

Troop movement and food habits of white-faced monkeys in a tropical-dry forest.

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Abstract: Home-range, movement and activity patterns and diet of a group of 16 white-faced monkeys (*Cebus capucinus*) were studied in a Costa Rican tropical dry forest at the end of the dry season (March and April) of 1982. The troop used an area of .67 km² and moved an average of 4.5 km ± 0.6 daily. Three basic daily activities were identified: resting, moving and feeding. Resting was greatest between 1000-1500 hours. Movement, which was strongly correlated with feeding, occurred most between 0500-0900 hrs and 1300-1800 hrs.

The primates were omnivores, feeding on parts of 27 species of plants, four species of insects and an *Anolis* lizard.

The white-faced monkey or capuchin, *Cebus capucinus imitator* Thomas (Primates: Cebidae), is found in a wide variety of forest types from Belize to Panama (Hall 1981). This monkey is omnivorous and feeds mainly on fruits and seeds but also on flowers, woody tissue, young shoots, insects, and small vertebrates (Defler 1979, Freese 1976, Freese and Oppenheimer 1981, Hladik *et al.* 1971, Oppenheimer 1960). However, troop movement has received little attention. The objectives of this study were to describe daily activity patterns and food habits of a *C. capucinus* troop in a tropical-dry forest during the latter part of the dry season.

STUDY AREA AND STUDY TROOP

The Dr. Rafael Lucas Rodriguez Caballero National Wildlife Refuge (hereafter referred to by its popular name, Palo Verde) is located on the northern bank of the Tempisque River, 20 kilometers from the river's outlet into the Gulf

of Nicoya, Guanacaste Province, Costa Rica. The refuge is found at 10°30' N and 85°30' W. Palo Verde is about 7,542 ha in size and situated in the tropical-dry forest life zone (Tosi 1969). Within the refuge, nine vegetation types were described: mangrove swamp, seasonal marsh, fresh-water flooded forest, lowland deciduous forest, deciduous forest on limestone hills, evergreen forest, overgrown pasture, *Acacia* scrubland and pasture (Vaughan *et al.* 1982).

Annual rainfall at nearby Puerto Humo for the 1961 to 1970 period averaged 2296 mm, 91% of which fell between May and October. Mean annual temperatures of 37°C are common. Elevation varies from 12 to 232m. The late-dry season months of March and April have little rain, relatively abundant fruit production, and extreme temperature differences between areas of different vegetation types.

The study area was about 100 ha in size and located on the southern slope of Cerro Guayacán, one of two prominent limestone hills within the wildlife refuge. Three forest types were described in this study area. These included: deciduous, semi-deciduous and evergreen, defined as individual trees retaining respectively,

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0-25%, 25-75% and greater than 75% of their leaves during the latter part of the dry season. The study troop consisted of three old and two young adult males, three adult females, seven juveniles and one infant for a total of 16 individuals.

METHODS

The study was conducted from 6 to 25 March and from 13 to 29 April 1982. Our observations began about 15 min before sunrise (0515 hrs) when capuchins were leaving their sleeping sites. The troop was followed until about 20 min after sunset (1800 hrs) when it settled into trees to sleep. A group of more than six monkeys was arbitrarily defined as a troop and a group of six or less, as a sub-group.

The focal animal technique (Altmann 1974) was used for collecting activity data, where a single capuchin was initially chosen at random and followed. Duration of each activity was recorded to the nearest minute which was the smallest time unit. Activity was grouped into hourly periods and for one statistical test, into two periods of four and one of five hours. When the focal animal separated from the troop or was lost by us, our observations were directed to the next capuchin seen. It was at times impossible to pursue monkeys close enough to observe feeding activities.

Four activities were studied: moving, resting, drinking and feeding. Movement was defined as travel. Resting was described as a variety of relatively stationary activities, including reclining with or without closed eyes, sitting alert, grooming, and play. Drinking involved ingestion of water from waterholes. Feeding occurred when the focal animal searched for, picked, bit or chewed a food source. The food unit was the plant part picked, bitten, or collected and partially or completely ingested. When the plant part was a fruit, the fruit part consumed was also annotated. For example, the *Spondias purpurea* tree was a food source and the fleshy mesocarp, the food unit. Each minute of feeding time usually included ingestion of one or more food units. Food units and the relative amounts of food discarded or dropped were determined by direct observation of feeding capuchins and when possible quantitative examination of fresh food remains beneath food sources.

Troop position and time of day were recorded on a map when abrupt changes occurred in capuchin direction of travel. Only relatively

large-scale directional travel was considered, while small-scale movements were excluded from the map. Daily distance traveled by the troop was calculated by summing all measured distances between consecutive estimated troop positions. Home range was estimated by using the minimum convex polygon of all troop positions calculated (Mohr 1947).

Statistical notation followed that of Sokal and Rohlf (1981).

RESULTS AND DISCUSSION

For each hour of the day, between 220 and 360 min ($x = 314.4$ min; S.D. = 45.2) of observation time was collected. The ratio of observations collected for adults and juveniles was 60:40, respectively. This approximated the age class composition of 50:50 of adults to juveniles for the study troop.

Troop home range. During March and April, the troop had a home range of 0.67 km². A significantly greater proportion of diurnal activity occurred in the evergreen forest compared to its total area in the study area ($x^2 = 8.4$, d.f. = 1, $P < 0.005$). The evergreen forest occupied only 5% of the home range, but the troop spent 32% of the daytime there (Table 1). In addition, 75% (12 of 16) of nights, about 50% of diurnal resting and a large proportion of feeding time, were spent in the evergreen forest. Sleeping and resting sites occurred mostly in leafy mango (*Mangifera indica*) and ojoche (*Brosimum alicastrum*) trees found in evergreen and semi-deciduous areas (Fig. 1).

On a daily basis, the troop occupied about 30-50% of their overall home range area; similar to what Baldwin and Baldwin (1977) described for the same species in Panama. In Palo Verde, there are seven evergreen forest patches, and waterholes are found in each. We observed daily visits to water sources by capuchin troops. The evergreen forest is an invaluable source of food, water and cover during the dry season for capuchins and other wildlife species.

Troop movement. Troop movement was recorded for six days from 0500-1800 hrs. Daily travel was 3.9, 4.0, 4.2, 4.5, 5.1 and 5.2 km ($x = 4.5$ km; S.D. = 0.6). The capuchin troop sometimes repeated a certain route four times a day (Fig. 2 and 3). They also crisscrossed established routes and even backtracked. Some

TABLE 1

*Diurnal use of forest types by a white-faced monkey
(Cebus capucinus) troop, Palo Verde,
(March-April, 1982)*

Forest Type	Home Range		Time Spent in Forest Type	
	ha	%	hrs	%
Evergreen	3.3	(5)	19.9	(32)
Semideciduous	6.0	(9)	9.3	(15)
Deciduous	22.1	(33)	15.5	(25)
Deciduous with evergreen pitches	35.6	(53)	17.4	(24)
Total	67.0	(100)	62.1	(100)

routes were highly defined, and capuchins moved through specific trees. Others were generalized, and the monkeys traveled in particular directions via many nearby paths.

Troop movements of *C. capucinus* were observed by Baldwin and Baldwin (1977) on the Burica Peninsula in Panama, with daily path lengths ranging from 0.6 to 1.5 km. Clutton-Brock and Harvey (1977) have listed some daily path lengths for 56 primate species belonging to eight families. Our value of 4.5 km. for *C. capucinus* exceeded the daily path lengths of all 56 species with the exception of three species of *Papio*. In their analysis of feeding and movement data for the 56 species, Clutton-Brock and Harvey (1977) found a negative association between daily path length and the proportion of foliage in the diet. The results for the Palo Verde *C. capucinus* troop conform to this trend: in March and April the capuchins spent only 4.6 and 3.6% respectively of total feeding time eating leaves and shoots, while they traveled large daily distances. Clutton-Brock and Harvey (1977) suggested that this trend would be expected since, compared to the reproductive parts of plants, foliage represented a dense and relatively predictable food supply.

Capuchins occasionally traveled to outlying parts of their home range and were observed eating food sources absent in the core area of the home range. For example, on 18 March there was an excursion to a large *Mastichodendron capiri* tree which had just begun to flower. The trips up the ridge on 25 March included extensive feeding on *Bursera simaruba* seeds (Fig. 2). Excursions to outlying parts of the home range occurred anytime before 1030 hrs and after 1430 hrs.

On many occasions, especially in deciduous forests, several adult capuchins walked at ground level while the remainder of the troop continued arboreally. These terrestrial movements covered up to 50 m, lasted up to six min and included foraging. Baldwin and Baldwin (1977) reported that *C. capucinus* foraged for insects for distances of more than 20 meters along the ground. Moreover, Defler (1979) observed that *C. albifrons* spent up to 50% of their active period foraging at ground level during the dry season (February) in Colombia.

Activity patterns. Feeding was significantly greater between 0500-0900 hrs than in the other four and five hour periods of the day ($H = 9.17$, d.f. = 2, $p < 0.010$). Feeding ceased by noon, then increased to 24% of total observation time from 1500-1700 hrs (Fig. 4). Movement was highly correlated with feeding throughout the day ($r = 0.7404$, d.f. = 11, $P < 0.05$). Resting occupied the majority of each hour between 1000-1500 hrs (Fig. 4). Resting bouts coincided with highest ambient temperatures in the refuge. In Colombia, Defler (1979) found the foraging period of *C. albifrons* to occur from 0500 to about 1300 hrs, followed by rest until 1500 hrs and then foraging until 1600 or 1700 hrs after which they slept. Baldwin and Baldwin (1977) reported *C. capucinus* usually spend between 50-70% of daily activity in foraging and travelling. Gundersen (1977) reported active foraging periods between 0800 and 1000 hrs and from 1600 to 1800 hrs for *Colobus badius* monkeys during the dry season in west Africa, which approximates our results. The same author noted that in the wet season, activity patterns are more flexible, and suggested

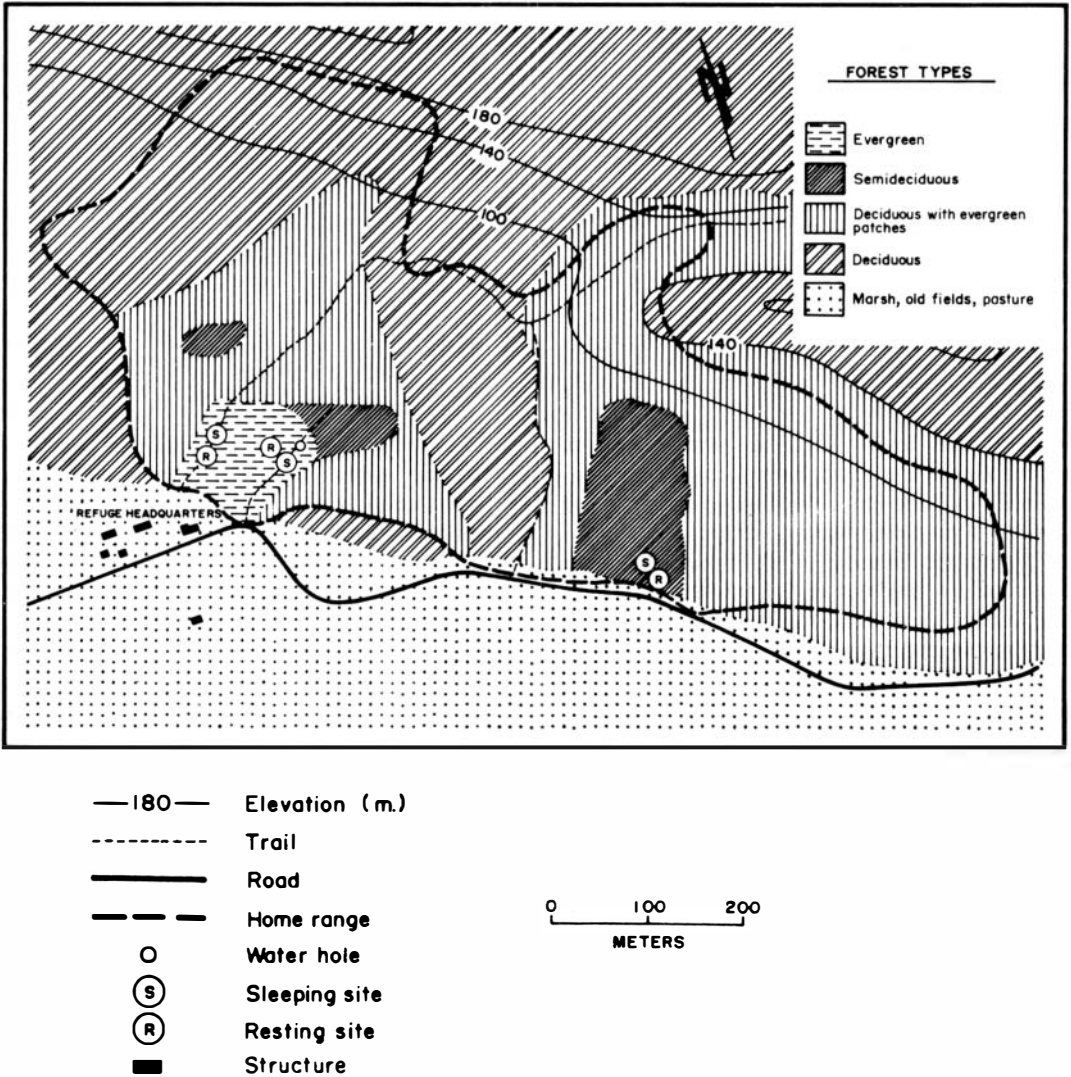


Fig. 1. Home range of a white-faced monkey (*Cebus capucinus*) troop. Palo Verde. March-April, 1982.

this was due to variation in daily temperatures and food sources.

Herbivory. Capuchins fed on 27 plant species (16 families), several insect species, and one vertebrate (Table 2). Plant parts eaten included; seeds, fruits, flowers, flower buds, leaves, young shoots, sap, and woody tissue.

Fruit was the primary food source in both months. Shifts from one plant food source to

another followed changes in the fruiting phenology in some cases. For example, ripe *Bauhinia* pods were abundant in March throughout the home range, but were absent in April. *Brosimum alicastrum* fruits were more plentiful in March than April, and *Muntingia calabura* was an abundant and much used food source in April.

The percentage of whole food units discarded or dropped and/or the portion of a unit

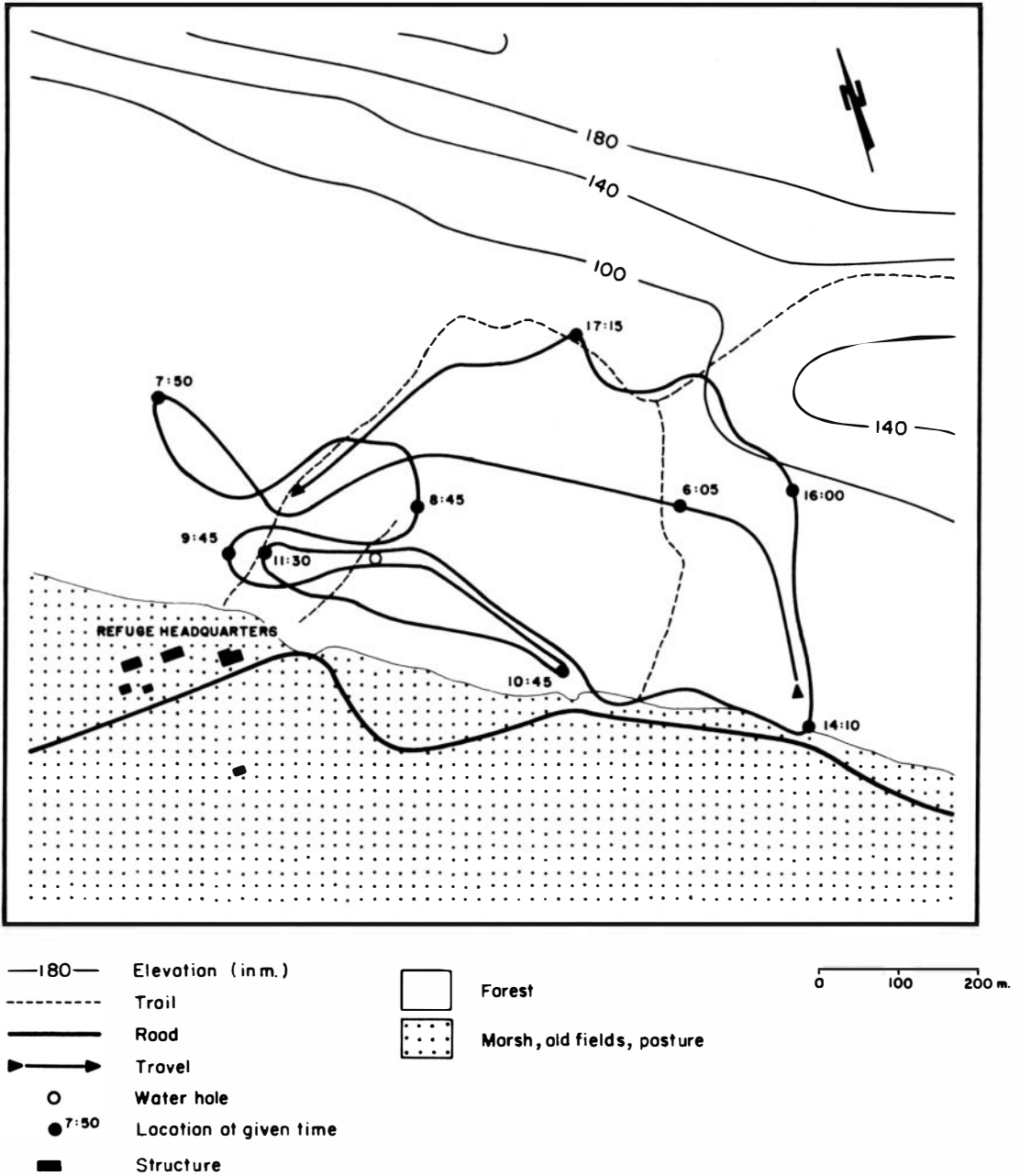


Fig. 2. White-faced monkey (*Cebus capucinus*) troop. movement. Palo Verde. March 12, 1982. Directed travel = 4.5 km.

rejected by a monkey varied between feeding events for a particular plant food. Discarded *Bauhinia* pods, for example, still contained an average 66% of their seeds, but some were picked clean of seeds. The capuchins ate 5 to 80% of the fleshy mesocarp of mangos. The

average percentages of seeds found in picked fruits after capuchin feeding was 70% in *Pithecellobium saman*, and 33% in *Brosimum alicastrum*. An average of 33% of fleshy fruit tissue of *Spondias purpurea* was rejected by capuchins. For *C. albifrons*, Defler (1979) found

TABLE 2

Percent of total feeding time spent on different foods by a white-faced monkey
(*Cebus capucinus*) troop. Palo Verde,
(March-April, 1982) a, b/

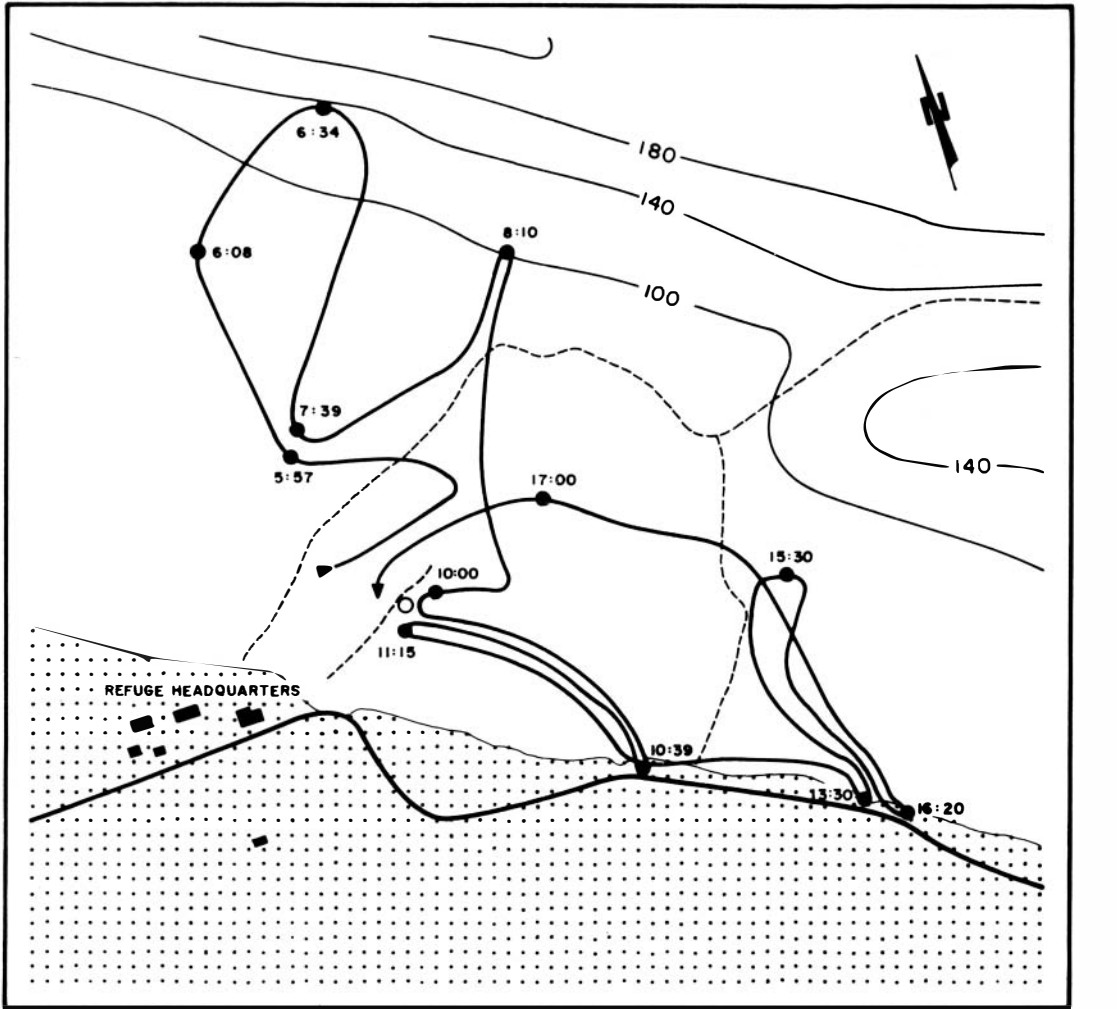
Species	Family	Plant Part Eaten.	Feeding Time (min.)	% of total feeding time
MARCH				
Fruits and seeds: c/				
<i>Bauhinia glabra</i>	Caesalpiniaceae	s	178	32.0
<i>Mangifera indica</i> *	Anacardiaceae	f	73	13.1
<i>Brosimum alicastrum</i>	Moraceae	s	47	8.5
<i>Muntingia calabura</i>	Elaeocarpaceae	s,m	40	7.2
<i>Spondias purpurea</i>	Anacardiaceae	f	40	7.2
<i>Bursera simaruba</i>	Burseraceae	f, ex,(s?)	40	7.2
<i>Pithecellobium saman</i>	Mimosaceae	s	21	3.8
<i>Ficus ovalis</i>	Moraceae	s, m	10	1.8
<i>Cecropia peltata</i>	Moraceae	fr	7	1.3
<i>Ceiba pentandra</i>	Bombacaceae	s	6	1.1
<i>Enterolobium cyclocarpum</i>	Mimosaceae	s	2	0.4
<i>Diospyros nicaraguensis</i>	Ebenaceae	s	2	0.4
<i>Xylosoma flexuosum</i>	Flacourtiaceae	fr	1	0.2
<i>Guazuma ulmifolia</i>	Sterculiaceae	s, (fr?)	(4)	
<i>Mastichodendron capiri</i>	Sapotaceae	?	(2)	
<i>Canavalia</i> sp.	Fabaceae	s	(2)	
Other Plant Parts:				
<i>Mastichodendron capiri</i>	Sapotaceae	flb	14	2.5
<i>Caesalpinia eriostachys</i>	Caesalpiniaceae	lf	13	2.3
<i>Astronium graveolens</i>	Anacardiaceae	sf	7	1.3
<i>Calycophyllum candidissimum</i>	Rubiaceae	flb	1	0.2
Unident. wood stick		wt	1	0.2
<i>Brosimum alicastrum</i>	Moraceae	sap	(1)	
<i>Enterolobium cyclocarpum</i>	Mimosaceae	flb	(1)	
Insects and Other Animals: d,e/				
unident., from ground			16	2.9
in/c:ast.			15	2.7
in/b:ast.			11	2.0
lizard (<i>Anolis cupreus</i>)			5	0.9
in/w, termite (Termitidae);				
<i>Trema micrantha</i>			4	0.7
in/w: <i>Guazuma ulmifolia</i>			2	0.4
in/dl.: ast.			(2)	
Total feeding time on fruits and seeds:			467	84.2
Total feeding on other plant parts:			36	6.5
Total feeding time on animals			53	9.6
Total observed feeding time			556	100.3
APRIL				
Fruits and seeds:				
<i>Muntingia calabura</i>	Elaeocarpaceae	s,m	361	54.9
<i>Brosimum alicastrum</i>	Moraceae	s	24	3.6
<i>Mastichodendrom capiri</i>	Sapotaceae	?	20	3.0
<i>Cassia grandis</i>	Caesalpinaceae	m, (s?)	14	2.1
<i>Cecropia peltata</i>	Moraceae	fr	13	2.0
<i>Ficus ovalis</i>	Moraceae	s,m	11	1.7
<i>Xylosoma flexuosum</i>	Flacourtiaceae	fr	10	1.5

Species	Family	Plant Part Eaten.	Feeding Time (min.)	% of total feeding time
<i>Astronium graveolens</i>	Anacardiaceae	?	10	1.5
<i>Guazuma ulmifolia</i>	Sterculiaceae	s, (fr?)	10	1.5
<i>Mangifera indica</i> *	Anacardiaceae	f	9	1.4
<i>Pithecellobium saman</i>	Mimosaceae	s	8	1.2
<i>Luehea candida</i>	Tiliaceae	s	8	1.2
<i>Acacia collinsii</i>	Mimosaceae	f,(s?)	3	0.5
<i>Sterculia apetata</i>	Sterculiaceae	s	2	0.3
<i>Spondias purpurea</i>	Anacardiaceae	f	1	0.1
<i>Piper tuberculatum</i>	Piperaceae	fr	1	0.1
<i>Enterolobium cyclocarpum</i>	Mimosaceae	s	1	0.1
Other Plant Parts:				
<i>Manilkara zapora</i>	Sapotaceae	fl	29	4.4
<i>Enterolobium cyclocarpum</i>	Mimosaceae	flb	21	3.2
<i>Caesalpinia eriostachys</i>	Caesalpinaceae	lf	16	2.4
<i>Pithecellobium saman</i>	Mimosaceae	fl	6	0.9
<i>Spondias mombin</i>	Anacardiaceae	st	2	0.3
<i>Enterolobium cyclocarpum</i>	Mimosaceae	wt	2	0.3
<i>Trichilia</i> sp.	Meliaceae	sap	2	0.3
<i>Mastichodendron capiri</i>	Sapotaceae	fl	1	0.2
Insects and Other Animals:				
in/b: <i>Enterolobium cyclocarpum</i>			14	2.1
in/b: ast			13	2.0
unident., from ground			13	2.0
in/dl. katydid (Tettigoniidae): <i>Sterculia apetata</i>			10	1.5
in/dl: ast			10	1.5
in/th: ast			6	0.9
in/w, andt (Formicidae): <i>Ceiba pentandra</i>			5	0.8
in/c: ast			1	0.2
wasp nets of <i>Polybia</i> sp. (nest, honey, larvae)			1	0.2
lizard <i>Anolis cupreus</i>				
Total feeding time on fruits and seeds			506	76.8
Total feeding time on other plant parts			79	12.0
Total feeding time on animals			73	11.2
Total feeding time			658 min	100.0

Key to symbols

- a/ For foods which lack feeding time data, the number of feeding events is given in parentheses.
- b/ A question mark in parentheses indicates that the plant part may or may not have been eaten.
- c/ Key to plant parts ingested
s = seed(s), f = fleshy mesocarp and/or endocarp, ex = exocarp,
m = sticky or juicy matrix surrounding seeds.
fl = flower, flb = flower bud, lf = leaf, st = young shoot, wt = woody tissue
sap = sap, fr = complete fruit including seed(s).
- d/ Key to insect foods (classified by method of procurement):
in/b = Insects obtained by stripping off bark,
in/w = Insects obtained by cracking or splitting woody tissue.
in/dl = Insects obtained through inspection of dead leaves on trees or shrubs,
in/th = Insects removed by hand from tree holes, and
in/c = Insects caught with cupped hand(s).
- e/ The plants harboring the insects are listed after the method of procurement symbols. ast = assorted plant sources.

(*) Not native to Guanacaste.



—180— Elevation (in m.)

----- Trail

———— Road

▶————▶ Travel

○ Water hole

● 7:39 Location of given time

■ Structure

□ Forest

▤ Marsh, old fields, pasture

0 100 200 m.

Fig. 3. White-faced monkey (*Cebus capucinus*) troop. movement. Palo Verde. March 25, 1982. Directed travel = 5.1 km.

80% of foraging time dedicated by monkeys to plant matter and 20% to animal matter. Hladik *et al.* (1971) reported an omnivorous diet for capuchins. The diet consisted of 65% fruit, 20% animals and 15% shoots, leaves and other vegetation.

During the dry season, in a tropical-dry forest in northwestern Costa Rica, Freese (1976) found *C. capucinus* to spend 11% of observed activity time feeding on insects and 26% on plants. The some author cited the most used fruit and seed sources in March and April as:

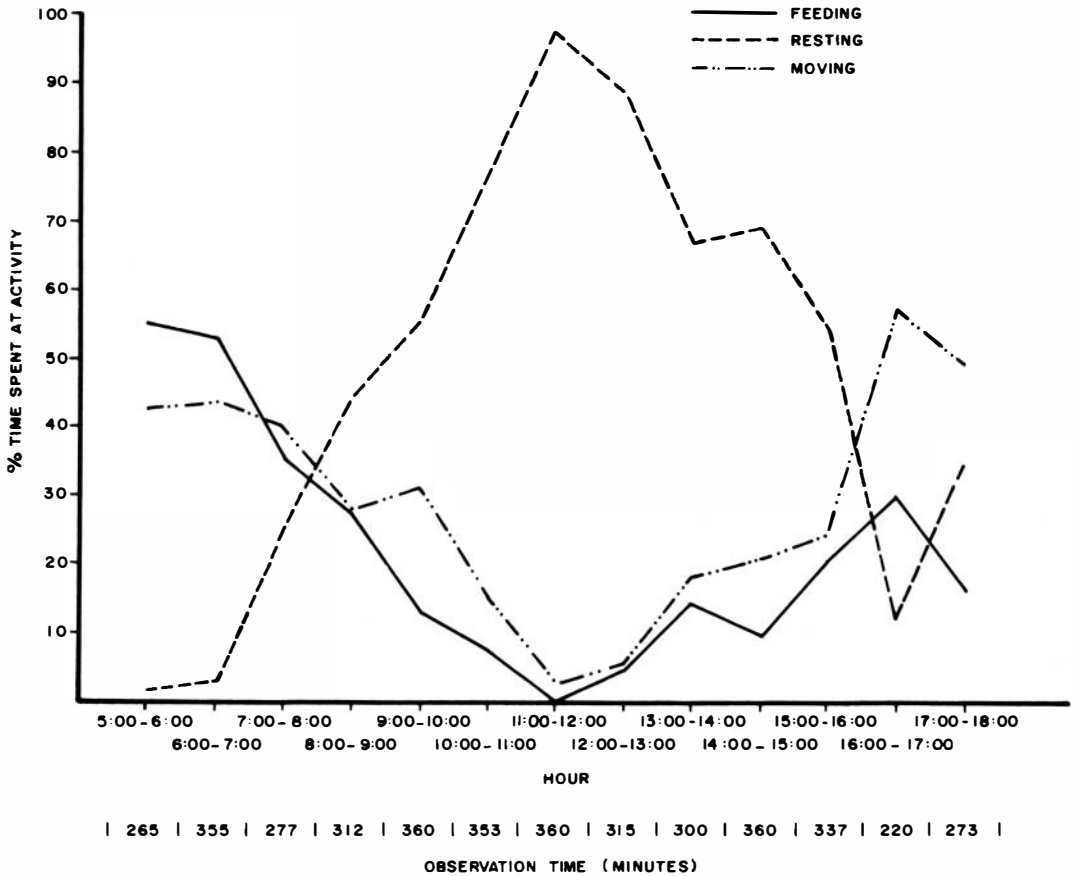


Fig. 4. Activity profile of a white-faced monkey (*Cebus capucinus*) troop. Palo Verde. March-April. 1982.

Bursera simaruba, *Ficus* sp., *Diptodendron costarricense*, and *Luehea candida*. Although *Bursera simaruba* and *Ficus ovalis* were also eaten in Palo Verde, they were not major food sources during the study period (Table 2).

Capuchins in Palo Verde spent only a small percentage of feeding time on foliage (4.6% in March and 3.6% in April). Hladik *et al.* (1971), in a comparative study of feeding habits of four sympatric monkey species on Barro Colorado Island, Panama, found that the leaf-eating howler monkey, *Alouatta villosa*, caught insects, while *C. capucinus* and *Saquinus geoffroyi*, spent 20 and 30% respectively, of their feeding time on animal prey.

Insectivory and Carnivory. Capuchins spent little time foraging on animals between 0500-0700 hrs and 1700-1800 hrs. Freese and Oppenheimer (1981) suggested that daily feeding begins with fruits because they are a readily

found carbohydrate source and that searching for insects is difficult under dim light conditions.

Feeding on animals in our study involved a variety of behaviors (Table 2). Adult capuchins frequently sought insects on the ground. Two monkeys caught and ate small *Anolis cupreus* lizards on the ground, one taking four min to consume all but the tail. Baldwin (1977) reported a capuchin grasping the tail of a large iguana (*Iguana iguana*) and after a struggle, breaking off the end segment and eating it. Capuchins in our study located a katydid, and thrust a cupped hand at the springing insect. During a one-hour period on 24 April, a young adult male fed on ten paper wasp nests (*Polybia* sp.), four of which harbored wasps. Swatting at the stinging insects, the monkey removed the nests thin outer layer and ate the honey and larvae-filled comb.

C. capucinus demonstrates considerable manual dexterity in removing seeds from fruits,

extracting insects from woody tissue, catching insects and other small animals, and other feeding behaviors. The superior manual abilities of this species were noted by various authors (Freese 1976, Jolly 1972, Moynihan 1976).

Drinking. The waterhole in the study area was found within the evergreen forest (Fig. 1) in close proximity to major sleeping and resting sites. Both evergreen forest and water availability influenced capuchin home range and movements during the dry season. At least during the dry season in Palo Verde we agree with Freese (1978) that *Cebus* troops are limited to areas where water is present.

Drinking was observed during all five study days in April, but on only two of five days in March. Our presence might have affected the monkey's behavior more in March when the troop was less accustomed to us. In April, adult males drank from one to three times daily between 0641 and 1736 hrs while females and juveniles drank less often, perhaps because they were more timid to our presence. Capuchins approached the waterhole cautiously, and of the three occasions in which the first drinker was observed, the leader was an adult male. Freese (1978) found that adult males led drinking processions.

Stress periods. This study was carried out during the latter part of the dry season, when water was a limiting factor and may have caused troop concentration around waterholes in addition to defense of these water sources by the monkeys. We did not observe any other *C. capucinus* troops in the evergreen forest during this study. Food sources seemed sufficiently abundant for the monkeys, as evidenced by the prolonged resting periods taken around midday. McCoy (1985) found that collared peccary (*Tayassu tajacu*) herds in Palo Verde showed variation in movement patterns, home range and activity and he suggested that this was correlated with food availability, increased movement in search of water or travel between foraging sites and cool bedding areas. Both Bigler (1974) and Day (1977) noted this latter trend with peccaries in Arizona. Perhaps year-long studies would show clear periods of food resource scarcity and an optimal foraging strategy for the primates, such as McCoy (1985) found for collared peccaries during November-

December and May-June when movement and home ranges increased and less than optimal foods were found in feces.

RESUMEN

El radio de acción, patrones de movimiento, actividad y dieta de una manada de 16 individuos de mono carablanca (*Cebus capucinus*) fueron estudiados en un bosque seco-tropical de Costa Rica a finales de la época seca (marzo y abril) de 1982. La tropa se desplazó en un área de 0.67 km², y recorrió un promedio de 4.5 km ± 0.6 diarios. Se identificaron tres actividades básicas diarias: descanso, movimiento y alimentación. Descansaron más entre las 1000-1500 hrs. El movimiento de la manada estaba fuertemente correlacionado con la alimentación y ocurrió más entre las 0500-0900 hrs y 1300-1800 hrs.

Los primates son omnívoros y consumieron partes de 27 especies de plantas, cuatro de insectos y una lagartija del género *Anolis*.

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