DISCUSSION

As predicted, intraspecific jacana aggression increased with jacana abundance, probably due to competition among conspecifics for food, mating territories, and other resources. At low jacana abuncances, interspecific jacana aggression increased with the number of gallinules, indicating that at low jacana density, gallinules may pose more of a threat to jacanas than other jacanas. However, at high jacana abundances, interspecific jacana aggression decreased with number of gallinules present. There may be a critical number of jacanas where jacana conspecifics become more threatening than gallinules.

Other environmental factors may affect jacana aggression. Ungerer et al. (1998) found that jacana density differs in different types of habitat within the Palo Verde marsh. However, our study was within plot they defined as homogenous habitat. Jacanas were clumped within plots in many of our trials and gallinules were also sometimes clumped. It may be that jacana aggression should be measured in terms of the distance to the nearest gallinule rather than as an average over an entire study area. Perhaps individual jacanas are more aggressive when gallinules are nearby. Time of day can also influence jacana aggression (Hourdequin et al. 1996), but because all of our observations were conducted during the middle of the day, diurnal patterns were not a factor.

Another possibility is that at the time of our study all of the young jacanas were too large to be eaten by gallinules. Jacana and gallinule chicks were seen in the area at the time of our study (R. T. Holmes pers. comm.) which suggests that breeding by these marsh birds is possible early in the dry season. Future studies should be done in the wet season to determine if gallinules pose more of a threat to jacanas then. If so, we would predict higher rates of aggression by jacanas towards gallinules.

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WILL THEY STOP MONKEYING AROUND? THE EFFECTS OF AN UNUSUALLY DRY YEAR ON HOWLER MONKEYS

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Abstract. We examined the behavior and troop composition of howler monkeys *(Alouatta palliata)* at Palo Verde National Park during an unusually dry year. Past studies allowed inter-annual comparisons. We hypothesized that the early dry season should alter howler behavior and troop composition patterns because of water and energy constraints. Consistent with this, we found an increase in alertness and a decrease in individual movement relative to the previous year. Contrary to expectations, population composition by sex and age class was similar to previous years, indicating that births and juvenile survivorship were similar. The two larger troops spent significantly more time moving and less time resting than the small troop, presumably because of their greater resource needs. This study contributes to a growing database of howler monkey behavior, troop size, and troop composition at Palo Verde National Park.

Key Words: Alouatta palliata, *time allocation, feeding patterns, troop composition*

INTRODUCTION

The mantled howler monkey, *Alouatta palliata*, is a common species at Palo Verde that is easily recognizable by the stentorian howls of adult males. Howler monkeys are territorial, living in multi-male, multi-female groups that average 10 - 18 individuals (Emmons 1997). They are almost exclusively arboreal and the vegetation and fruit they consume is usually their only source of water (E. Gonzales, pers. comm.).

Water may be a limiting resource for howlers during the dry season, because many trees are not fruiting and deciduous species lack leaves. In 1997, the wet season at Palo Verde was much dryer than usual. The rains, which usually begin in April, did not start until July, and then rainfall was lower than normal (E. Gonzales, pers. comm.). Moreover, during our first four days at Palo Verde, two howler infants from the troop at the Palo Verde OTS field station were seen in a weakened condition and subsequently found dead.

Our first objective was to examine the impact of a dry year on Palo Verde's howler monkeys by comparing their behavior and troop composition with that recorded in previous years (Bird et al., 1996, Cover et al., 1997). We hypothesized that howlers in this dry year should attempt to conserve energy and water by spending less time moving and more time resting. We also predicted that fewer infants and juveniles would be present in the troops, indicating a decline in births and juvenile survivorship.

Our second objective was to examine how troop size affects howler monkey behavior during a dry year. We hypothesized that the two larger troops, because of greater food requirements, should spend more time moving than the small troop.

METHODS

We observed three troops of howler monkeys on 13 - 14 January 1998 at Palo Verde National Park, Costa Rica. We found the troops at sunrise by following the howls of male monkeys. One troop was located 1 km west of the OTS Biological Station in a mango grove, one 200 m up the southern slope near the Sendero Pizote trail, and one 200 m east of the Ojo de Agua (watering hole).

After locating each troop, we watched it for 30 min to count the number of members and to categorize them by sex and age (adult male, adult female with infant, lone adult female, and juvenile). We minimized movement, avoided eye contact, and remained quiet during observation.

We observed and recorded the behavior of randomly selected individuals using 10 min focal samples. Sampling was done *ad lib.*, without a schedule rule, i.e., we did not set explicit times for collection of focal samples (Altmann 1974). We recognized four behavior categories: resting (relaxing or sleeping),

alertness (scanning, on guard), feeding, and moving (motion within and between trees). For each 10-minute focal sample, we recorded the time spent in each behavior class. Time budgets were developed by averaging the proportions of each bout devoted to each behavior. However, individual monkeys almost never engaged in more than two recognized behaviors within an observation bout, so the data were also suited to categorical analyses of the presence and absence of particular behaviors. A total of 53 h (316 focal samples) of observation was compiled between 06:30 and 17:00 on 13 January and between 06:30 and 16:30 on 14 January.

We pooled data from all three troops and calculated the proportion of time spent resting, alert, moving and feeding, and compared these data to those presented graphically by Cover et al. (1997). We used chi square analyses to compare troop compositions between 1998 and 1996 and to compare behavioral patterns among our three troops.

RESULTS

All three troops of howler monkeys tended to do most of their moving and feeding in the mornings (07:00 - 10:00) and evenings (15:00 - dark) and rested with little activity during midday. We observed them eating unripe mangoes, leaves of *Enterolobium cyclocarpum*, *Cecropia*, and *Acacia*, and some other flowers, buds and green leaves. Males tended to be stationed high in the canopy, around the perimeter of the group.

TABLE 1. Troop compositions in 1998.

Troop	Lone Females	Females with Infants	Males	Juveniles
Mango	10	7	4	6
Watering hole	2	2	5	3
Slope	1	1	2	0

TABLE 2. Total composition by sex and age class in 1998 compared to that reported by Bird et al. for 1996.

Year of study	Lone Females	Females with infants	Males	Juveniles	Total
1996	10	18	20	10	58
1998	13	10	11	9	43

TABLE 3. Comparison of behavior by *Alouatta palliata* between data collected by Cover et al. (1997) and present study in Palo Verde National Park.

Behavior	Sex and age class	Proportion of activity in 1997	Proportion of activity in 1998	% Change
Resting	Female with Infant	0.46	0.46	0
	Lone Female	0.52	0.59	14
	Male	0.47	0.43	-9
Alert	Female with Infant	0.15	0.28	87
	Lone Female	0.07	0.08	14
	Male	0.11	0.33	200
Moving	Female with Infant	0.25	0.16	-36
	Lone Female	0.21	0.09	-57
	Male	0.23	0.13	-44
Feeding	Female with Infant	0.14	0.10	-29
	Lone Female	0.17	0.24	41
	Male	0.18	0.11	-39

TABLE 4. Proportion of observation bouts with specified behavior.[a] Chi-square statistics tested the null hypothesis that proportions were equal across troops.

Troop Size	Total Observation Bouts	Behavior: Resting	Alertness	Moving	Feeding
Small	106	0.70	0.35	0.11	0.22
Medium	46	0.58	0.30	0.25	0.21
Large	163	0.42	0.38	0.30	0.34
Chi Square		11.06***	2.07	6.45*	6.20*

* P < 0.05; ** P < 0.01; *** P < 0.001

[a] Note that proportions sum to >1.0 because observation bouts were classified as including up to two behaviors.

The mango grove troop had 27 individuals, the watering hole troop had 12, and the slope troop had four (Table 1). Composition by sex and age class in 1998 was very similar to that in 1996 ($\chi^2 = 3.15$, $P > 0.05$; Table 2).

Compared to January 1997, time spent moving tended to decrease for females with infants, lone females, and males while there was some increase in alertness, particularly among males (Table 3). No change in either feeding or resting was evident between the study by Cover et al. (1997) and the present study (Table 3). Of the troops we observed, the two larger troops rested less and moved more than the small troop (Table 4). The large troop spent more time feeding than the two smaller troops (Table 4).

DISCUSSION

Contrary to our prediction, the proportion of juveniles and infants were similar to previous years. However, our study was conducted near the beginning of the normal dry season, and it is possible that drought related mortality within these monkey troops was just beginning as food and water resources declined. Behavior patterns appeared different from previous years. The reduction in time spent moving relative to 1997 might be attributable to conservation of water and energy. The shift towards increased alertness from 1997, particularly among males, could represent an increased investment in defending limited resources during this particularly dry year. However, we saw no signs of poor health beyond the two infant deaths that motivated the study. Those two deaths could have been unrelated to the drought, possibly due to a localized pathogen.

Behavior patterns differed with troop size. The small troop never ranged more than 80 m in two days, whereas the larger troops traveled 200 - 500 m each day. This could be because larger troops require more resources, and deplete local resources more quickly, than small troops. However, it could also be due to inherent differences in habits between the particular troops that we observed. These alternatives can only be resolved with studies that include multiple troops per size category.

It was difficult to make comparisons between years, partly because the data from previous years could not be reanalyzed. However, repeated studies of this type could yield valuable information about the annual variation in behavior, size, and composition of Palo Verde's howler monkey troops. Our data are summarized in Appendix 1 to facilitate inter-annual comparisons.

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APPENDIX 1. Complete data set for individual classes in Mango, Slope, and Waterhole troops in Palo Verde National Park, Costa Rica (Troop Size: large = 27, medium = 12, small = 4). Each bout was classified as including one or two behaviors.

				Percent of bouts with activity			
Troop	Time	Age/Sex	Total observation bouts	Rest	Alert	Move	Feed
Mango (Large)	Morn	F	10	20	20	50	70
		FWI	8	25	63	63	38
		J	5	20	40	40	80
		M	11	27	45	55	36
	Mid	F	21	86	10	5	10
		FWI	6	67	33	17	0
		J	8	75	38	25	13
		M	15	27	80	13	7
	Aft	F	9	22	33	22	56
		FWI	5	0	40	60	80
		J	3	33	0	67	100
		M	5	40	40	20	40
Waterhole (Medium)	Morn	F	13	46	23	38	38
		FWI	12	42	58	42	17
		J	14	50	7	50	43
		M	18	44	50	22	17
	Mid	F	18	89	11	6	11
		FWI	17	76	24	12	0
		J	18	72	28	0	17
		M	20	85	15	5	5
	Aft	F	9	44	0	22	56
		FWI	8	25	38	63	25
		J	7	14	43	43	71
		M	9	22	89	67	0
Slope (Small)	Morn	F	5	100	20	0	0
		FWI	6	83	50	0	17
		J	6	67	0	33	50
		M	12	67	58	8	8
	Mid	F	2	100	0	0	50
		FWI	1	0	100	0	0
		M	5	40	40	0	40
	Aft	F	2	100	50	0	0
		FWI	1	100	0	0	0
		J	1	100	0	100	0
		M	5	40	20	20	40