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Drinking from Arboreal Water Sources by Mantled Howling Monkeys (*Alouatta palliata* Gray)

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Abstract. Mantled howling monkeys (*Alouatta palliata* Gray) were observed to drink from arboreal water sources during the wet season but not during the 5 month dry season. The lack of drinking in the dry season is attributed to seasonal differences in their activity patterns and food selection, the water content of the food, and the absence of plant secondary compounds in their dry season diet.

Introduction

Mantled howling monkeys (*Alouatta palliata* Gray) on Barro Colorado Island have been studied periodically for more than 40 years, yet have never been reported to drink [CARPENTER, 1934, 1965; COLLIAS and SOUTHWICK, 1952; SOUTHWICK, 1955; ALTMANN, 1959; BERNSTEIN, 1964; CHIVERS, 1969; RICHARD, 1970; MITTERMEIER, 1973]. In other neotropical areas studies of howler species have produced similar results [BALDWIN and BALDWIN, 1972; NEVILLE, 1972]. Several investigators have reported that howlers came to the ground near water but were not observed to drink [CARPENTER, 1934; RACENIS, 1951; IZAWA, 1975]. CARPENTER [1934] suggested that howlers obtained water from their food or by licking dew or rain from the surrounding environment, thereby eliminating the need for drinking.

This paper describes seasonal drinking by mantled howling monkeys that was associated with the lack of succulent new leaves during the wet season and the concomitant increased ingestion of plant secondary compounds contained in mature leaves. These observations were made during the course of a 14-month study (June 1972 through August 1973) concerned with resource utilization and social behavior of mantled howlers in Guanacaste Province, Costa Rica [GLANDER, 1975].

Methods

The 13 member study group (2 adult males, 6 adult females, 5 juveniles) was observed for 2,071 h, using the focal animal technique [ALTMANN, 1974] during 172 days for an average of more than 12 continuous hours of animal contact observation per day. Every behavior of one focal animal per day was recorded. *Ad libitum* sampling [ALTMANN, 1974] of nonfocal animals was opportunistic.

In order to insure unambiguous individual recognition, unique leather collars with colored metal tags were placed around the necks of the females [SCOTT *et al.*, 1976]. Males were easily identified by physical markings and infants and juveniles could be differentiated by their association with tagged females.

The study group's home range consisted of 9.9 ha of forest, containing 1,699 numbered trees [for a detailed description of the habitat see GLANDER, 1975, in press]. Meteorological data were collected at a government weather station located 600 m from the study site.

Results

Even though the howlers came to the ground and fed in trees whose branches touched the water, they were never seen to drink from the river or any other ground water. Drinking from arboreal cisterns was observed 38 times, all during the wet season (May–November, table I). Only one instance of licking rain water was noted. Not all members of the group were seen to drink from the cisterns during the study. However, on a return visit in July 1976, I witnessed all group members drink several times from the cistern in Tree 463.

The drinking posture, in all but one case, was assumed by inserting the head and shoulders into the cistern while anchoring the tail on a nearby branch (fig. 1A, 2). The one exception occurred when a juvenile dipped his hand into the cistern and then licked the drops of water from his hand (table I). After all drinking bouts water was seen to drip from the animal's hand or mouth. To verify the presence of water, I climbed to one of the cisterns where I found 2 inches of stagnant water containing decaying leaves, aquatic insects, and a frog (fig. 1B).

A majority (82%) of the observed drinking bouts occurred in one tree (Tree 463, table I). The reason for this is unknown. Possibly this tree con-

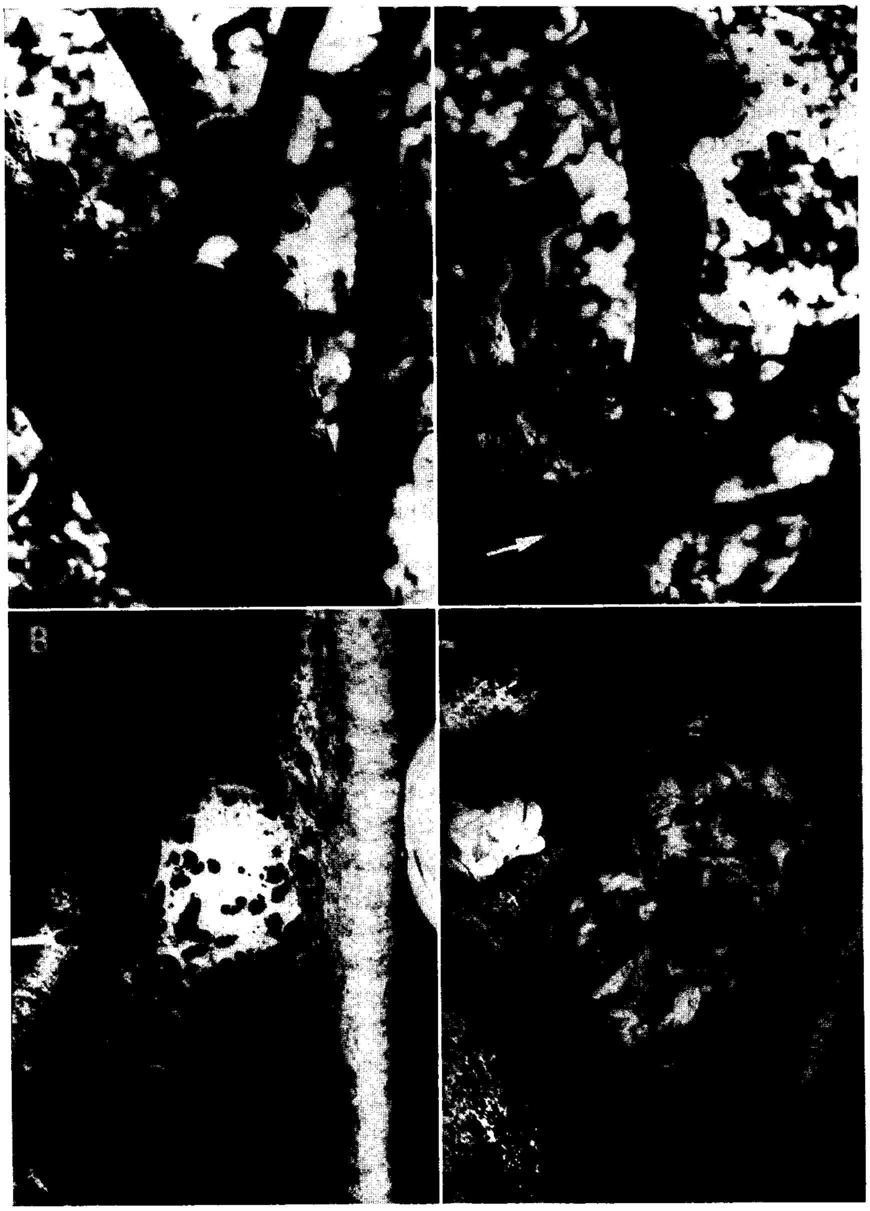

Fig. 1. A A howler, head down, drinking from the cistern in Tree 463. *B* 2 inches of water collected in the cistern in Tree 112. Note the leaves in the water. This picture was taken immediately after Scar had drunk on 6/22/73 (table I). *C* 2 females waiting their turn to drink while a third (arrow) drinks from the cistern in Tree 463. Note the collars around the necks of the females. Each collar is uniquely colored for positive individual identification. *D* The same cistern as in *B* except during the dry season.

Fig. 2. A cut-away view of a howler drinking from an arboreal water source.

tained more water or had a longer lasting supply of water than the other occasionally utilized trees.

Location of the trees in the home range did not appear to determine which cisterns were used, since all of the trees containing the cisterns were visited regularly for other activities. However, the water source in Tree 463 may have influenced the daily pattern of travel. Several times animals made obvious detours or retraced their paths to drink from that cistern.

Interactions frequently occurred around the cistern in Tree 463. The linear dominance hierarchy, documented from other activities [GLANDER, 1975], was apparent in the order of drinking (table I). For instance, males supplanted females, and high ranking females could easily supplant lower ranking females

Table I. Drinking bouts

Date	Time	Animal	Tree No.	Dura-tion, sec	Comments
10/ 2/72	07.09	Yellow	463	nd	
10/ 8/72	05.40	Y-juvenile	395	nd	
	07.46	Green	463	nd	
10/16/72	16.55	Green	109	nd	
	16.56	Y-juvenile	109	nd	
10/24/72	07.30	Whitered	463	240	
	07.35	Green	463	2	supplanted by Yellow
	07.35	Green	463	2	supplanted by Yellow
	07.37	Y-juvenile	463	30	
	07.38	WR-juvenile	463	–	dipped hand in and licked
	07.39	Yellow	463	nd	Green tried to force her way in
	07.40	Whitered	463	57	
	07.43	Yellow	463	50	
	07.44	Y-juvenile	463	15	
	07.45	Green	463	195	everyone else had left
10/28/72	06.20	Y-juvenile	463	73	Yellow standing nearby
	09.07	Y-juvenile	463	nd	
10/29/72	14.48	Green	463	nd	
11/ 7/72	05.35	Green	463	nd	
	05.38	Whitered	463	nd	supplanted by Scar
	05.40	Scar	463	100	
	05.42	Whitered	463	100	Green waiting her turn
	05.45	Green	463	100	Scar – Whitered had left
11/18/72	15.46	Whitered	463	75	Green waiting her turn
	15.48	Green	463	126	
11/19/72	15.34	Yellow	463	50	supplanted her juvenile
	16.01	Whitered	463	139	
11/21/72	06.33	Whitered	463	190	supplanted her juvenile
	15.24	Scar	463	112	
12/ 3/72	16.40	?-juvenile	713	nd	
12/15/72 to 4/27/73 dry season; no drinking					
5/ 4/73	06.12	Yellow	463	nd	
5/12/73	07.36	Scar	380	nd	
5/28/73	09.53	?-juvenile	226	nd	
6/12/73	10.04	Yellow	463	140	infant on her ventrum
6/22/73	10.50	Scar	112	nd	
7/ 9/73	09.45	Scar	463	35	
7/16/73	11.05	Scar	463	30	
7/19/73	14.23	Blue – Baker	734	–	licked water from leaves
8/ 7/73	17.10	Green	463	nd	

nd = Not determined; tree 463, 112, 713 = *Sloanea terniflora;* tree 109, 380 = *Anacardium excelsum;* tree 395, 226 = *Mastichodendron tempisque.*

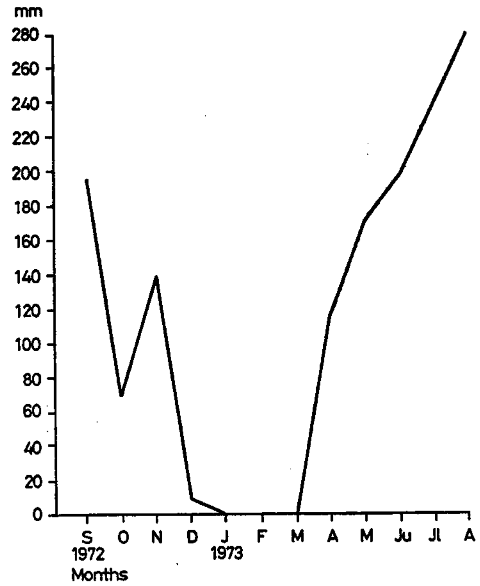

Fig. 3. The monthly distribution of rain during the study.

from the cistern. Sometimes several animals were lined up waiting to drink (fig. 1C).

Discussion

The drinking pattern reported here (drinking in the wet but not the dry season) is the opposite of the expected pattern. Generally the dry season is assumed to be the period of maximum water stress (fig. 3). But, why drink only during the wet season, hypothetically the less stressful season? And, why did the howlers not drink from the river when the arboreal cisterns dried up? Did their seasonal water requirements change? Was there a change in the water content of their food?

In terms of environmental stress, the dry season is a time of higher average monthly temperatures (fig. 4), higher average daily and monthly hours of sunshine (table II) and lower average monthly relative humidity (fig. 5). Higher temperatures and lower humidity during the dry season should increase the heat load, thereby increasing the water requirement [Taylor and Lyman, 1967]. Water loss, a critical variable for animals under heat stress, is affected

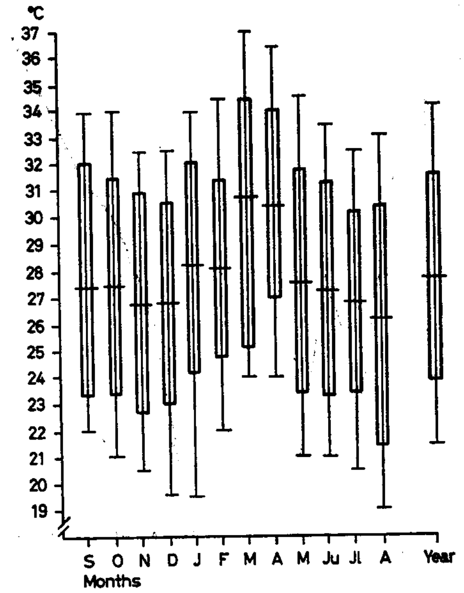

Fig. 4. The monthly temperature averages and extremes. Single line represents the maximum–minimum temperature. Double lines represent the average maximum and average minimum temperatures.

by the water vapor pressure gradient, i.e., water vapor moves from high vapor pressure to low vapor pressure [LOWRY, 1969]. Vapor pressure is a direct measure of water in the atmosphere. The wet season vapor pressure was greater than the dry season vapor pressure ($t = 8.00$, $p < 0.001$, $df = 312$), supporting the assumption that the dry season is more stressful (higher gradient between an animal's lung vapor pressure and the ambient vapor pressure). Yet the howlers maintained their water balance without drinking during this more stressful season. Conversely, they drank during the less stressful wet season to maintain their water balance. To explain the lack of correspondence between expected drinking patterns and meteorological parameters, other factors must be considered.

The seasonal diets are very different and the difference reflects the availability of the various trees' phenophases. During an average wet season day the howlers spent 30 min (25.3% of their feeding time) eating mature leaves and 47 min (31.2%) eating new leaves, compared to 21 min (11.5%) eating mature leaves and 104 min (56.5%) ingesting new leaves during the dry season [GLANDER, 1977]. The mean water content of new leaves is significantly greater

Table II. Average hours of sunshine for the study site recorded during a 10-year period

		1972				1973								
		Sep	Oct	Nov	Dec[1]	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Year average
Day	$\bar{x}$	4.9	4.9	5.6	6.9	7.8	9.2	8.8	8.0	6.2	4.7	4.5	5.9	6.4
Month	$\bar{x}$	147.9	151.5	166.9	213.6	242.5	260.5	278.6	239.0	193.4	140.0	140.2	159.5	193.5

[1] December through April, dry season.

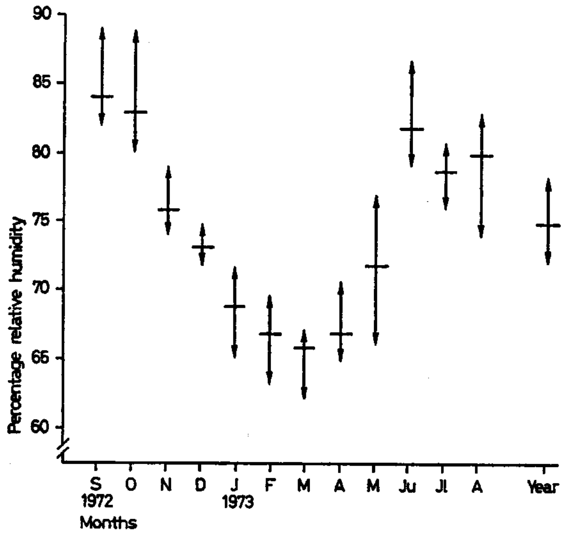

Fig. 5. The average relative humidity recorded at La Pacifica, Guanacaste Province, over a 5-year period. The arrows indicate the average maximum and minimum.

than that of mature leaves (72.2–56.6%, $t = 9.18$, $p < 0.001$, $df = 51$). Thus, the dry season diet provided significantly more water than the wet season diet.

In addition to the seasonal differences in feeding behavior, there were differences between the howlers' wet and dry season activity patterns which may relate to water conservation. The average time of first movement and feeding as early as 04.00, 1–½ h before sunrise. Also, during the dry season wet season. On several mornings during the dry season the animals began feeding as early as 04.00, 1–½ h before sunrise. Also, during the dry season most of their morning movement and feeding was completed by 07.30, and the animals rested through the heat of the day, beginning to stir again after 15.00. In comparison, during the wet season they did not begin to move or feed until after 06.30 and then continued to move and feed sporadically throughout the day. Seasonally, the overall time spent in each activity was not significantly different.

This seasonal change in the time of activity by the howlers and their preference for new leaves with high water content may represent a behavioral adaptation similar to that reported for desert eland [*Taurotragus oryx,* TAYLOR and LYMAN, 1967]. By avoiding the noonday sun and selecting succulent food, the eland were able to live independent of water.

Are the seasonal differences in the howlers' activity patterns and the seasonal variations in the amount of water in their food sufficient to explain their lack of drinking during the dry season? These factors may account for the observed drinking behavior. However, the seasonal presence of plant secondary compounds in the howlers' diet must be considered as an important variable when interpreting the water and nutrient needs of these animals.

The ubiquitous occurrences of plant-produced chemical compounds [WHITTAKER, 1970] influenced the study group's feeding behavior [GLANDER, in press]. Given the choice between mature and new leaves of the same tree, the howlers preferentially selected new leaves. In some instances they ingested large quantities of the tree's new leaves yet never consumed its mature leaves. Phytochemical screening showed that the mature leaves of those trees contained large amounts of alkaloids while the new leaves of the same trees did not contain alkaloids [GLANDER, in preparation]. New leaves were relatively rare on all food trees during the wet season, forcing the howlers to increase their ingestion of mature leaves by 13.8% over the dry season. An increase in mature leaves (more toxins) during the wet season, as well as the lowered water content of mature leaves, may force howlers to drink supplemental water. One of the primary detoxification pathways (microsomal enzymes located in the liver and kidneys) produces water-soluble metabolites [FREELAND and JANZEN, 1974]. Thus, additional water – water that cannot be obtained from their food – may be needed during the wet season to flush the toxins out of their bodies.

The absence of drinking every day during the wet season indicates varying water needs and lends support to the succulent leaf – secondary compound hypothesis. Though rare, new leaves did occur throughout the wet season. Ingestion of available succulent new leaves would decrease the need to drink.

A lower wet season water vapor gradient and less heat stress reduces water loss, and the selection of mature leaves with low secondary compound content reduces water needs for detoxification. All of these factors, acting together, alters the daily water needs. Whether or not the howlers drink depends on the daily/weekly variability in the tree phenophases available and climatological parameters.

Drinking, or the lack thereof, in howlers seems to be linked more with the kinds of food available than with water availability. The selection of seasonally available succulent new leaves that are low in secondary compounds and the avoidance of the midday heat during the dry season allows the howlers to obtain sufficient water from their food without coming to the ground where they would be exposed to predators. In a similar fashion, the howlers' ability to meet their increased wet season water needs from arboreal water sources is advantageous in terms of reducing their exposure to ground predators.

Similar evaluations of other primates' activity patterns and food choices (in terms of the water content of food, heat stress, and the presence of plant-produced chemicals) may help explain the great deal of variability in drinking, both within and between primate species, reported in the literature.

Summary

Despite occasional trips to the ground and feeding in trees whose canopies touched the river, mantled howling monkeys were never seen to drink from any ground water. Drinking from arboreal cisterns was observed, but only during the wet season (meteorologically the less stressful season but phenologically the more stressful season). The lack of sufficient new leaves during the wet season forced the howlers to ingest more mature leaves which contained significantly less water. To compensate for the lowered amount of water in their food, the monkeys utilized arboreal water cisterns. The cisterns dried up during the dry season, but the howlers maintained their water balance by altering their time of activity and selecting a diet comprised largely of succulent new leaves. The effect of plant-produced secondary compounds on drinking also was discussed.

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