceived the new setting as more threatening.

Animals in the MG did not spend significantly less time on the ground following the move to novel space, and in fact they significantly *increased* the time they spent on the ground from the first to the second post-move period. While it is impossible to generalize from one group, this finding suggests a relatively profound role for males in enabling the use of novel space by other members of their group. Consistent with this idea, it was the male in this group who first exited the indoor compound, and he was quickly followed by most of the group's females. Van Schaik and van Noordwijk (1989) reported that wild adult male tufted capuchins lead the group during travel, and place themselves between predators and the rest of the group. Their protector role may be especially meaningful to other members of the group in a novel environment. Alternative explanations cannot be discounted however. For example, the AFG group may have experienced a relatively greater disruption by virtue of having both of their males removed, and thus may have experienced the move as more stressful in general.

All animals groomed less frequently following the move, but had a greater average number of partners in close proximity or contact (at least on the first and third post-move observation periods). Grooming involves attention focused on another individual as opposed to focused on potential predators; the drop in grooming rates may therefore have reflected greater vigilance in the new space. Having partners in contact, conversely, increases the chances of predator detection by increasing the number of eyes to potentially spot a threat. These changes, then, are consistent with predation-avoidance strategies (Boinski et al. 2000). Spending time in proximity or contact has also been noted to reduce captive primates' physiological and behavioral signs of stress in novel environments (Hennessey 1984; Jordan et al. 1985).

Descriptively, group cohesion seemed greater in the MG: animals were frequently noted to form large congregations that involved the adult male and most other group members. Such mass huddles were never observed in the AFG. This perhaps reflects a role of the male in promoting group cohesion; if so, this would be another mechanism by which males' presence serves to protect their group. However, we cannot discount differences between the groups in the perceived stress of the move.

Both the time spent on the ground and social behavior varied across post-move data collection periods, though not in a linear way. Increasing familiarity with the new enclosure can therefore not account for this variation. It is possible that temperature differences across observation periods contributed to the variability: subjectively, temperatures during the second observation period—when social contact and grooming were low and time on the ground was high—seemed cooler, and this was the observation period during which data collection was terminated early due to rain. We unfortunately did not record temperature data, and therefore can neither support nor refute its impact. However, if temperatures were significantly cooler during the second observation period, one would expect that this would cause greater social contact rather than the decrease we observed.

It is perhaps meaningful that time spent on the ground varied inversely with the various social behavior measures: time on the ground was highest during the second post-move data collection period relative to the first and third, whereas the opposite was true for grooming and time spent in contact. This perhaps reflects the mutually exclusive nature of some social and exploratory behavior. What drove the variation, however, is not clear from our data.

In summary, juvenile capuchin monkeys and those carrying infants were more likely than others to stay above ground in novel spaces. This is what would be expected based on their relative vulnerability and the relatively uncertainty inherent in novel space. The presence of an adult male may have supported the secure use of new space, and may encourage group cohesion. The extent to which these results generalize to other groups, species or a non-captive situation is unclear. Furthermore, given that even the MG did experience the culling of one male prior to release in new housing, we cannot know the effect that this social disruption had on our results. Future research in both captive and wild settings can assess the generality of our findings. Of particular interest from the perspective of captive management would be to confirm the influence of an adult male. If males in general have as profound an impact as our data suggest, their presence may be a vital aspect of smooth transitioning to new housing. This might be particularly important in groups with large numbers of juveniles or mothers with dependent infants.

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