Table 1. Defensive actions of *P. spinicola* in control, clipping and crushing treatments. Values are means ± SE.

Treatment	Ejection Time (s)	Aggression [a]	Time to First Encounter (s)	Encounter Frequency (s-1)
Control	29.4 ± 11.9	71.2 ± 9.8	4.0 ± 1.7	0.27 ± 0.22
Crushing	37.8 ± 23.1	82.0 ± 8.2	5.6 ± 2.6	0.43 ± 0.40
Clipping	17.6 ± 6.4	80.0 ± 20.0	11.0 ± 2.9	0.18 ± 0.19
P-value	0.81	0.31	0.19	0.43

[a] % of encounters characterized as aggressive [b] Treatments compared with a Kruskal-Wallis non-parametric test

Table 2. Defensive responses of *P. spinicola* to the control, clipping and crushing treatments. Values are mean ranks within treatment groups as determined by a Kruskal-Wallis analysis.

Treatment	Ejection Time (s)	Aggression (%)	Time to First Encounter (s)	Encounter Frequency (1 / s)
Control	9.0	6.0	6.1	8.3
Crushing	7.8	7.8	7.0	8.8
Clipping	7.2	10.2	10.9	5.6

Perhaps encounter rates decreased and time to first encounter increased because the ants were directed to other activities, such as moving disturbed egg sacs to a safer location (pers. obs.). Alternatively, these trends might be caused by decreased search areas resulting from an increase in ant turning rates triggered by pheromones (Janzen 1983). The clipping treatment produced the strongest effect in all four measured variables, and crushing was intermediate in three (Table 2); this suggests that the crushing and clipping treatments represent an increasing gradient of disturbance and pheromonal release that might lead to more effective defense of the ant-Acacia system.

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MONKEY BUSINESS: ALOUATTA PALLIATA BEHAVIOR AS A FUNCTION OF AGE AND SEX

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Abstract. The hierarchical social structure in *A. palliata* might be reflected in differences between sex and age classes in the amount of time allocated to various behaviors. We tested this hypothesis by observing behavior in howler monkeys (*Alouatta palliata*) in Palo Verde National Park, Costa Rica. Adult males, females with infants, and females without infants all had very similar activity budgets (time spent resting, moving, feeding, and being alert). Juveniles tended to spend more time moving and less time being alert than adults. Age and sex classes of A. palliata differed less than expected in their activity budgets, perhaps because the social hierarchy exerts its impact in other areas such as reproductive competition and foraging advantage.

Key Words: Alouatta palliata, *howler monkeys, behavior, social hierarchy*

Introduction

Behavior in primates and other animals often reflects social organization and an individual's status within the social hierarchy (Chapman 1987, Chapman 1990, Chapman and Lefebvre 1990). The mantled howler monkey, *Alouatta palliata*, is a diurnal folivore typically found in mixed age and sex groups of 3-44 individuals (Eisenberg 1989) that includes several adult males associated with multiple adult females. Individual troops are organized into a linear hierarchy in which males are dominant to females (Glander 1983). Dominant individuals benefit from increased access to resources but face costs of intraspecific aggression and group defense (Robinson 1981). We hypothesized that the behavior of individual monkeys would reflect their status within the social hierarchy. Specifically, we predicted that the proportion of time allocated to feeding, moving, resting, and alertness, would differ among adult males, females with infants, females without infants, and juveniles. We tested these predictions by recording the behaviors of individual howler monkeys on 9-10 January 1996 in Palo Verde National Park, Costa Rica.

Methods

To quantify activity patterns of individual monkeys, we used focal animal sampling (Altmann 1974). Focal individuals in four age and sex classes (adult male, adult female with infant, adult female, and juvenile) were chosen so that individuals of each age and sex class were observed once before repeating observations of any class. During 10 minute sampling periods, we recorded the amount of time spent on five behaviors: resting (sitting or lying without any other activity), moving (walking and climbing not accompanied by other activities), feeding (searching for and manipulating food), alertness (cautiously scanning surrounding ground and vegetation), and other (activities not fitting into above categories). We calculated the proportion of observation time spent on each activity by an individual during each sample period. Observations of behavior after 08:30 on 10 January were not analyzed because the entire group entered a resting period that differed greatly from behavior during other sampling periods. We pooled the data from all other observational periods for analyses, and used Kruskal-Wallis ranked sums tests to compare the proportion of time spent in each activity across different age and sex classes.

Results

We observed three groups of 9, 21, and 26 *A. palliata* near Hacienda Palo Verde and the Estacion Biologica OET. We recorded 580 min of observations on 58 individuals: 20 males, 18 females with infants, 10 females without infants, and 10 juveniles. The activity budgets of *A. palliata* across age and sex classes (Figure 1). All classes spent 15-20% of their time resting and 20-30% of their time feeding ($X^2 = 0.93$ df =

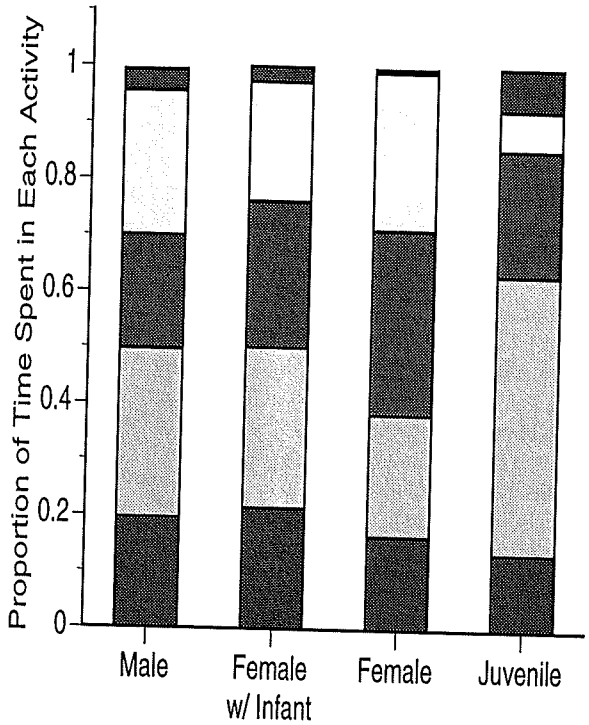

Figure 1. Proportion of time allocated to different activities within four age and sex categories of mantled howler monkeys, *Alouatta palliata*, at Palo Verde National Park, Costa Rica.

2, P = 0.82 and X^2 = 2.23, df = 2, P = 0.53, respectively). Juvenile monkeys spent considerably more time moving (50% vs 20-30%; X2 = 7.44, df = 3, P = 0.059) and less time alert than adults (7% vs 20-30%; X^2 = 7.31, df = 2, P = 0.06, respectively).

Discussion

Our observations of *Alouatta palliata* showed very similar activity budgets across the three adult age classes, and a trend for greater movement and less alertness by juveniles. These results were unexpected given that other studies have shown both age- and sex-dependent behavior patterns in several species of monkey. Dominant individuals are generally more vigilant (male *Cebus capucinus*; Rose 1994) and occupy more advantageous foraging positions (female *C. nigrivittatus*; Robinson 1981). If these patterns existed in *A. palliata*, we would expect adult males to have increased alertness and decreased feeding time. Juveniles, who exhibit lower levels of alertness and increased movement, do seem to rely upon adults to provide protection rather than assuming responsibility themselves.

The hierarchical structure of *A. palliata* may be less pronounced than in other species, but it seems more likely that the dominance hierarchy manifests itself in other areas of behavior such as reproductive competition and foraging advantage. Studies focusing on both patterns of behavior and resource use may better illuminate age and sexual class differences within groups of *Alouatta palliata*.

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