Habitat, Diet, and Activity Patterns of Free-Ranging Woolly Spider Monkeys (*Brachyteles arachnoides* E. Geoffroy 1806)

Katharine Milton[1]

*Results of a 10-month study of the ecology and behavior of free-ranging wool-ly spider monkeys (*Brachyteles arachnoides*) in Brazil show that these animals are strongly folivorous. Leaf-eating accounted for more than 50% of the total feeding time in all samples but one and accounted for more than 80% of the total feeding time in three samples. Mature foliage was routinely eaten. Woolly spider monkeys consistently spend more than 50% of each day quietly resting and sleeping. Animals travel little except when actively feeding and show low levels of social interaction. Such an activity profile suggests that woolly spider monkeys may often be living near the limits of their energetic resources. The social organization of the species is unusual for a folivorous primate in that small groups of females and associated immature animals confine their activities to discrete home-range areas, whereas males are itinerant, traveling over the home ranges of various female groups. Animals sharing a common home-range area show no permanent daily pattern of association other than that of mother-dependent offspring. Foraging alone or with few conspecifics should maximize each individual's returns from foraging by minimizing the day range that must be traveled each day to locate foods while simultaneously lowering interference competition for higher-quality dietary resources.*

[1]Department of Anthropology, University of California, Berkeley, California 94720.

INTRODUCTION

Woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroy 1806), with an adult body weight of 12–15 kg, are the largest primates in the New World and the largest endemic mammals of Brazil (Aguirre, 1971; S. Rodrigues and J. C. Magalhães, personal communication). This genus is placed in the subfamily Atelinae, along with spider monkeys (*Ateles*) and woolly monkeys (*Lagothrix*). Unlike the latter genera, which are polytypic and show a wide geographical distribution, *Brachyteles* is a rare monotypic geographic isolate, entirely confined to one restricted area of southeastern Brazil and currently threatened with extinction due to massive habitat destruction (Aguirre, 1971; Kinsey, 1982; *Veja*, 1982). Once estimated to number as many as 400,000 individuals, the total population may now consist of no more than 200–2000 individuals, living in remote montane areas or in protected forest on private land (Aguirre, 1971; *Veja*, 1982; personal observation).

Brachyteles individuals are buff-gold in color with darkly pigmented faces and extremities; they use the brachiating locomotor mode, lack a thumb on the manus, and have fully prehensile tails. Woolly spider monkeys show little or no sexual dimorphism in body size and animals of both sexes have canines scarcely larger than incisors (Zingeser, 1973; Kinsey, 1982; personal observation). Data on the ecology and behavior of the species are almost nonexistent, and it has remained one of the most poorly known and least studied of the New World primates.

STUDY SITE

Between 5 August 1982 and 1 July 1983, my assistant, Carlos de Lucca, and I carried out a series of systematic observations on members of a woolly spider monkey population living in protected forest on a private ranch, Barreiro Rico, in São Paulo State, Brazil. This ranch, located at 22°40'40"S latitude and 48°11'10" longitude, elevation 480 m above sea level, contains 3259 ha of forest, divided into five patches. All patches were repeatedly censused for *Brachyteles,* and animals were located in three; the total *Brachyteles* population for Barreiro Rico is estimated at 85–100 individuals, making it the largest known extant population of these rare animals.

All systematic observations other than censusing work were carried out in a 422-ha forest patch, Sarâ, which I estimate contains approximately 45 *Brachyteles.* Four other primate species occur sympatrically with *Brachyteles* in this forest (*Alouatta fusca, Callicebus personatus, Cebus apella,* and *Callithrix aurita*), as well as a large number of other mammal species including deer, peccary, coati, squirrel, agouti, ocelot, and, on the forest periphery, puma. Over the years, some logging has taken place, particularly on the forest

periphery but also in some sections of the interior. The central portion of the forest, however, including the core area used by the habituated animals, consists of tall, primary growth, occasionally interspersed with second growth or patches of bamboo. Woolly spider monkeys show a clear preference for the older and taller areas of the forest, venturing into low areas primarily to feed on vines. To facilitate the study, over 19,000 m of trail, laid out in 200 × 300-m sections, were cut through the forest and mapped to scale.

The study area is characterized by a rainfall pattern which divides the year into approximately 6 months of intensive rain and 6 months of notably lesser rainfall. As calculated from 20 years of daily rainfall collection (Fig. 1), the average annual rainfall for Barreiro Rico is 1262.96 mm (SE, 241.13 mm). Most rain (> 120 mm/month) falls between October and March; the two wettest months of the year are December and January, with > 200 mm of rainfall per month. Less rain (< 75 mm/month) falls from April to September, with the two driest months of the year being July and August, with < 35 mm of rain per month. The annual temperature generally ranges between 35 and 8°C, cooling noticeably at night. Frosts, with temperatures near 0°C, occur occasionally.
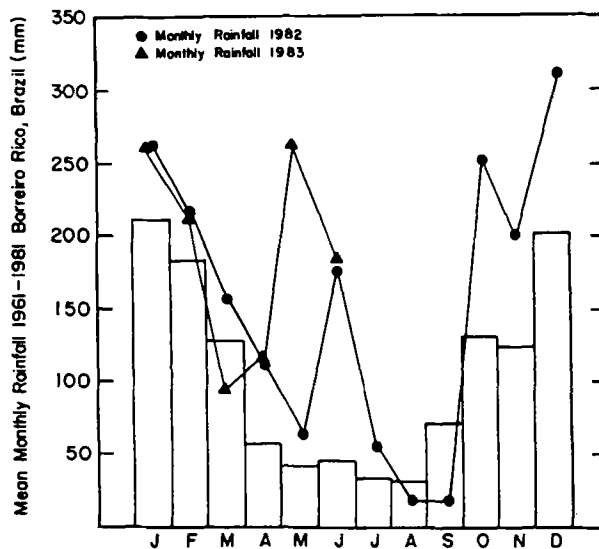

Fig. 1. Mean monthly rainfall 1961–1981, Barreiro Rico, Brazil
Note: Monthly rainfall for 1982 indicated by circles and line; monthly rainfall for 1983 indicated by triangles and line.

Table I. Tree Species Data From 30,000 m² of Forest, Barreiro Rico

Family, species, and common name	Number of individuals ≥19 cm DBH				Relative density (%)
	Plot A	Plot B	Plot C	Total	
Apocynaceae					
Aspidosperma nemorale Handro (guatambú)	2	3	21	26	4.4
Aspidosperma peroba Saldanha da Gama (peroba)	7	4	6	17	2.9
Anacardiaceae					
Astronium graveolens Jacq. (guaritá)	6	7	12	25	4.2
Annonaceae					
Duguetia lanceolata St. Hil. (pindaiba)	6	10	9	25	4.2
Xylopia brasiliensis Spreng. (erva doce)	1	1	0	2	0.3
Araliaceae					
Didymopanax morototoni Deene. and Planch. (mandioqueiro)	1	0	1	2	0.3
Caricaceae					
Jacaratia spinosa Aublet. (jaracatia)	0	2	0	2	0.3
Cyperaceae					
Rhynchospora exhaltata Kunth. (navalha de macaco)	1	0	0	1	0.17
Elaeocarpaceae					
Sloanea monosperma Vell. (ourico)	1	0	1	2	0.3
Euphorbiaceae					
Alchornea triplinervia Muell. Arg. (tapiazeiro)	2	6	6	14	2.3
Croton floribundus Spreng. (capexingui)	2	6	8	16	2.7
Gonatogyne brasiliensis Muell. (guaraiúva branca)	1	0	0	1	0.17
Pachystroma illicifolium Klotzch. (canxim)	14	2	0	16	2.7
Securinega guaraiuva Kuhlm. (guaraiúva)	38	50	49	137	23.5
Lauraceae					
Cryptocaria moschata Nees. and Mart. (batalheira)	3	3	9	15	2.5
Nectandra sp. (canela cheirosa)	5	1	2	8	1.3
Ocotea spixiana Nees. (canelão)	6	0	0	6	1.0
Ocotea acutifolia Nees. (canela preta)	11	23	21	55	9.4

Ocotea sp. A (canela)	0	1	1	2	0.3
Ocotea sp. B (canela)	0	1	0	1	0.17
Unknown	2	0	0	2	0.3
Lecythidaceae					
Cariniana estrellensis Raddi (jequitiba)	1	1	0	2	0.3
Leguminosae					
Copaifera langsdorfii Desf. (pau de óleo)	4	2	5	11	1.9
Hymenaea courbaril L. (jatobá)	0	1	1	2	0.3
Inga striata Benth. (ingá)	0	1	0	1	0.17
Piptadenia gonoacantha (pau jacare)	0	1	0	1	0.17
Zollernia ilicifolia Vog. (pau jantar)	1	1	0	2	0.3
Unknown ("Copaifera branco")	1	1	3	5	0.8
Meliaceae					
Cabralea sp. (canjarena)	7	7	1	15	2.6
Melastomataceae					
Miconia sp.	1	0	0	1	0.17
Mouriri sp. (pitanga brava)	23	6	1	30	5.1
Moraceae					
Ficus sp. (figueira)	2	0	0	2	0.3
Myrtaceae					
Myrciaria sp. (jabuticabeira)	0	0	2	2	0.3
Unknown	3	0	0	3	0.5
Rutaceae					
Esenbeckia intermedia Mart. (canela de cotia)	0	0	5	5	0.8
Esenbeckia leiocarpa Engl. (guaranta)	49	35	1	85	14.6
Pilocarpus pauciflorus St. Hil.	2	0	0	2	0.3
Sapindaceae					
Diatenopteryx sorbifolia (maria preta)	2	1	0	3	0.5
Ulmaceae					
Celtis spinosa Spreng. (galinha choca)	1	1	1	3	0.5
Vochysiaceae					
Qualea jundiahy Warm. (goiaba do mato)	0	0	3	3	0.5
Unknown					
1. "Canela amarella"	10	2	7	19	3.3
2. ?	0	3	0	3	0.5
3. ?	1	0	5	6	1.0
4. ?	0	0	1	1	0.17
5. "Quaresmeira"	0	0	1	1	0.17
6. ?	0	0	1	1	0.17

POTENTIAL FOOD SOURCES

Habitat. The limited geographical range of woolly spider monkeys in comparison with both spider and woolly monkeys suggested that they might have very specific habitat requirements. Thus I was particularly interested in collecting data on forest composition and phenological patterns of forest trees. The semideciduous forest characteristic of Barreiro Rico once extended over large areas of São Paulo State as well as Minas Gerais and Goias (H. de F. Leitao, personal communication). Today, little remains of this forest. In São Paulo State, for example, only an estimated 4% of the original precontact forest cover is still in existence (*Veja,* 1982). The Barreiro Rico forest is believed to be representative of the original forest type once prevailing in this geographical region (H. de F. Leitao, personal communication) and inhabited by woolly spider monkeys (Aguirre, 1971; Kinsey, 1982).

Forest Composition. To sample forest composition, all stems $\geq$ 19 cm diameter breast height (DBH) in each of three 1-ha, noncontiguous forest plots were located, measured, tagged, and in most cases identified as to species (Table I). Two plots were in mature forest areas of Sarâ and one plot was in a mature forest area of Viraeiro, a nearby 611-ha forest patch, also inhabited by *Brachyteles*. Results of combined data from this sample show an average of 194.7 $\pm$ 19.4 (SD) stems $\geq$ 19 cm DBH per hectare. Combined data (30,000 m²) show a total of only 46 tree species ($\overline{X}$ per hectare = 30.0 $\pm$ 2.65). Members of Euphorbiaceae and Lauraceae are particularly well represented. Seven species accounted for > 65% of the total tagged stems in the combined data, and one species alone, *Securinega guaraiuva* (Euphorbiaceae), accounted for 23.5%. This forest type therefore is considerably different from that characterizing most moist lowland forest areas of South and Central America, which typically show a very high species diversity and low densities of individual species. For example, a total of 350 stems ($\geq$ 15 cm DBH) representing 179 species was found in a single 1-ha forest plot near Manaus, Brazil (Prance *et al.,* 1976). In central Panama, older areas of moist lowland forest show an average of 171 stems ($\geq$ 19 cm DBH) and 56 species per hectare (Milton, 1980). The low species diversity and strong species dominance characteristic of the Barreiro Rico forest lower the potential dietary diversity for primary consumers living in this forest.

The relative paucity of tree species in this forest type is offset to some degree by a number of vine species growing in the tree crowns. Examination of 200 tagged trees from the two sample quadrats in Sarâ forest (100 trees per quadrat selected by drawing random numbers) showed that 85 and 88%, respectively, contained at least one vine species and 19 and 25%, respectively, contained three or more. Destructive sampling of three vine tangles (three tangles cut down and all vine species growing in each counted) gave a total

of 15 vine species ($\overline{X}$ number of vine species per tangle = 7.7 ± 0.6). The precise number of vine species in the forest is unknown but is surely in excess of 30. Vine species include a minimum of 10 Bignoniaceae and one or more Leguminosae, Dilleniceae, Hippocrateaceae, Cucurbitaceae, and Sapindaceae as well as other vine families and various aroids (Araceae), particularly *Philodendron* sp. (H. de F. Leitao, personal communication).

Phenology. To monitor changes in the relative availability of seasonal plant foods from canopy tree species, 125 trees, representing a total of 36 species, were examined every 10 days from 14 August–4 December 1982 for new leaf, flower, and fruit production as well as the presence/absence of mature leaves. In all, 12 such samples were taken. These were divided into two data sets, set A, the first 6 samples (14 Aug.–4 Oct.), and set B, the last 6 samples (14 Oct.–4 Dec.). Theoretically, according to the standard rainfall patterns for this geographical region, set A should represent conditions in the forest during a drier portion of the year than set B (Fig. 1). In actuality, this was the case during the study, although June, typically a month of low rainfall, was unusually wet in 1982, perhaps triggering some flushing/flowering activities slightly earlier than normal. Data from set A show that in August–September, 36% of the tree species sampled had only mature leaves, 56% had at least some flush, 25% had flowers, and 28% had fruit. In set B, October–first week December, every species in the sample (100%) showed some evidence of phenological activity. Seventy-eight percent of the species in set B produced at least some new leaves, 61% flowers, and 36% fruit.

Vine species were not monitored for phenological activity. However, data from the destructive sampling activities mentioned above show that in September, 47% (seven species) of the vine species counted had only mature leaves and 53% (eight species) had some new leaves and/or flowers. In November, of 10 vine species examined, 100% had some new leaves and 1 also had flowers.

Leaf fall in the forest was monitored from 14 August to 14 December by means of six 1-m² litter traps that were examined and cleaned every 2 weeks. Leaf fall was generally high during all of September and October, peaking sharply between 14 and 29 September, with an estimated 802 leaves/m². Between 14 and 29 October, litter fall was estimated at 477 leaves/m². By late November–early December, (29 Nov.–14 Dec.), leaf fall had slackened considerably and was estimated at only 100 leaves/m².

Thus data both from phenological monitoring of tree species and from litter fall show that this study began during the time of year when phenological activity in the forest was low and progressed into a period of high leaf drop, high leaf flush, and notable flowering activity. By December, however, leaf fall, leaf flush, and flowering activities had begun to taper off, various species had set fruit crops, and a few species had ripened fruit crops.

METHODS

Study Subjects. The first weeks of the study were spent habituating woolly spider monkeys in Sarâ forest so that they would remain calm in the presence of human observers. Though woolly spider monkeys have not been hunted in the Barreiro Rico forests for many decades, they still fear humans and rapidly flee from them. For 15 days, my assistant and I followed animals living in the western area of the forest until several individuals ceased to panic whenever we appeared. These individuals, in turn, had a calming effect on other individuals. Systematic data collection was not started until this core group of woolly spider monkeys was habituated enough for accurate observations. At the end of the first sample period (22–27 August), animals were sufficiently habituated so that we could walk directly under them and speak in a normal tone of voice without causing alarm. Our habituated animals consisted of three adult females, two subadult females, one juvenile, and one infant estimated to be no more than a few months old. These animals were often accompanied by one or two subadult males and occasionally by various fully adult males.

Woolly spider monkeys have a fluid grouping structure previously associated with strongly frugivorous primates, particularly chimpanzees and spider monkeys. The only permanent daily association pattern is that of mother–offspring. Small groups (three–five) of females, their immature offspring, and one or two subadults occupy discrete portions of the forest (home range) and can be encountered repeatedly month after month within their particular areas. In contrast, subadult and adult males are itinerant and travel through the forest, either alone or in all-male groups of up to eight individuals, apparently searching for estrous females. During this study, a variety of different males continuously entered the home range of our habituated females and associated with one or more of them for periods lasting from a few minutes to over a week before traveling away into other sections of the forest. For this reason, observations are biased in favor of females since they were observed much more consistently than males. The unusual social structure of this species is discussed in detail in another paper (Milton, in preparation).

Diet and Activities. Data on the diet and activities of woolly spider monkeys were collected during a series of samples, spaced as indicated in Table II. For convenience, activities were divided into four mutually exclusive categories — feeding, resting, traveling, and other (calling, social behavior, mating behavior, etc.). On each sample day, from 0630 until 1830 hr, the activity being performed by each visible woolly spider monkey was recorded at 5-min intervals. Each of these was counted as an activity record for the corresponding 5-min interval. Percentages for each activity — feeding, resting, traveling, and other — were then calculated in relation to the total activi-

Table II. Average Percentage Feeding Records per Sample Day Devoted to Different Dietary Categories ($\bar{X} \pm$ SD)

Sample period	Leaves	Fruit	Flowers
22 Aug–27 Aug. ($N = 6$) 12-hr sample days)	74.7 ± 8.1	12.5 ± 8.5	12.8 ± 4.4
11 Sept.–17 Sept. (2 groups 16 Sept.; $N = 7$; no data 12 Sept.)	91.4 ± 9.6	7.3 ± 6.6	1.3 ± 3.4
29 Sept.–3 Oct. ($N = 5$)	80.6 ± 12.7	5.2 ± 4.6	14.2 ± 9.3
15 Oct.–20 Oct. (2 groups 17, 19, & 20 Oct.; $N = 9$	92.7 ± 9.8	4.2 ± 8.4	3.1 ± 5.6
31 Oct.–Nov. 6 ($N = 7$)	51.4 ± 11.1	26.4 ± 11.1	21.9 ± 8.2
16 Nov.–22 Nov. (2 groups 18 Nov.; $N = 8$)	62.3 ± 16.1	10.4 ± 9.8	27.6 ± 15.6
1 Dec.–6 Dec. ($N = 6$)	61.2 ± 17.2	5.5 ± 7.9	33.5 ± 18.2
4 Jan.–9 Jan. ($N = 6$)	56.5 ± 5.0	28.5 ± 8.0	16.3 ± 14.2
25 Mar.–30 Mar. ($N = 6$)	41.2 ± 10.4	58.8 ± 10.4	0
26 Apr.–1 May ($N = 6$)	68.8 ± 9.5	31.2 ± 9.5	0
26 May–29 May	69.5 ± 11.3	30.5 ± 11.0	0
27 June–1 July ($N = 4$)	54.4 ± 12.4	29.6 ± 6.3	15.8 ± 12.3

ty record for each 5-min interval. These percentages were added together and divided by the total number of 5-min intervals in each sample day (144 intervals per 12-hr day), to arrive at the percentage of time spent at each activity (see also Milton, 1980). Only full sample days (12 hr of observation) were used for this purpose (in all, 75 days or 900 hr). Occasionally, as indicated in Table II, while one observer followed the habituated animals, the other followed woolly spider monkeys living in another section of the forest. In this way, some additional full days and many partial days of observation were also collected on the behavior of other less habituated woolly spider monkeys. These data are in full agreement with those collected on habituated animals.

Feeding time included the inspection of food, bringing it to the mouth, biting, chewing, and swallowing. Whenever an animal was feeding, the food species (when known) and the food category (leaf, fruit, flower) were recorded as well as the relative maturity of the dietary item (young leaf, mature leaf, unripe fruit, and so forth) and the portion consumed (bud, petiole, leaf tip, and so forth). To calculate the percentage of feeding time spent on different food species and categories, I related the feeding activity records for each food category and species to the corresponding activity records for the 5-min intervals and proceeded as described above (see also Milton, 1980). The resulting percentages were divided by the percentage of total time spent feeding in the sample days to get estimates of the time spent on each food species, category, and part.

In addition to this systematic sampling data, 7–10 days per month between 5 August and 7 December were spent censusing woolly spider monkeys in forests on Barreiro Rico. During censusing work, group composition and locale were recorded, as well as any food items seen eaten by these monkeys. In all, during the total study period, in excess of 1200 hr of direct observation was carried out on the activities of the Barreiro Rico *Brachyteles* population.

RESULTS

Diet

Food Categories. Woolly spider monkeys are entirely primary consumers and feed exclusively on plants. Animals were not observed to eat any foods from the second trophic level during the entire study period. Plant foods included leaves (both young and mature), fruits (generally unripe but occasionally ripe), and flowers (both buds and open flowers). Foods from these three categories were taken from both tree and vine species; leaves, petioles, or fruits were also eaten from hemiepiphytes and aroids. Woolly spider monkeys are wholly arboreal and were never observed to come to the ground to feed. Tree species used as preferred food sources tended to be among the largest and tallest in the forest. Vines were eaten from trees of all heights, and monkeys frequently moved into areas of low second growth on the forest periphery to feed on the copious vines growing in huge tangles in these sunlit areas.

Leaves. Overall, woolly spider monkeys devoted the overwhelming proportion of their feeding time during the entire sample to eating leaves (Table II). As shown in Table II, leaf-eating accounted for > 50% of the total feeding time in all but one sample period, and in three samples leaf-eating accounted for > 80–> 90% of the total feeding time. Overall, considerably more feeding time was devoted to immature than to mature foliage (Table III). However, mature leaves, particularly mature leaves from three tree species (*Xylopia brasiliensis, Mouriri* sp., and *Aspidosperma peroba*), were important dietary constituents, and leaves from one or more of these three species (generally mature, occasionally young) were included in the diet on 86% of all sample days. *Xylopia brasiliensis* has a relative density of only 0.3% and is a rare species, yet its leaves accounted for 11% of the total feeding time during the sample (all food categories) and it was by far the most important tree leaf source and was the only tree species used for continuous leaf-eating bouts lasting as long as an hour or more. Leaves from *Mouriri* sp. accounted for 5% of the total feeding time (relative density of *Mouriri* sp., 5.1%), and leaves from *A. peroba* for 2% of the total feeding time (rela-

Table III. Median and Range of Leaf-Eating
Records per Sample Devoted to Mature Foliage
(Percentage)[a]

Sample dates[b]	Median (%)	Range (%)
22 Aug.–27 Aug.	28	18–70
11 Sept.–17 Sept.	33	18–51
29 Sept.–3 Oct.	32	16–53
15 Oct.–20 Oct.	48	6–62
31 Oct.–6 Nov.	26	0–49
16 Nov.–22 Nov.	27	4–31
1 Dec.–6 Dec.	53	24–80
4 Jan.–9 Jan.	31	15–52
25 Mar.–30 Mar.	27	15–44
26 Apr.–1 May	31	28–67
26 May–29 May	49	42–61
27 June–1 July	45	15–71

[a]Total number of records per day scored for mature
leaf-eating divided by total number of records
scored for eating leaves per sample day. Minimum
estimates—leaves known to be mature vs all
leaves eaten per day, including leaves of unknown
maturity.
[b]Number of sample days per sample period as
indicated in Table II.

tive density of *A. peroba*, 2.9%). In contrast, extremely abundant tree species such as *Securinega guaraiuva* (relative density, 23.5%) and *Esenbeckia leiocarpa* (relative density, 14.6%) accounted for only a trace amount of foliage in the diet. Indeed, overall, in terms of tree species used as leaf sources, with the exception of the three preferred species cited above and several species of Lauraceae (two *Ocotea* spp. and one unknown species) which were fed on sufficiently frequently to be recognized, most other canopy tree species used as leaf sources contributed little to daily feeding time (generally ≤ 5 min per day per species used).

As shown in Table IV, a considerable proportion of the total feeding time per sample was devoted to eating vine leaves, generally young but occasionally mature. Unfortunately, the vines used as leaf sources could not be identified as to species both because of a lack of botanical information and because of the tendency for many vine species to occur in the canopy in large clusters, making it difficult to discern from below which leaves were actually being eaten. As a food category, however, vine foliage is an important dietary resource for woolly spider monkeys, and in some samples vine leaves accounted for as much as 37–47% of the total feeding time.

Fruits. In 6 of the 12 samples, fruit-eating accounted for < 15% of the total feeding time. It is noteworthy that fruit, particularly ripe fruit, is

Table IV. Percentage Total Feeding Records per Sample Period
Scored for Vine Leaves Plus Median and Range Per Sample[a]

Sample dates[b]	% Total feeding records scored for vine leaves	Median (%)	Range (%)
22 Aug.–27 Aug.	32	31	18–46
11 Sept.–17 Sept.	35	35	29–39
29 Sep.–3 Oct.	40	39	24–52
15 Oct.–20 Oct.	47	37	22–58
31 Oct.–6 Nov.	23	27	13–28
16 Nov–22 Nov.	38	32	22–40
1 Dec.–6 Dec.	11	12	8–28
4 Jan.–9 Jan.	31	37	16–47
25 Mar.–30 Mar.	37	32	23–48
26 Apr.–1 May	33	29	19–54
26 May–29 May	21	25	21–27
27 June–1 July	13	11	4–25

[a]Percentage total feeding records spent eating vine leaves calculated by summing all 5-min intervals scored as feeding on vine leaves and dividing this figure by the total number of 5-min intervals scored for feeding for the total sample period. Medians and ranges represent the daily scores—5-min intervals scored as feeding on vine leaves divided by the total number of 5-min intervals scored as feeding per sample day.
[b]Number of sample days per sample period as indicated in Table II.

generally an extremely rare commodity in this forest. In March, however, an average of 58.8% of the daily feeding time was spent eating fruit. In this sample, animals concentrated most fruit-eating on immature fruit of *Esenbeckia leiocarpa*. This species has a relative density of 14.6%, which helps to explain why the percentage of time devoted to fruit-eating in this month was unusually high. Although several fruit species were eaten in each sample period (Table V), generally such fruit was taken from rare tree or vine species and was eaten unripe. Between August and December, only one tree species, *Myrciaria* sp. (relative density, 0.3%), an understory tree, produced what could be described as a notable fruit crop. Woolly spider monkeys entered the trees while the fruit was still green, eating quantities of it and knocking hundreds of other fruits to the ground. When feeding, animals bit through the tough outer portion of the fruit and discarded it, chewing and swallowing only the immature seeds and surrounding white matrix. Woolly spider monkeys were also voracious seed predators on immature fruits of *Inga striata* and *Pachystroma ilicifolium*. They chewed seeds of *Esenbeckia leiocarpa*, but many of these apparently were defecated intact. The animals also served as seed dispersal agents for *Mouriri* sp., two species of *Ficus,* and an unidentified species of Myrtaceae.

Flowers. As a dietary category, flowers are a more seasonal resource for woolly spider monkeys than either leaves or fruit. In three sample peri-

Table V. $\bar{X}$ Day Range and Number of Food Species Eaten per Sample Period

Sample period	Day range $(\bar{X} = SD)$	Species (total, median, and range per sample period)		
		Tree leaf[a]	Fruit	Flower
22 Aug.–27 Aug.[b]	678.0 ± 149.6	13	5	4
		5.5	0	1
		5–8	0–1	1–2
11 Sept.–17 Sept.	750.0 ± 158.1	10	3	1
		7	0.5	0
		3–10	0–1	0–1
29 Sept.–3 Oct.	680.0 ± 182.4	10	3	5
		6	1	2
		4–10	0–2	2–4
15 Oct.–20 Oct.	568.7 ± 201.7	9	3	2
		5	0	1
		4–8	0–1	0–1
31 Oct.–6 Nov.	814.3 ± 267.0	14	3	4
		5	2	1
		2–8	1–3	1–3
16 Nov.–22 Nov.	700.0 ± 300.0	11	5	8
		4	3	3
		2–8	0–4	1–5
1 Dec.–6 Dec.	314.5 ± 138.1	9	4	6
		6	1.5	3
		5–6	0–2	1–4
4 Jan.–9 Jan.	566.7 ± 60.6	9	3	4
		2.5	2	1
		2–6	2–3	0–3
25 Mar.–30 Mar.	618.7 ± 78.6	4	3	0
		1	2	0
		0–1	1–3	0
26 Apr.–1 May	656.7 ± 90.7	7	5	0
		4	3	0
		1–4	1–3	0
26 May–29 May	522.5 ± 148.8	3–5	1	0
		2	1	0
		1–3	1	0
27 June–1 July	690.0 ± 101.6	9–10	4	1
		2	3	1
		1–5	2–4	1

[a]Vine species omitted from all leaf calculations but not fruit and flower calculations, since it was possible to distinguish vine flowers and fruits as to individual species but generally impossible for foliage.
[b]N's as indicated in Table II.

ods, no flowers were eaten (Table II), and in two other sample periods, flower-eating accounted for < 4% of the total feeding time. During November and December, however, flowers accounted for 28–33% of the total feeding time. Not only were there a number of flower species available in the forest during this period, but several of these species either produced very abundant

flower crops or produced flower crops over a period of weeks such that animals could repeatedly exploit them. In early November, an unidentified and fairly common vine (Bignoniaceae) produced a substantial crop of yellow flowers that were heavily exploited for several days by woolly spider monkeys. For all of November, lasting into December, two tree species — *Duguetia lanceolata* (relative density, 4.2%) and an unidentified and rare species of Lauraceae — produced flower buds and flowers that were heavily eaten by the monkeys. Toward the end of November, lasting into December, *Croton floribundus* (relative density, 2.7%) began to produce flower buds and flowers and accounted for 12% of the feeding time in the 16–22 November sample and 23% of the feeding time in the 1–6 December sample. Individuals of *Croton floribundus* occur in clumps and, for this reason, may be particularly worthwhile to exploit, since travel to an area where there is one *C. floribundus* usually gives animals from two to five other individuals of this species to exploit as well.

   Time Spent Feeding Per Food Category. There were notable differences between sample periods in the amount of feeding time animals devoted to different food categories (Table II). In the first four sample periods, covering August, September, and October, by far the greatest amount of feeding time was devoted to leaves. By early November, animals had begun to devote considerably more time to eating flowers and somewhat more time to eating fruit. By March and April, fruit had become of considerable importance in terms of its overall contribution to total feeding time, but flowers were not eaten at all. This pattern of food exploitation strongly parallels production patterns of the tree species in the forest. As shown in Fig. 1, the two driest months of the year in this geographical region are usually July and August. Rainfall increases in September, becoming heavy in October. As noted, in 1982, June was an unusually wet month (Fig. 1) and this may have precipitated some phenological activity, particularly leaf flush, somewhat earlier than usual. However, the fact that leaf fall peaked sharply in the latter half of September, right about the time when the heavy rainfall is generally expected to begin, indicates that, in general, phenological patterns were not greatly altered by an unusually wet June. Data collected on the phenological activities of trees from mid-August to early December show that the most intense new leaf production as well as flowering activities and fruit setting took place during the October–December portion of the phenological sampling program, not the August–September portion. Overall, woolly spider monkeys appear to be strongly opportunistic feeders, tracking the relative availability of seasonal dietary resources and using the edible seasonal foods of different dietary categories as they become available. Young vine leaves, very abundant in second-growth areas on the forest periphery, and the mature leaves of select tree species serve as dietary buffers, helping to carry animals through portions of the year when most seasonal plant foods are in scant supply.

Table VI. Activity Patterns of *Brachyteles arachnoides*[a]

Sample dates[b]	Rest	Travel	Feed	Other
1982				
22-27 Aug.	63.0 ± 6.1	8.4 ± 2.8	26.0 ± 5.0	2.6 ± 5.0
11-17 Sept.	62.4 ± 3.1	11.3 ± 2.5	24.4 ± 3.7	2.0 ± 1.0
29 Sept.-3 Oct.	63.8 ± 5.6	9.0 ± 3.2	26.4 ± 4.3	1.4 ± 0.6
15-20 Oct.	63.4 ± 6.2	9.6 ± 3.3	26.5 ± 6.1	1.3 ± 0.5
31 Oct.-6 Nov.	60.6 ± 3.6	11.2 ± 2.1	26.4 ± 3.9	2.1 ± 0.8
16-22 Nov.	64.1 ± 6.5	8.2 ± 2.8	26.1 ± 7.0	1.7 ± 0.8
1-6 Dec.	54.5 ± 4.1	6.7 ± 2.0	35.7 ± 6.4	3.0 ± 2.7
1983				
4-9 Jan.	67.2 ± 4.8	7.8 ± 2.9	24.7 ± 1.8	0.8 ± 0.4
25-30 Mar.	66.0 ± 4.5	8.2 ± 1.7	25.2 ± 3.3	1.3 ± 0.8
26 Apr.-1 May	57.8 ± 4.3	12.2 ± 1.6	29.2 ± 3.7	1.0 ± 0.2
26-29 May	56.8 ± 1.7	11.5 ± 2.5	29.3 ± 1.9	1.4 ± 0.7
27 June-1 July	52.8 ± 1.6	12.8 ± 1.3	33.4 ± 2.5	0.9 ± 0.7

[a]$\bar{X}$ ± SD of summed percentages per 12-hr sample day for each sample period.
[b]Number of sample days as indicated in Table II.

Activity Patterns

Rest. Activity patterns for each sample are presented in Table VI. These data show that woolly spider monkeys spend an average of at least 6 hr per day resting. The standard deviation for resting activity is small, indicating that this daily rest is a persistent and habitual pattern of behavior for these monkeys. Woolly spider monkeys tend to be late risers. In 8 of the 12 sample intervals, the median getting-up time was 0820 hr or later (range, 0728-0950), and in the remaining four samples it ranged between 0728 and 0750 hr. In four sample intervals, the median getting-up time was 0920 hr or later. In contrast, *Cebus apella* in this same forest are actively moving about at first light. Woolly spider monkeys also show a persistent pattern of uninterrupted afternoon rest, generally beginning at about 1200 hr and ending at about 1430-1530 hr. Animals settle down for the night as light begins to fade and can be found the next morning in the same sleep tree and sleep site, indicating that they do not move around after dark. Thus woolly spider monkeys are extremely inactive primates, spending more than half of their daylight hours and all of their nighttime hours quietly resting or sleeping.

Feeding. On average, woolly spider monkeys spend about 3 hr a day in feeding activities (Table VI). This works out to about 14.6 min a day spent feeding for each kilogram of body weight (assuming that the average weight for an adult woolly spider monkey is about 13 kg). The only notable exception to this pattern came in December, when animals increased their daily feeding time to slightly more than 4 hr. This sample period also showed the highest percentage of feeding time devoted both to mature leaves and to flowers. As a category, mature leaves require longer to chew before swallowing

than immature leaves (Milton, unpublished data), and the increase in feeding time may be due in part to the added processing time related to a high proportion of mature foliage in the diet. However, during this same sample period animals were also spending considerable time eating flowers and flower buds of *Croton floribundus,* as noted, a tree species which tends to show a clumped spatial distribution. As many flowers from this species could be found within a very restricted area, the increase in feeding time for this sample may also represent opportunistic feeding on an unusually abundant and concentrated high-quality dietary resource. As is the case for resting, the standard deviation for feeding activity is not large.

Travel. The amount of time animals devoted to travel each day averaged about 1 hr, ranging between 50 and 104 min (Table VI). Animals travel an average of 630 ± 128 m per day (Table V). The longest single day range recorded was 1400 m, and the shortest 350 m. Traveling and feeding usually occurred during the same time interval. Animals would begin to travel, moving from tree to tree and feeding, generally briefly, on whatever edible items they encountered in each tree until they appeared satiated. They would then stop traveling and rest. This pattern of feeding while traveling is different from the pattern shown by mantled howler monkeys *(Alouatta palliata).* Howlers tend to travel steadily over several hundred meters, rarely stopping to feed, until they reach a particular food tree or grove of food trees where they then feed heavily (Milton, 1980). The difference in these two travel patterns, both related to resource exploitation but one strongly goal-directed and one fluid, suggests, in turn, that howler monkeys are more selective feeders than woolly spider monkeys.

Each day's travel was plotted onto a scale map of the study area. Over the entire study period, the study animals entered an area corresponding to some 53 ha in the gridded section of the forest and an additional 18–20 ha off the grid on the western border of the forest. Home-range size for female woolly spider monkeys is estimated at about 70 ha. I cannot comment on home-range size for males because most males appear to move about over wide areas of the forest. Within the first four sample periods, the study animals had moved over the area corresponding to the major portion of their home range, and most other samples primarily involved variations in the use of different sections of this delineated home-range area (Fig. 2). Animals frequently rested and slept and could be encountered in a particular area of the home range some 4 ha in size, which can be regarded as a core area. No defense of any area was noted, though there is a dominance hierarchy between females and between males and any male apparently can displace any female. (Dominance was judged by the ability of one individual to supplant another at feeding or rest sites, to completely monopolize a food tree, or by the rapid withdrawal of one individual at the approach of another, usually larger individual.)
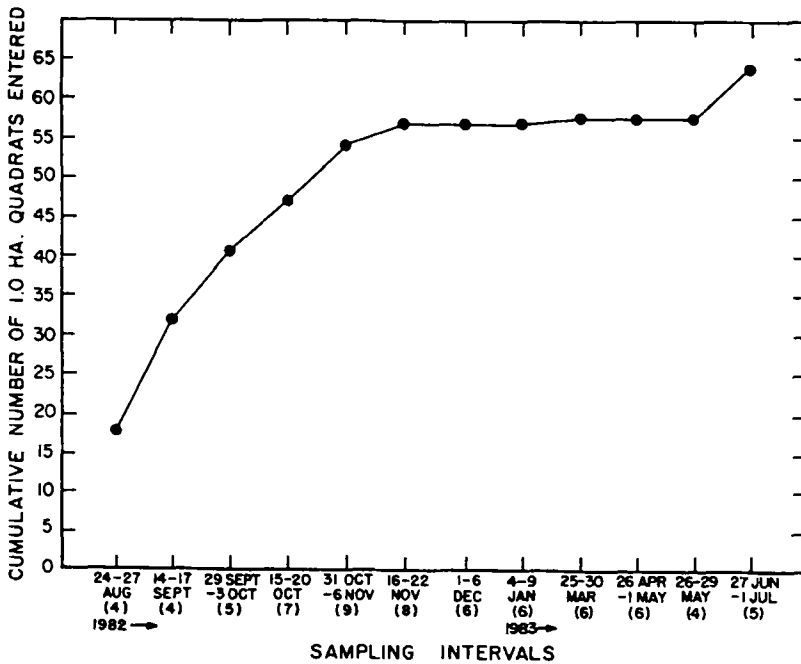
Fig. 2. Cumulative home-range size. Note: The number in parentheses below the sample interval date represents the number of days of continuous data from which cumulative quadrat use was extracted for each interval.

Other Activities. Animals were observed to drink water from tree holes after 15 October when heavy rainfall had begun. Various animals would drink from the same tree hole, either in the company of other individuals or alone, indicating that many of these tree holes are known to all individuals using this section of the forest. In general, animals devoted very little time to activities other than feeding, traveling, and resting. On average, < 1% of each day is devoted to social behavior (one animal interacting with another animal that is not a dependent offspring). Adult individuals of both sexes were frequently observed to deposit fresh urine on the hands and, occasionally, the ventral surface of the tail (Milton, in press). Such urine presumably carries information about the sex and identity of the individual and, in the case of females, the reproductive state. Animals also communicate with calls, and during the study a total of eight distinct calls (Table VII) was identified. The probable function of these calls is discussed in Table VII. Grooming between adult individuals was not observed, though a mother may groom her immature offspring. Animals also show a highly ritualized greeting gesture, used by two animals who apparently recognize one another but have not been together recently. When two such individuals come together, they

Table VII. Calls of *Brachyteles arachnoides*

Call	Animals heard giving call	Context/function
1. Low belch	Adult females and probably adult males	An alert call; also appears to function as a contact call between a foraging female and her independently locomoting offspring.
2. Scream — a loud, piercing cry	Any age	Generally used when one animal is alone to ascertain the locations of other individuals. Call is often answered by whinnies from other conspecifics.
3. Whinny — a neighing sound similar to that made by *Ateles*. There are many variations on this call, given at different levels of intensity.	Subadults and adults, both sexes	Used between feeding animals, out of sight of one another, apparently as a contact call. Often heard in the early morning — perhaps to indicate the general path of foraging and again in the late afternoon, perhaps to indicate the location of the sleeping area to any conspecifics within auditory range.
4. Staccato chutter-whinny	Adult females and probably adult males	Used when two animals come into contact that have not met recently.
5. Bark	Subadults and adults, both sexes	Alarm and irritation. Usually directed toward the observer.*
6. Shrill yip	Subadults and adults, both sexes	Alarm and irritation; usually precedes bark.
7. Keening	Immatures	Probably to get attention of the mother — immature not in body contact with mother when call is given.
8. Mating twitter	Sexually receptive females	Used when female is very much interested in sexual attention from males.

*When irritated, animals also slap leaves with the hand, forcefully pull back branches and let them go, bounce forward (lunge; seen even in small infant of 4–6 months), and defecate copiously if the source of annoyance is on the ground.

begin to give a staccato chuttering call (staccato chutter-whinny) and then embrace one another forcefully with the forearms. The head of one participant is often pressed into the shoulder of the other and this embrace may be held for over 60 sec. While embracing, animals may draw back the corners of the lips in an open-mouthed grimace showing very little of the teeth. Females give this embrace to females and males give it to males (male observation, C. de Lucca), but it does not appear to be used intersexually.

Sexual behavior in this species is very striking. A female appears to communicate her sexually receptive condition by means of pheromone cues in

her urine, which she deposits on her hands and then transfers to the substrate as she travels over her home range while foraging. Many males (seven to nine individuals) rapidly appear in her home range within a few hours, and these males follow the female continuously for 24–48 hr, copulating with her whenever possible. When the female is in this maximally receptive condition, she constantly gives an unusual twittering call (mating twitter). Sexual behavior in this species is discussed in detail in another paper (Milton, in preparation). During the study, 31 copulations were observed, many at very close range, permitting the collection of considerable data on the mating behavior of this rare species.

DISCUSSION

From an examination of museum specimens, Zingeser (1973) predicted that woolly spider monkeys might show folivorous tendencies, citing as evidence a number of similarities between the maxillary premolars and molars of this species and those of *Alouatta,* the howler monkey. This study fully supports his prediction. Woolly spider monkeys are overwhelmingly folivorous; furthermore, they have both the low activity level and low level of social behavior often characteristic of leaf-eating primates (Jolly, 1972; McNab, 1978; Milton, 1980). Prior to this study, howler monkeys were regarded as the most folivorous of the New World primates (Hill, 1962; Jolly, 1972; Milton, 1980). Woolly spider monkeys are fully as folivorous as howler monkeys and also include higher percentages of mature leaves in the diet on a more regular basis than is the case for howlers (Glander, 1975; Milton, 1980: Gaulin and Gaulin, 1982). Leaves are a notoriously poor source of readily assimilable energy (McNab, 1978; Grand, 1978), generally containing less than 4% nonstructural carbohydrates per unit dry weight (Milton, 1979). This raises the question of where woolly spider monkeys obtain dietary energy when living on diets composed primarily of leaves.

The abundant structural carbohydrates of leaves (cellulose and hemicelluloses) can provide energy for leaf-eating animals if the animals possess sufficiently large colonies of cellulolytic bacteria and protozoa in the gut. These microorganisms, in contrast to the digestive enzymes of vertebrates, have the ability to degrade the cellulose and hemicelluloses of leaves in the process known as fermentation, producing energy-rich volatile fatty acids as a by-product. These fatty acids, in turn, can often be absorbed by the host animal and may make an important contribution to its energy budget. Howler monkeys ferment structural carbohydrates in the cecum and colon and appear to derive important energetic benefits from this process [Milton *et al.,* 1980; Milton and McBee, 1982; see also Bauchop and Martucci (1969) and Bauchop (1978) for discussion of fermentation processes in the sacculated stomach

of Old World colobines]. I suggest that woolly spider monkeys, like howler monkeys, also carry out fermentation processes in the hindgut.

Woolly spider monkeys, like all New World primates including howlers, are monogastrics; but they show considerable volume in the cecum and colon (Hill, 1962), indicating that these sections of the gut may serve as fermentation chambers. Fresh fecal matter of woolly spider monkeys has the same distinctive pungent odor as that of howler monkeys and, likewise, shows a high content of endogenous fecal nitrogen (Milton *et al.,* 1981; Milton, unpublished data). Both of these features indicate that fermentation activities occur in the cecum and upper colon of woolly spider monkeys. Interestingly, a single trial with an adult female woolly spider monkey in the São Paulo Zoo, to determine food passage rates, showed that this animal began to turn over gut contents 8 hr after the initial feeding of colored markers and food (Milton, 1984). This initial turnover time is considerably more rapid than is the case for mantled howler monkeys, which are smaller animals and yet begin to turn over gut contents some 18-23 hr after the initial feeding (Milton *et al.,* 1980; Milton, 1981a). (The rapid initial passage rate for the captive female *Brachyteles,* however, could result from the fact that the zoo diet is high in fruit and low in fiber in comparison to the usual diet in the wild.) In addition, however, in contrast to howler monkeys, whose defecation patterns are not notable, woolly spider monkeys in the wild defecate copious amounts of fecal matter very frequently. Field data from calm, habituated animals show that adult woolly spider monkeys of both sexes generally defecate notable quantities of fecal matter from 10 to 14 times per 12-hr day ($N = 6$).

In combination, all of these features suggest that the digestive strategy of woolly spider monkeys may differ in certain important respects from that of howler monkeys. Like howlers, woolly spider monkeys are opportunistic feeders in that they tend to exploit whatever edible fruits or flowers are available in the habitat at any particular time, but members of both species routinely eat large quantities of foliage each day. However, when eating leaves, woolly spider monkeys appear to be somewhat less selective feeders than howlers, as noted, generally taking some foliage (including vine foliage) from each tree visited until satiated, rather than traveling to a select tree or trees for much of their daily leaf-eating activity. Woolly spider monkeys also include more mature foliage in the diet and doubtless also take in a considerably greater volume of food per day. Since woolly spider monkeys are larger than howlers (some 12-15 vs 6-9 kg), this larger body size should confer greater energetic lability, enabling them to exploit a coarser dietary matrix (Parra, 1978). The quantities of plant material eaten by woolly spider monkeys are presumably passed from the stomach through the small intestine, where the soluble nutrients are absorbed. The less digestible, more fibrous portion of the diet then passes into the cecum and upper colon, where I predict that

cellulolytic gut flora degrade the less lignified and more rapidly fermentable portion of the plant fiber. After a limited fermentation treatment, directed only at the more degradable portion of the cell wall material, the undigested plant matter appears to be expelled from the gut in regular pulses during the day. Thus the digestive strategy of woolly spider monkeys, in contrast to that of howler monkeys, appears predicated more on the rapid turnover of lower-quality plant food, whereas that of the howler monkey appears predicated on the more efficient, slow digestion of higher-quality plant foods (Milton, 1980, 1981a, 1984).

In general, monogastric hindgut fermenters of moderate body size (beavers, porcupines, howler monkeys) obtain only some 18–33% of their estimated required daily energy from fermentation end products (Johnson and McBee, 1967; McBee, 1978; Milton and McBee, 1982). When living on diets composed primarily of leaves, woolly spider monkeys may well be near stress with respect to meeting their daily requirements for energy. Certainly the activity patterns and other behaviors characteristic of this species suggest adaptations to a diet low in available energy. Late rising, long periods of rest during the day, limited daily travel associated with feeding, and a low level of social behavior all appear to represent adaptations functioning either to lower daily energetic expenditure or to conserve available energy. Indeed, animals often feed or defecate from a prone rather than sitting or standing position, apparently to conserve energy.

I suggest that the fluid pattern of social organization of woolly spider monkeys may also be viewed as an adaptation to a limited energetic substrate. Milton and May (1976) have shown that in primates, typically, the larger the social group, the larger the home range. If, within a given time interval, the primate group covers the same proportion of its home range using the same movement patterns as a solitary individual, the individual primate in the social group may have to expend more energy in travel than would be the case if it foraged alone (Milton and May, 1976). Because of its large body size, the vertical component of travel is assumed to be very costly for woolly spider monkeys. Though brachiation may lower the costs of arboreal travel per unit distance (Milton, 1980), woolly spider monkeys cannot always brachiate, and travel through the trees is predicted to involve a considerable output of energy (see, for example, Taylor et al., 1972). Therefore, by foraging alone or in small groups, a woolly spider monkey may minimize the distance it must travel each day for food, thus lowering foraging costs. In addition, foraging alone or with few conspecifics should permit each individual to harvest the most select dietary items from each tree visited without interference (Wrangham, 1977). The fact that males are itinerant also permits females to feed frequently without dietary competition from males, which, since they are dominant to females, can displace or exclude females from particular food sources (personal observation). Permanent large

foraging parties (and a high degree of sociality) may in fact represent luxuries that this monogastric, leaf-eating primate simply cannot afford, particularly in a forest habitat characterized by low species diversity, notable species dominance, and marked seasonality in the phenological patterns of many forest trees.

There is a striking similarity between the fluid grouping pattern shown by woolly spider monkeys and that described for chimpanzees and spider monkeys (Wrangham, 1977; Klein and Klein, 1977). Both chimpanzees and spider monkeys are very strongly frugivorous, and in both cases a fluid grouping pattern has been viewed as a response to the patchy distribution patterns of ripe fruit in tropical forests (Wrangham, 1977; Klein and Klein, 1977; Milton, 1981b). The fact that a species as strongly dependent on leaves in the diet as the woolly spider monkey shows a similarly fluid grouping pattern indicates that it is not the dietary category per se (i.e., fruits vs. leaves) that is the critical factor underlying this fluid social structure, but rather the nature of the interaction between the distribution patterns of key foods of whatever category, and the body size and energetics of the feeder. Fruit is high in energy but is very patchily distributed in tropical forests relative to leaves (Milton, 1980). Both spider monkeys and chimpanzees must travel extensively as a general rule to locate sufficient ripe fruit to meet their daily energetic needs (Wrangham, 1977; Rodman, 1984; Milton, 1981a). The tendency for spider monkeys and chimpanzees to forage alone or in small subgroups appears to represent a similar response to the same basic set of selective pressures as those faced by woolly spider monkeys — namely, the pressure to minimize individual day range when foraging while simultaneously maximizing foraging returns from each tree visited by lowering the possibilities for interference competition from more dominant animals (Wrangham, 1977; Milton, 1981c). All three of these species are sufficiently large in body size so that aggregation for predator protection is not assumed to be of strong significance in terms of the size of foraging units. In turn, the fluid distribution pattern of adult females in these species should make it very difficult for any one male to control sexual access to a particular group of females. This factor may contribute to the strong degree of male bonding noted in these species, as well as the low level of intermale aggressiveness in mating encounters and the lack of any strong sexual dimorphism in body or canine size (Wrangham, 1977; Milton, 1984, personal observation).

ACKNOWLEDGMENTS

REFERENCES

Aguirre, A. C. (1971). O Mono *Brachyteles arachnoides,* Academia Brasileira de Ciências como Contribuicão ao Programa Biologico Internacional, Rio de Janeiro, pp. 1-53.

Bauchop, T. (1978). Digestion of leaves in vertebrate arboreal folivores. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores,* Columbia University Press, New York, pp. 193-204.

Bauchop, T., and Martucci, R. W. (1968). Ruminant-like digestion in the langur monkey. *Science* 161: 698-700.

Gaulin, S. J. C., and Gaulin, C. K. (1982). Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *Int. J. Primatol.* 3: 1-52.

Glander, K. E. (1975). *Habitat and Resource Utilization: An Ecological View of Social Organization in Mantled Howler Monkeys,* Ph.D. dissertation, University of Chicago, Chicago.

Grand, T. I. (1978). Adaptation of tissue and limb segments to faciliate movement and feeding in arboreal folivores. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores,* Smithsonian Press, Washington, D.C., pp. 231-242.

Hill, W. C. O. (1962). *Primates: Comparative Anatomy and Taxonomy, Vol. 4,* Interscience, New York.

Johnson, J. E., and McBee, R. H. (1967). The porcupine cecal fermentation. *J. Nutrition* 91: 540-546.

Jolly, A. (1972). *The Evolution of Primate Behavior,* Chicago University Press, Chicago.

Kinsey, W. G. (1982). Distribution of some Neotropical primates and the model of Pleistocene forest refugia. In Prance, G. T. (ed.), *Biological Diversification in the Tropics,* Columbia University Press, New York, pp. 455-482.

Klein, L. L., and Klein, D. B. (1977). Feeding behaviour of the Colombian spider monkey. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes,* Academic Press, London, pp. 153-181.

McBee, R. H. (1978). Fermentation in the hindgut. In Clark, R., and Bauchop, T. (eds.), *Microbial Ecology of the Gut,* Academic Press, London, pp. 185-217.

McNab, B. K. (1978). Energetics of arboreal folivores: Physiological problems and ecological consequences of feeding on an ubiquitous food supply. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores,* Smithsonian Press, Washington, D.C., pp. 153-162.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: A test of some hypotheses of herbivore leaf choice. *Am. Nat.* 114: 362-378.

Milton, K. (1980). *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics,* Columbia University Press, New York.

Milton, K. (1981a). Food choice and digestive strategies of two sympatric primate species. *Am. Nat.* 117: 476-495.

Milton, K. (1981b). Estimates of reproductive parameters for free-ranging ranging *Ateles geoffroyi. Primates* 22: 574-579.

Milton, K. (1981c). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *Amer. Anthrop.* 85: 534-548.

Milton, K. (1984). The role of food processing factors in primate food choice. In Rodman, P., and Cant, J. (eds.), *Adaptations for Foraging in Non-Human Primates,* Columbia University Press, New York, pp. 249-279.

Milton, K. (1984). Urine washing behavior in the woolly spider monkey. *Z. Tierpsychol.,* in press.

Milton, K., and May, M. L. (1976). Body weight, diet and home range in primates. *Nature Lond.* 259: 459-462.

Milton, K., and McBee, R. H. (1982). Structural carbohydrate digestion in a New World primate, *Alouatta palliata. Comp. Biochem. Physiol.* 74: 29-31.

Milton, K., Van Soest, P. J., and Robertson, J. (1980). Digestive efficiencies of wild howler monkeys. *Physiol. Zool.* 53: 402-409.

Parra, R. (1978). Comparison of foregut and hindgut fermentation in herbivores. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores,* Smithsonian Press, New York, pp. 205-230.

Prance, G. T., Rodrigues, W. A., and da Silva, M. F. (1976). Inventario florestal de um hectare de mata de terre firme km 30 da Estrade Manaus-Itacoatiara. *Acta Amazon.* 6: 9-35.

Rodman, P. S. (1984). Foraging and social systems of orangutans and chimpanzees. In Rodman, P. S., and Cant, J. (eds.), *Adaptations for Foraging in Non-human Primates,* Columbia University Press, New York, pp. 134-160.

Taylor, C. R., Caldwell, S. L., and Rountree, V. J. (1972). Running up and down hills: Some consequences of size. *Science* 178: 1096-1097.

Veja (1982). Vol. 708, p. 82.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes,* Academic Press, London, pp. 504-538.

Zingeser, M. R. (1973). Dentition of *Brachyteles arachnoides* with reference to Alouattine and Atelinine affinities. *Folia primatol.* 20: 351-390.