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SHORT COMMUNICATIONS

Seasonal and Habitat Differences in the Abundance of Primates in the Amazon (Tapajos) National Park, Brazil

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ABSTRACT. Twelve species of primates occur in the Amazon (Tapajós) National Park. The abundance of these species varies with habitat type and extent of human disturbance. Seasonality of rainfall and river level significantly affect the abundance of primates in seasonally inundated forest but not in upland forest types.

INTRODUCTION

The distribution and abundance of primates in the Amazon (Tapajós) National Park are determined by a complex set of historical, human and environmental factors. Species ranges are in part limited by the Tapajós River (SICK, 1967; ÀVILA-PIRES, 1974). Six primate species occur on a particular side of the river, six others are common to both sides, and two species have distinct subspecies on each side of the river (HILL, 1962; HERSHKOVITZ, 1963) (Fig. 1).

The Tapajós River, like other rivers in the Amazon Basin, is subject to an annual rise and fall in river level which largely corresponds with the seasonal distribution of rainfall. Recent studies have shown that the regularity of these cycles has favored the development of complex interactions between flooded forest and aquatic communities (GOULDING, 1980). However, very little is known about the relationship between seasonality in riverine forests, or other Amazonian forest types in general, and terrestrial animal communities. The only published report on primates of the Amazon (Tapajós) National Park is a brief survey by AYRES and MILTON (1981). In the present study the distribution and abundance of primates were examined in upland and riparian forests during the wet and dry seasons as part of a general faunal survey of the park.

METHODS

STUDY AREA

The Amazon (Tapajós) National Park is located on the Transamazon Highway, 54 km south of Itaituba, Pará, Brazil, between 3°50′ and 5° S, 56°15′ and 57°32′ W. It incorporates about 1,000,000 ha on the northwest bank of the Tapajós River, a southern clear-water tributary of the Amazon River. The inclusion of an additional 10-km wide band running the length of the park on the southeast side of the Tapajós River has been proposed (IBDF/FBCN, 1979). This strip was included in the survey.

The major forest type in the park is high forest (15–30 m) occurring on *terra firme* (ground that never floods), with interspersed patches of low forest (10–15 m) characterized by an abundance of lianas. *Varzea* forest (PRANCE, 1978) occupies the narrow flood plain of the Tapajós

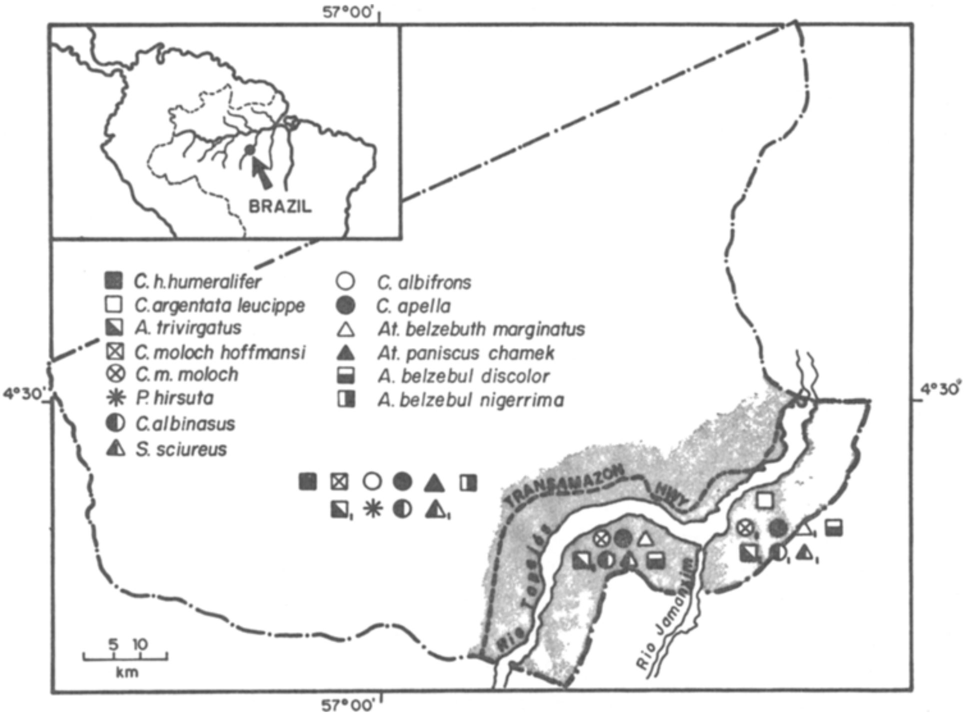

Fig. 1. Distribution of primates in the Amazon (Tapajós) National Park. Symbols with subscript 1 represent species which were not sighted during this survey in a particular area but were reported by local residents. Park boundaries show the new limits proposed by IBDF/FBCN (1979). Censusing was confined to the shaded area.

River and its tributaries and floods between January and April or early May. Slash and burn agriculture and road building have created second-growth formations along the river and the Transamazon Highway. Forests along the first 20 km of the Transamazon Highway in the park and near Pimental, a village on the southeast side of the river, have been selectively logged.

The mean annual rainfall for the area is 1,754 mm (1971–1977, Meteorological Station No. 82445, Itaituba) with a pronounced dry season from July to November. Highest rainfall generally occurs in February and March and is about five times that of August, the driest month.

SURVEYS

Primate surveys were conducted on foot, by canoe and by motor boat from August 1978 to November 1979. Most were undertaken between the months of March and May as river levels began to drop and between July and November during the height of the dry season (Table 1). Surveys were not conducted during rain or between 1200–1400 hours when primate activity was low.

Transects (trails 3–20 km long) extended roughly perpendicular to the river and the Transamazon Highway throughout the length of the park, traversing *varzea* and primary (high and

Table 1. Distances censused (km) according to habitat type and season.*

River margin	Season	Secondary forest	Select. cut	High forest	*Varzea*	Low forest
Southeast	W	0.82	—	15.84	14.38 1)	—
		—	—	—	57.33 2)	—
	D	9.69	1.20	29.50	26.13	3.86
Northwest	W	7.66	14.68	18.28	8.05 1)	5.05
		—	—	—	63.88 2)	—
	D	12.45	7.91	20.63	8.81	6.05
Total		30.62	23.79	84.25	22.43 1)	15.41
					121.21 2)	
					34.94	

*Censuses were conducted on foot, 1) by canoe, or 2) motor boat. W: Wet; D: dry.

low), secondary, and selectively-cut *terra firme* forests. Surveys were conducted while walking slowly (about 1.5 km/h) and recording the number of paces in each habitat along the transect with a mechanical counter. Paces were multiplied by mean pace length to estimate distances.

All trails surveyed in the wet season, and some additional trails, were surveyed during the dry season. *Varzea* areas which were censused by canoe during April and May were surveyed on foot from July–September. Data from canoe surveys were recorded and analyzed in the same manner as surveys on foot except distance traveled was estimated in 5-m intervals.

The margins of the Tapajós River and a small tributary, Igarapé Tracôa, were surveyed by motor boat only during the wet season; the shoreline was impossible to navigate during the dry season. Observations from the boat were made on one river margin at a time while traveling 3–10 km/h. Distances were estimated using travel time over known distances and maps.

For all primate sightings during and outside survey hours, the locality, time, weather, habitat, height of vegetation, group size and activity were noted. Detection distance (distance of the group from the observer when first seen) was also recorded during censuses on trails.

Variation in number of groups sighted among transects was high even within a particular habitat type, but estimates of this variation are not presented because raw data for individual transects were lost in a fire and only summarized tables remained. Though absolute densities are often derived from transect censuses of primates (Freese et al., 1982; Cant, 1978, etc.) and are necessary for solving certain problems, primates do not fit many of the assumptions which underlie transect models (see Eberhart, 1978, for discussion of assumptions of transect censusing; see Janson & Terborgh, in press, for review of these techniques as applied to primates). This is a special problem when surveying several species simultaneously. Therefore I used an index of density (number of groups seen/10 km of transect) and did not attempt to derive absolute densities by correcting for species-specific differences in detection distances and other behavioral biases. Detection distance (expressed here as the average of the maximum and mean detection distance for all sightings of a species) is simply given as one indicator of the difficulty of sighting a species. A measure of variance is not reported since these data were also lost.

RESULTS AND DISCUSSION

General Abundance and Biases in Census Methods

With a total of 333 km censused, this survey revealed 10 of the 12 species known to be in the area (Table 2). *Aotus* is usually nocturnal and was not recorded. *Callithrix argentata*

Table 2. Indices of density (groups/10 km censused) for each species according to habitat and season.*

			Habitat				
Species	*N*	Season	Second.	Sel. cut	Low	High	*Varzea*
Callithrix humeralifer	7(1)	W	6.52	0.68	1.98		(0.16)$^{2)}$
	0	D					
Callicebus moloch	1	W	1.18				
	0	D					
Saimiri sciureus	1	W				0.29	
	0	D					
Cebus apella	20(3)	W	1.18	4.77		2.05	2.23$^{1)}$(0.25)
	12	D	1.36		1.93	1.20	0.29
Cebus albifrons	0	W					
	1	D	0.80				
Pithecia hirsuta	2(1)	W	1.31	0.68			(0.16)$^{2)}$
	0	D					
Chiropotes albinasus	9(1)	W		1.36		0.88	1.78$^{1)}$(0.08)
	5	D				0.80	0.29
Alouatta belzebul	15(13)	W		0.68		1.17	4.46$^{1)}$(0.82$^{3)}$,1.20$^{4)}$)
	4	D		3.29			0.29
Ateles paniscus	0	W					
	1	D				1.13	0.18
Ateles belzebuth	2	W					1.39$^{1)}$
	4	D				1.36	

*Data are from foot and 1) canoe censuses with motor boat census in parentheses; 2) sightings along Igarapé Tracôa; 3) index for *A. belzebul discolor*; 4) index for *A. belzebul nigerrima*. W: Wet; D: dry.

leucippe was sighted only during the initial phases of the survey by another researcher (Vivo, 1979). It is restricted to a small portion of the proposed area, south and east of the Tapajós River to the Jamanxim River (Hershkovitz, 1977) (Fig. 1). Though range maps for *Lagothrix lagothricha* include the area occupied by the park (Àvila-Pires, 1974), this species was not encountered in this survey and according to knowledgeable inhabitants of the area occurs only further south on the Tapajós River.

Surveys on foot and by motor boat and canoe were not equally effective in sampling primate populations in the park. Ten species were recorded from forest trails, but only three species (*Cebus apella*, *Alouatta belzebul* and *Chiropotes albinasus*) were observed from the motor boat along the main Tapajós River (Table 2). *Alouatta belzebul* accounted for 93% of the sightings from the motor boat. The three species observed on the main Tapajós River from the motor boat, as well as *Ateles belzebuth*, were also sighted inside the *varzea* forest from a canoe. The differences in sightings along the river and trails are partly due to habitat preferences of the species, but discrepancies between motor boat and canoe censuses also suggest possible biases in the techniques. In the same section of *varzea* forest, the number of sightings of howler monkeys relative to all other species combined was higher in the motor boat surveys than in canoe surveys. With a larger sample size this difference ($\chi^2 = 3.81$, $d.f. = 1$, $p = 0.051$) may be statistically significant. The time of the survey appeared to be particularly important with motor boat surveys. In early morning and late afternoon groups of howler monkeys occupied large emergent trees and were visible from a considerable distance on the river. Approximately equal distances of shoreline were covered during all periods of the day from 0630 to 1730. Twelve groups of howler monkeys were encountered between 0630–0730 and 1600–1730. Only one group was seen outside these hours and this was during a period of heavy rain at 1530. With other census methods primates were sighted throughout the day.

Combining data for all census methods, three species (*C. apella*, *Alouatta belzebul* and *C.*

albinasus) accounted for 79.6% of the sightings, and *Ateles belzebuth* and *Callithrix humeralifer* another 13.6%. In some cases the apparent rarity of other species probably truly represents the population in the censused area, but the low numbers of some species may result from sampling or visibility biases. *Callicebus moloch* was encountered only during the wet season, but was heard vocalizing during both seasons. Numerous residents of the area mentioned its occurrence in the second growth distributed in patches in the park. *Cebus albifrons* was encountered only once during censuses, but was sighted five times outside of census hours in *varzea* and secondary forests during the wet and dry seasons. *C. moloch* and *C. albifrons* are probably both more common than survey data indicate.

Ateles paniscus and, particularly *Saimiri sciureus,* occur in fairly large groups, are often noisy, and not likely to be overlooked in a survey. *A. paniscus* is sensitive to human disturbance and may be more abundant in inaccessible areas of the park. *S. sciureus* was sighted only once and was in a mixed band with *C. apella.* This species occupies a wide range of habitats, but appears to prefer river margins (MITTERMEIER & COIMBRA-FILHO, 1977). The low numbers in the park may be a function of the relatively narrow flood plain along the Tapajós River.

DETECTION DISTANCE AND GROUP SIZE

No relationship was found between habitat and the detection distance of *C. apella,* the only species recorded in all habitats (One Factor Analysis of Variance, $F_{4,12} = 0.38, p<0.50$). In general all habitats were relatively dense and visibility did not change appreciably. Sufficient data were collected to test for seasonal trends in detection distances of the three most commonly sighted species. There were no significant differences between the wet and dry season (paired t-test, $t_2 = 1.43, p<0.20$). Therefore data on detection distance were combined for the five forest types over both seasons.

Detection distances differed considerably among species (Table 3) and in part reflect differences in the response of the species to the observer. *Ateles belzebuth* and *C. albinasus* had the largest detection distances. These species generally vocalized profusely and remained stationary or came closer to the observer rather than fleeing immediately. *C. apella* usually bounded noisely away from the observer. *Pithecia hirsuta*[1] was always extremely quiet and had the smallest detection distance. I often located *C. humeralifer* by vocalizations. Small body size probably contributed to the low detection distance in this species.

Group sizes were compared for wet and dry season for each species using a Student's t-test. Since no significant differences were found at $p<0.05$, overall means are given for minimum counts (minimum number of animals in a group) and best counts (groups in which I am reasonably sure all individuals were counted) (Table 3). Most group sizes reported here fall within the range of values reported for the same species in other studies (see MITTERMEIER & COIMBRA-FILHO, 1977; COIMBRA-FILHO & MITTERMEIER, 1981; for reviews), but few comparative data are available for *C. humeralifer humeralifer* and *Alouatta belzebul.* RYLANDS (1981) observed *C. humeralifer intermedius* in groups of 4 to 13 individuals, but repeated counts on four groups yielded group sizes ranging from 8 to 12. He noted that individuals

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1) This name is based on the ranges given by HERSHKOVITZ (1979) in his revision of the genus *Pithecia.* Since I became aware of this work after my survey, I did not confirm the distinguishing characteristics of this species in the field and recorded it as *P. monachus.*

Table 3. Detection distance, minimum group count and best group count for each species.

		Detection distance1)	Minimum counts			Best counts		
Species	*N*	(m)	*N*	$\bar{X}\pm$S.D.	Range	*N*	$\bar{X}\pm$S.D.	Range
Callithrix humeralifer	7	27.5	7	4.49±1.70	1–6	4	5.67±0.58	5–6
Callicebus moloch	—							
Saimiri sciureus	1	20.0	1	8				
Cebus apella	22	45.0	27	5.61±3.29	1–14	6	7.83±4.79	2–15
Cebus albifrons	1	40.0	1	3				
Pithecia hirsuta	2	27.3	3	1.00±0		3	1.00±0	
Chiropotes albinasus	10	51.0	14	7.21±3.66	1–15	5	9.40±4.22	4–15
Alouatta belzebul	4	29.8	18	4.60±1.81	2–8	10	6.19±1.32	5–8
Ateles paniscus	1	40.0	1	6				
Ateles belzebuth	4	58.5	6	4.17±3.09	1–12	4	7.25±4.86	1–12

1) Average of the maximum and mean detection distances for each species.

or pairs often traveled separately from the main group for extended periods of time, which suggests that my counts for *C. h. humeralifer* may be low. *Alouatta belzebul* occurs in fairly small groups, comparable to or slightly smaller than the group size of *A. seniculus* and *A. caraya*, but about one-half to one-third the size of those reported for *A. palliata*. (For review of group size in *Alouatta*, see NEVILLE, 1972.)

HABITAT PREFERENCES

Approximately the same number of species were encountered in all habitats except low forest, but indices of density for individual species differed greatly among habitats (Table 2). All primates except *Ateles* spp. tolerated some degree of human disturbance. In other studies *Ateles* has been recorded in secondary forest (e.g., GREEN, 1978), and its restriction to primary forest in the park may result from increased hunting pressure in disturbed areas which are usually near houses and settlements rather than from habitat modification. *C. albinasus* and *Alouatta belzebul* were found in all areas with reasonably tall forest. *C. h. humeralifer* was most abundant in disturbed areas, often near houses, or in natural low forest. These observations are consistent with RYLAND's (1981) conclusion that *C. h. intermedius* requires dense vegetation or disturbed forest. The only sighting of *C. h. humeralifer* in riparian forest was at the edge of the *varzea* adjacent to an agricultural plot on *terra firme*. MITTERMEIER, BAILEY and COIMBRA-FILHO (1977) commented on the absence of callitrichids from flooded forest and suggested that the small primate niche was filled by *S. sciureus* in some areas. In this study *C. apella* was the smallest primate regularly recorded in the *varzea* and used the greatest range of habitats. The adaptability of this species is well documented (MITTERMEIER & ROOSMALEN, 1981). More data are needed to determine habitat preferences for the other species.

SEASONAL PATTERNS

For most reasonably common species, there was an overall trend of lower abundance in the dry season in all areas (Table 2). However, the only statistically significant seasonal difference within a habitat was in *varzea* (paired *t*-test, $t = 3$, $d.f. = 4$, $p < 0.05$). With a larger sample size, seasonal differences in primate abundance might also be apparent in secondary forest

($t = 2.44$, $0.05 < p < 0.10$). Observed group sizes did not vary with season, but the number of sightings was reduced.

The increased density of primates in the *varzea* during the wet season may result from ranging of animals from adjacent *terra firme* forest into *varzea*. If this were so there should be a drop in primate numbers in *terra firme* forest during the wet season and a rise in the dry season. This trend was not detected which suggests that animals may be moving over long distances. Alternatively, the addition or removal of animals from *terra firme* forest may not be apparent above the inherent variability encountered while censusing since the *varzea* forest has a maximum width of about 600 m in the study area and accounts for a very small area in comparison to the *terra firme*.

Seasonal changes in behavior in response to resource availability have been documented far more extensively for primates than for other rain forest mammals, including switching of food sources, changes in group dispersion and modification of ranging behavior (see CLUTTON-BROCK, 1977, for review). No data are available on the phenology of the Tapajós River which might serve as a basis for evaluating the seasonal availability of food for primates in the area. However studies of the Tocantins River, a neighboring tributary on the Amazon which has a similar flood regime, show that phenology is closely tied to river level and rainfall. In the flooded forest, fruit production begins as the water rises; mature fruit falls as the water recedes; fruiting activity is very low during the dry season (REVILLA, pers. comm.). Fruiting activity in the upland forest does not exhibit this pronounced synchrony. Generally tree species diversity is lower in *varzea* forests (PRANCE, 1978) than upland forests and may thus result in higher densities of any one species in fruit at a given time. Studies in other parts of the central Amazon Basin have shown that insects, which serve as prey for omnivorous primates such as *C. apella*, increase during the wet season in both upland and flooded forests (PENNY & ARIAS, 1982). This phenomenon is particularly notable in *varzea* forest where arthropods migrate up trees to escape the rising water (ADIS, 1977). If these patterns of fruiting and insect abundance hold for the Tapajós River, food for primates may be particularly abundant in *varzea* forest during the four months of inundation and more widely distributed in time and space in the upland forest. The distribution of primates in the park may largely reflect this pattern.

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