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The Time Budget of a Group of Wild Woolly Monkeys *(Lagothrix lagotricha)*

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I studied a group of woolly monkeys (Lagothrix lagotricha) *for 1800 hr from early 1985 until September 1987 near the lower Apaporis river of the Vaupés Department in the eastern Colombian Amazon. The group had an activity budget of 29.9% rest, 38.8% move, 25.8% forage, and 5.5% other activities during 720 hr of observations evenly spaced throughout this year. The only significant change in these activities during the study period was social activity, which increased as a function of increased food supply. Average diurnal activities of resting and moving are negatively correlated, and each activity show significant changes during the day, while foraging show no significant change. The activity budgets of the adult males and females are not significantly different, but the activities of the juveniles and infants showed much more social activity than the adults. High moving scores may be correlated with the comparative infertility of the soils of the Caparú forest, which require increased effort to maintain the energy levels necessary for maintenance and reproduction in* Lagothrix.

KEY WORDS: Lagothrix lagotricha; time budget; activity budget.

INTRODUCTION

An understanding of how animals divide up their activities throughout the day and the year is important for understanding their lifestyles. Most animals spend a great deal of their time in feeding-related behaviors, while spending much less time in social behavior. Time budgets indicate in a

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general way how primates interact with their environment temporarily, and they imply the investment in energy and time that is necessary for activities important for the animals' survival and reproduction.

Woolly monkeys (*Lagothrix lagotricha*) are large frugivores, averaging about 7 kg, though adult males usually weigh more than adult females do, and males possess much more developed canines and more heavily developed bodies (Hernández-C. and Defler, 1989; Defler, personal observation). Their diet obligates them to travel quite a lot and to exhibit large home ranges, since increased group weight and frugivory correlate positively with travel time and home range size (Milton and May, 1976; Oates, 1987; Dunbar, 1988). However, these dietary correlations are confounded by the characteristics of food patch size and other variations in different home ranges (Strier, 1987), which in turn may be influenced from site to site by factors such as soil fertility and precipitation (Janzen, 1974; Emmons, 1984; Junk and Furch, 1985; Gentry and Emmons, 1987). It may be easier to describe the physicochemical characteristics that effect food patch sizes from site to site than to describe the actual variation in food patch size throughout the year. But all of these features — proximate and ultimate — are needed to understand intraspecific differences in group characteristics such as time budgets.

I report data on the activity budget of a group of woolly monkeys in eastern Colombia and compare them to conspecifics at another site. The Caparú forest may represent in its edaphic poverty a habitat that is more representative of great extensions of the Amazon basin than other research sites, which are often picked for their high primate biomass. Comparisons between divergent Amazonian sites promise to define ecosystemic processes that may seem overly simplified if studied only at fertile sites (NRC, 1980).

METHODS

The Study Site

The Estación Biológica Caparú (1°15′S, 69°35′W) is located north of an oxbow lake formed from the lower Apaporis River in the Department of Vaupés in extreme eastern Colombia (Fig. 1). The area used by the study group consists of primary rain forest growing as the following communities: (1) igapó or seasonally flooded blackwater forest, (2) Pleistocene river terrace, (3) dissected low clay soil hills of Plio-Pleistocene origin, and (4) floodable lowlands along various creeks (Carvajal *et al.*, 1979). This lowland primary Amazonian forest has an annual mean temperature of 25.1°C and an annual precipitation of 3995 mm (n = 8 years), as measured at the research site.

Fig. 1. Map of location of study site (Estación Biológica Caparú) in SE Colombia.

Data Collection

I collected data for 5 days each month from October 1986 through September 1987 after previously habituating the group with other observations totaling about 1100 hr. I used a slow data scan patterned after Altmann (1974) and Robinson (1981). This consists of an effort twice each hour to record what each member of the group was doing for ≥5 sec per individual. I began a scan at 5 min after the hour and 35 min after the hour. Each complete scan lasted ≤20 min as I attempted to record the activity of as many independently locomoting individuals as possible. I moved from place to place to obtain adequate views. Since the animals had been well-habituated by my earlier observations, moving about on the forest floor generally caused no change in ongoing behaviors. My daily observations began at 0535 and finished during the period 1705–1725, though I usually accompanied the monkeys for 20–30 min after this time, to mark their sleeping positions on the map so as to facilitate locating them early the next morning.

I recorded the following activities on a prepared data sheet for each scan sample.

Rest: Any immobile position, whether standing, sitting, reclining, or suspensory, that did not include obvious interactions with another individual or with another object, except for objects such as substrates.

Move: Any mobile activity, whether walking, running, climbing, jumping, swinging, or brachiating within the same tree or between different trees.

Foraging: Any handling, ingestion, chewing, or obvious search for foods.

Social Behaviors: Any direct interaction between two or more individuals, including playing, grooming, contact, or agonistic — fighting or displacement.

Nonsocial Behavior: Other individual activities such as urinating, autogrooming, chest-marking, or defecating that did not involve an obvious direct interaction with another individual.

I considered a mother carrying an infant a special case with respect to the following: I recorded the mother's behaviors such as moving and foraging as such, irrespective of the attached infant. I scored only independently locomoting infants in focused observations.

The observations for the activity budget represent 720 hr of direct observation. I scored a total of 8863 individuals during 1434 slow scans for an average of 6.18 individuals per scan. The scored individuals are as follow: adult male (1102), adult female (2376), juveniles (600), infants (472), and individuals not identified to age/sex class (4313).

The focal group varied from a subunit of 3 individuals to 24. One complete count of the group on March 13, 1987, yielded 4 adult males, 11 adult females, 1 juvenile male, 2 juvenile females, and 6 infants, for a total of 24 subjects. I rarely obtained complete counts, and I saw unknown animals, especially females, occasionally.

Adult animals are the largest in the group. Adult males had well-developed and pendant testicles and heavy musculature around the shoulders and head. The males are the most easily recognized as individuals, due to scarring around head and body. The single juvenile male was almost as large as a female, but he did not have large, well-developed testicles or the well-developed musculature of an adult male. Juvenile females are smaller than adult females. They sometimes associated with a larger female. Infants are sometimes or often carried. They belonged to a cohort of small animals that were similar in size, due to the birth season from April to September, which facilitated their recognition.

Of the 4757 individuals identified to age class, 23.2% are adult males, 50% are adult females, 14.5% are juveniles, and 8.1% are infants. The actual makeup of the group is about 22% adult males, 34.8% adult females, and 44% juveniles and infants. Adult females are slightly overrepresented

Table I. Comparison of Two Methods to Calculate Time Budget[a]

Activity	Frequency (total score)	Proportion (average monthly score)
Rest	0.285	0.299
Move	0.39	0.388
Forage	0.253	0.258
Social	0.055	0.048
Nonsocial	0.007	0.007

[a] $T = 6, n = 5, p > 0.05$ (Wilcoxan matched pairs test).

in the sample, while the younger age classes are slightly underrepresented. Perhaps increased confidence on the part of adults and their size, allowed them to be more easily seen in the foreground.

I converted raw data for each day to a percentage of 1 so as to reduce biases arising from unequal samples. I averaged them across each month to produce monthly and annual scores (NRC, 1981; Struhsaker, 1975). Later, I compared the overall activity budget obtained by converting each scan to a percentage score to that obtained by calculating behavior frequencies by adding all activity records over the entire 720 hr. There is little difference between the two annual activity budgets obtained from the two methods (Wilcoxan matched-pairs test, $T = 6$, $n = 5, p = 0.05$; Table I). This allowed me to perform further analysis based on both the percentage conversion — monthly budgets and average diurnal time budgets — and the total frequencies of the scan sample — age-sex budgets.

Phenology

I compared the time budget to phenological data collected on the availability of mature fleshy fruits — the major dietary component of *Lagothrix*. It represents 83.2% of the diet of my study group (T. Defler, in preparation). New leaves represent 11.4% of the diet of this group (T. Defler, in preparation) per research of Sara Defler (in preparation) for the same period and for the same plant communities utilized by the study group (Figs. 2 and 3). We collected data via monthly observations on phenological events of all trees >12 cm DBH from 10 plots established at random (measuring 50 × 20 m per plot) from each of the major plant communities — igapó, river terrace, and hill. The phenological events include developmental state and number of fruits, percentage of new leaves,

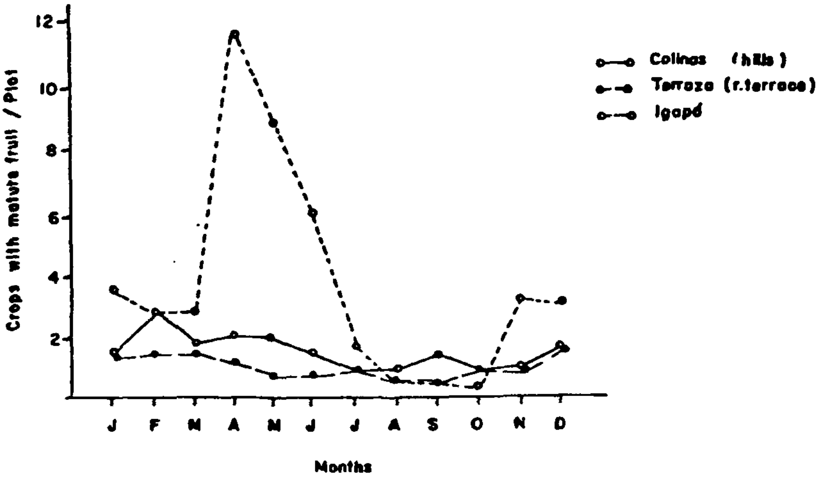

Fig. 2. Monthly average number of trees (crops) with mature fruits per plot in each of the major plant communities. Plots measured 50 × 20 m; 10 plots studied per plant community (S. Defler, in preparation).

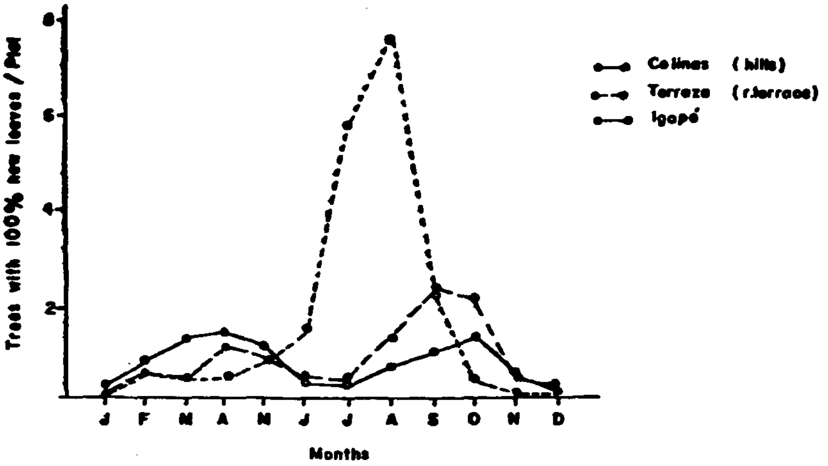

Fig. 3. Monthly average number of trees with new leaves per plot in each of the major plant communities. Plots measured 50 × 20 m; 10 plots studied per plant community. Each individual with new leaves was weighted by the percentage of canopy that is new, e.g., 1 individual with 10% + 1 individual with 90% = 1 (S. Defler, in preparation).

Table II. Time Budget for *Lagothrix lagotricha*

Sample time	Rest	Motion	Forage	Social behavior	Nonsocial behavior
Oct. 1986	33.2	44.4	20.7	1.2	0.5
Nov. 1986	40.4	32.6	24.8	1.9	0.3
Dec. 1986	28.4	36	28.8	6.5	0.3
Jan. 1987	27.6	38.3	27.5	6.1	0.5
Feb. 1987	24	44.9	22.4	7.4	1.3
Mar. 1987	21.6	39.9	29.1	9	0.4
Apr. 1987	32.4	32	26	8	1.6
May 1987	22.1	39.1	33	5.5	0.3
June 1987	22.6	45.8	27.5	3.2	0.9
July 1987	33.1	39.1	20	6.6	1.2
Aug. 1987	31.7	39.6	27.5	1.1	0.1
Sept. 1987	41.5	33.9	22.2	1.7	0.7
Mean	29.9	38.8	25.8	4.85	0.675
SD	6.747	4.635	3.88	2.864	0.473
Variance	45.53	21.49	15.06	8.2	0.22
Median	30.05	39.1	26.75	5.8	0.5
G test	16.163	10.341	6.244	21.0402	9.1796
p (df = 11)	>0.5	0.5	>0.9	<0.05	>0.5

and quantities of buds and flowers. We did not collect phenological data for vines, even though they represent about 26.5% of the monkey's diet.

RESULTS

Annual and Monthly Activity Budgets

The Caparú woolly monkeys average 29.9% resting, 38.8% moving, 25.8% foraging, 4.8% in social activity, and 0.7% in "nonsocial activities" (Table II). No significant variation in the frequency of resting, moving, and foraging was found, although there was a significant variation in the frequency of social behavior during the year ($G = 21.04016$, $p > 0.025$) when the G test was applied to each category, where the observed monthly percentages were compared to the expected value, which was considered to be the mean of the monthly means.

Average Diurnal Time Budget

Figure 4 shows the average diurnal activity cycle for resting, moving and foraging. Average diurnal resting exhibits a significant high around

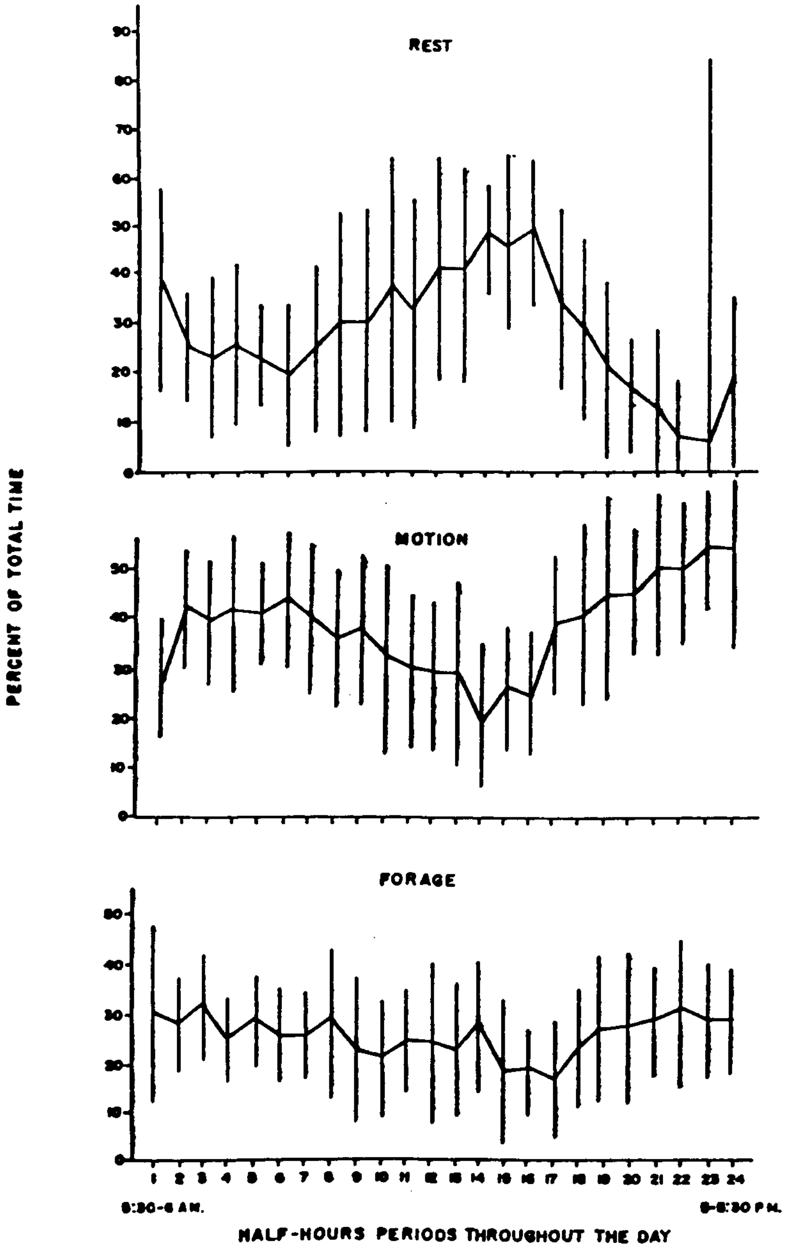

Fig. 4. Average diurnal activity cycles.

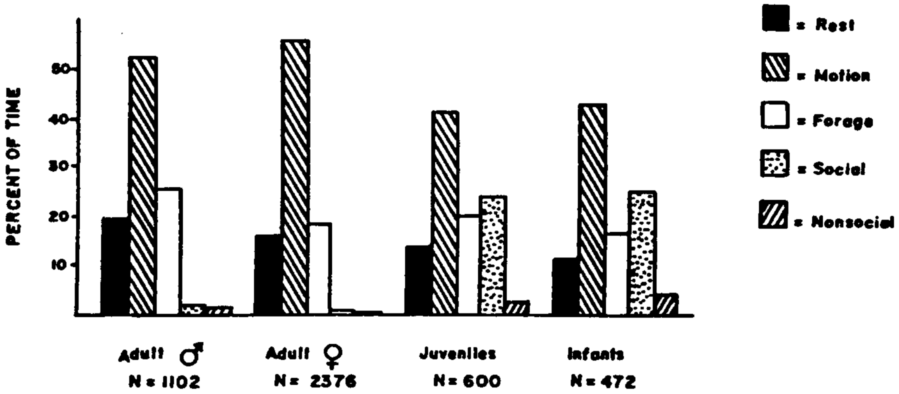

Fig. 5. Comparison of activity budgets in different age-sex categories.

midday ($G = 93.525, p < 0.005$). Average diurnal motion also shows a significant negative change at midday ($G = 53.514, p < 0.005$), and average diurnal resting behavior is inversely correlated with diurnal movement ($r = -0.94704$, $N = 24$, $p < 0.001$). Average diurnal foraging exhibits no statistically significant change throughout the day.

Age–Sex Classes

Since there is very little difference between the conversion into monthly percentage scores (Table I) and the percentage/time budget calculated over the entire frequency score for the complete study period, and because there were time periods when infants and juveniles were not observed, I analyzed age and sex classes based on the entire annual scores, rather than using the conversion to monthly scores.

Figure 5 is a comparison of the time budgets for four classes of individuals: adult males, adult females, all juveniles, and all infants. The analysis is based on 4757 (53.7%) observations of individuals, in which the adult sex and age class and the unsexed age class of youngsters were identified. The rest, motion, and forage scores are not significantly different between adult males and females (RE, $T = 17$, df $= 11, p > 0.05$; MO, $T = 17, p > 0.05$; FO, $T = 32$, df $= 11, p > 0.05$). Moreover, the juveniles and infants are not significantly different from each other when the overall average scores are compared ($T = 7, n = 5, p > 0.05$). In Fig. 5,

Table III. Time Budgets for Atelinae and Several Other Primate Species

Species	Rest	Move	Forage	Other
Lagothrix lasotricha Defler (this study)	29.9	38.8	25.8	5.5
Stevenson *et al.* (1994)	36	24	36	5.8
Ateles belzebuth (Klein & Klein, 1977)	63	22.2	14.8	
Ateles geoffroyi (Richard, 1970)	51.1	10.8	27.6	7.5
Brachyteles arachnoides Strier (1986, 1987)	49.3	29.4	18.8	2.5
Milton (1984)	61	9.7	27.8	1.5
Alouatta seniculus (Gaulin & Gaulin, 1982)	78.5	12.7	5.6	3.2
Alouatta palliata (Milton, 1980)	66.2	15.6	13.4	4.8
Cebus albifrons (Terborgh, 1983)	18	21	61	
Cebus apella (Terborgh, 1983)	12	21	66	1.0
Saimiri sciureus (Terborgh, 1983)	11	27	61	1.0
Saguinus fuscicollis (Terborgh, 1983)	44	20	32	4.0
Saguinus imperator (Terborgh, 1983)	25	21	51	3.0
Cacajao calvus (Ayres, 1986)	29	35	36	

the greatest differences in activity budgets are between the adults and the nonadults. Adults rested much more than the nonadults did, while juveniles and infants devoted much more of their time to social interactions.

DISCUSSION

Interspecific Comparisons of Time Budgets

A comparison of the Caparú woolly monkey time budget with several other Neotropical primate species and groups (Table III) shows that at Caparú *Lagothrix lagotricha* devote much more than most other primate species to motion, which correlates positively with their high day ranges (x = 2880 m) and extraordinarily large home range [760 ha (Defler, 1994a)]. It seems likely that these scores reflect the exigencies of this specialized fruit-eater in searching for enough nutriment for yearly maintenance coupled with the rather poor and infertile region that they inhabit. In a future paper I will describe fruit availability at Caparú, since the dispersal of fruit is probably the main environmental characteristic that leads to high move scores (Dunbar, 1988).

The Caparú Biological Research site is located at a transition zone between the generally infertile upper-Amazonian dissected Plio-Pleistocene origin clay terrain (Amazon Planalto), which, although infertile, is not as poor as the Guianean shield elements against which the clay soils abut and with which they interdigitate (Bigarella and Ferreira, 1985; Ibarra *et al.,* 1976; Jordan, 1985a, 1985b). The Guianean Shield soils are far more ancient and, consequently, are very weathered and leached, draining the classic black waters, which are nutrient-poor (Janzen, 1974; Junk and Furch, 1985). There are extensive ranges of low granitic and sandstone hills immediately north of Caparú that support a specialized type of vegetation locally called sabana (Carvajal *et al.,* 1979) and that is better known as caatinga forest. These communities are less diverse than any supported by the extensive Plio-Pleistocene clay soils that seem to be dominant throughout wide expanses of the middle Amazon and that are typical of the greater Amazonian valley.

Strier's (1987) comparisons of activity budgets of two groups of *Brachyteles archnoides* at two different sites (Milton, 1984; Strier, 1986) suggested that increased locomotion by one of them is correlated with increased size of the group. One could expect similar-sized groups of *Lagothrix lagotricha* in more fertile sites to exhibit less motion and either more rest or more social behavior. At Caparú, as available food sources increased, social behavior also increased significantly ($G = 21.0402$, $p < 0.05$), since the increased food supply of the strong seasonal fruit production of the igapó (Fig. 2) allows much more time for social interaction, usually in the form of grooming.

A recent, unpublished study of a 14-member group of *Lagothrix* on the whitewater Duda River in Tinigua National Park (Colombia) showed a time budget with 36% rest, 24% move, 36% forage, and 5.8% other (Stevenson *et al.,* 1994) — less movement instead of more, despite the smaller group. These differences may indicate a more fertile site with more numerous and larger fruit crops (food patches) than at Caparú.

There are no ecological data to characterize the soil fertility and food patch size at the Duda river site, though its position near the Cordillera de los Andes on a whitewater river suggests higher fertility than Caparú (Junk and Furth, 1985; Defler, 1994a). There is no study correlating soil fertility with food patch size in canopy trees and vines — the source of the majority of woolly monkey fruits — but fruit and flower density and species richness correlate with soil fertility in understory plants in the lowland tropics (Gentry and Emmons, 1987). This is very suggestive when considering the influence of soil fertility on fruit crop size, which is the most likely determinant of moving and day ranges (Defler, 1994a).

Diurnal Patterns

The diurnal patterns of the Caparú group are not unusual, especially so close to the equator (1°15″S), where there is little daily and seasonal variation that could confound daily patterns at higher latitudes. However, this is not always the case, since *Brachyteles* at 19°50′S exhibited similar trends to Caparú *Lagothrix* despite their distance from the equator (Strier, 1987).

Other primates such as guenons (Aldrich-Blake, 1970), macaques (Southwick *et al.*, 1965), and red uacari (Ayres, 1986) rest during midday, though this is by no means universal. One might expect a more variable pattern for foraging as well, but this expectation is not borne out at Caparú. Correlations between resting and moving occur commonly in other studies and probably reflect the usual mutually exclusive nature of these categories (Dunbar, 1988).

Although sexual dimorphism in *Lagothrix* implies that there might be a difference in the time budget between the sexes (Clutton-Brock, 1977), my study does not support this hypothesis. Possibly the lack of sexual difference at Caparú may be due to increased feeding in females, which are lactating, as demonstrated in several other studies (Smith, 1977; Altmann, 1980). Such increased feeding by females could provide average female time budgets equal to the time budgets of the larger males. However, my data are inadequate to test this possibility, since I did not distinguish between lactating and nonlactating females. Another possibility is that the sexual differences in body weight may not be sufficiently great to register significant sexual differences in the Caparú data.

It is not surprising to find that the greatest difference between adults and young occurs in the social behavior score, due mostly to play. That increased social behavior is attained by lower motion scores versus those of adults seems surprising, but this may be due simply to the nature of the game, as these playful youngsters tumble through the forest following their elders.

CONCLUSIONS

More intraspecific comparisons from different sites with soils of different fertility should increase our knowledge and modify conclusions about primate densities, primate community diversity, specific adaptability, and distributions. Some of these ecological details could be collected while pursuing other research objectives and could perhaps be included in all field studies routinely, so that comparisons of results among sites would be more meaningful.

Two sites where *Lagothrix lagotricha* have been studied show different time budgets, which may demonstrate how the species reacts to sites of different fertility throughout its wide area of distribution (Defler, 1994a). *Lagothrix* seems to possess a wide ecological amplitude that may not be characteristic of many other primate species. Since this ecological amplitude does not extend to tolerance of human beings and their activities, its remarkable ability to survive in primary lowland tropical forest ought to be examined in more detail after first setting aside areas that will ensure its survival into the future.

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