*aculeata*. There is also no indication of what allows *P. aculeata* to thrive in both aquatic habitats and extreme dry areas with only periodic flood water. A study of the variation in root structure between underwater and dry area roots may yield some insight into how phenotypic change might allow growth in both extreme environments. Finally, further study of the population structure of this tree may be more instructive in the large expanses dominated by *P. aculeata* on the south side of the marsh, which does not have the same history of human disturbance.

Overall, *P. aculeata* appears to be highly tolerant of both water stress and grazing pressure. While its primary area of occurrence is within the marsh, it appears that seedling establishment may only occur in these areas during rare, extended dry seasons. Though *P. aculeata* appears competitive with other tree species in dry, open canopy areas outside the marsh, it may be both shade intolerant and incapable of growing to a height sufficient to avoid being overshaded by taller canopy trees. The combination of its shade intolerance and its resistance to grazing appears to make *P. aculeata* more competitive in areas of human disturbance to canopy trees or cattails and in areas of heavy cattle grazing.

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# *ALOUATTA PALLIATA* TIME BUDGETS IN THE EARLY DRY SEASON

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*Abstract*. Howler monkeys, *Alouatta palliata*, vary their diet according to location and time of year. We studied howler monkeys during the early dry season in Palo Verde National Wildlife Refuge. We hypothesized that due to decreased fruit abundance during the dry season, howlers would forage mostly on foliage and would spend more time resting than foraging. The howler monkeys observed did forage exclusively on foliage and spent most of their time resting after a morning foraging peak. We expect howlers to spend relatively less time resting when fruit is more available.

## INTRODUCTION

The mantled howler monkey, *Alouatta palliata*, is a highly social animal with a wide variation in troop size, averaging approximately 14 individuals (Smith 1977). Howler troops including several males are common throughout lowland and montane forests in Costa Rica (Glander 1983).

Howlers show a variety of dietary preferences, including leaves, flowers and fruit, according to their location and the time of year. During the dry season, when fruit abundance is decreased, most of their diet consists of foliage (Glander 1983). Due to the low energetic content of leaves and the large amount of time required for digestion, we hypothesized that *A. palliata* would spend a greater amount of time resting than actively foraging.

## METHODS

We studied howler monkeys in secondary dry forest near the Sendero Venada trail, in Palo Verde National Wildlife Refuge, Guanacaste, Costa Rica. Our observations took place on 11 and 12 January 1995, which was the beginning of the dry season.

We followed two different troops of *A. palliata* which we named Big Lips' and Dave's after distinguishing features of prominent males. Big Lips' troop consisted of fourteen individuals, including four males, eight females and three young. Dave's troop consisted of ten individuals, of which three were males, four were females and three were young. We located each troop at dawn by means of their distinctive territorial calls. Once we located the troop, we avoided eye contact and remained silent to acclimate the monkeys to our presence and reduce the disturbance of their normal behavioral patterns.

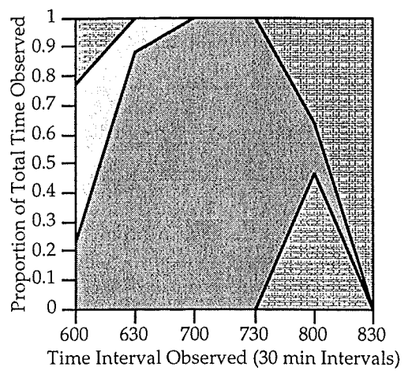
On 11 January, we observed Big Lips' troop from 0615 to 0845 and on 12 January, Dave's troop from 0620 to 1130. We used scan sampling at five minute intervals to create quantitative time budgets for each troop. These five minute intervals were grouped into 30 minute blocks for analysis. Behaviors were classified in one of the following five categories: traveling, resting (including grooming), feeding, vigilance, and territoriality. We interpreted howling as an expression of territoriality, and watching as an indication of vigilance. We also took detailed field notes of social interactions, spatial distribution of individuals within the troop, and specific foods consumed.

## RESULTS

### *Time Budgets*

Both troops were active in the early morning, with vigilance (some presumably due to our presence) and territoriality as the dominant behaviors (Figs. 1, 2). The monkeys then rested for one to two hours before beginning a period of feeding and traveling. Although the two troops

followed the same general pattern of resting and activity, they differed in the length of time of each type of behavior. For example, Big Lips' troop was relatively inactive until 0800 when they began to travel and feed (Fig. 1), whereas Dave's troop had a brief resting period from 0600 to 0630 and then was active until 0830 (Fig. 2). Resting comprised the largest proportion of the time budget for both troops, though observation time on Big Lips' troop was limited.



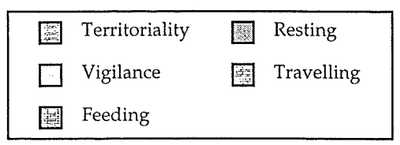
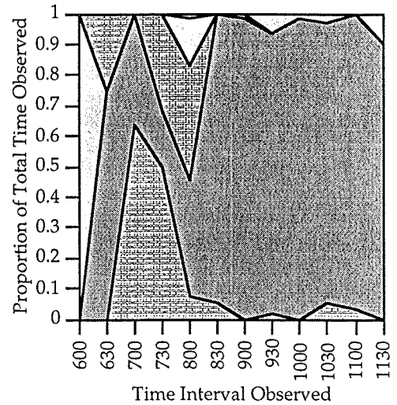




FIG. 1. Time Budget for Big Lips' Troop, 11 January, 1995.

*Observations*

All the monkeys of a troop generally slept in groups, within one or two trees, centered around a single male. They fed independently, spreading over 5-10 trees. The young tended to eat while holding on to their mothers. They fed primarily on leaves of Guanacaste trees (*Enterolobium cyclocarpum*), and occasionally on those of Raintree (*Pithecellobium saman*) and Moraceae (*Brosimum sp.*). Leaves of *Chomelia espinosa* (Rubiaceae) were eaten by one male. We observed three methods of feeding: sitting on a branch biting off leaves with their mouths only, picking leaves off the tree with their hands, and hanging from their tails and stripping leaves off the trees below with their teeth.



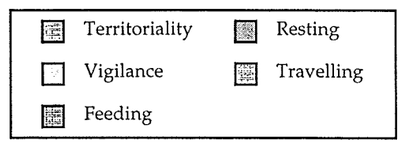




FIG. 2. Time Budget for Dave's Troop, 12 January, 1995.

When the monkeys moved from tree to tree, they traveled in a single line along the same path, using the same branches. The females with young seemed to initiate troop movement most of the time, with the males following shortly after.

## DISCUSSION

Early in the Guanacaste dry season, fruit production is low, so primates must depend on leaves as their main food source. According to Milton (1980), leaves provide considerably less ready energy than fruit. In addition, leaves require more time to digest than fruit. These two factors should result in less time spent foraging and more time spent resting and digesting. Our data supports this hypothesis since the monkeys we examined spent the major proportion of time resting as opposed to foraging. Further study should address the proportion of time *A. palliata* spends resting during different





periods of fruit production throughout the year.

Howlers tend to stay in large groups while resting, possibly indicating they come together for protection. However, the monkeys do not stay together while foraging, suggesting that food limitation during the dry season may force them to separate. Therefore, we might expect them to stay closer together while foraging during the food-rich wet season. The time spent foraging and possibly spatial distribution during foraging appear to be related to the current abundance of the howlers' preferred food source.

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