

## Ecological Strategies of Woolly Monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia

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Information on the use of space, activity patterns, diet, and social interactions were recorded for a group of woolly monkeys (*Lagothrix lagotricha*) during 13 months at Tinigua National Park, Macarena, Colombia. In this region, fruit abundance changes throughout the year with a peak during March–April (beginning of the rainy season) and less fruit during September–November (end of rainy season). Woolly monkeys spent most of their time in mature forest where fruit abundance is higher than in open-degraded or flooded forests. Changes in habitat used by monkeys were coupled with changes in fruit supply across vegetation types. On an annual basis, woolly monkeys spent 24% of point samples locomoting, 36% resting, 36% feeding, and 4% on other activities. However, these proportions varied across the year depending on fruit availability. Based on instantaneous samples, the diet consisted mostly of fruits (60%), arthropods (23%), vegetative parts and flowers (17%), and other items (1%). Non-lactating females and juveniles spent more time eating insects than adult males and lactating females; however, significant differences between classes were detected only during the period of fruit scarcity. These differences are probably due to the high extent to which non-lactating females and juveniles were excluded from fruiting trees by males. The high proportion of arthropods in their diet is unusual for primates with large body size and is a possible factor influencing group cohesiveness in woolly monkeys. © 1994 Wiley-Liss, Inc.

**Key words:** woolly monkeys, *Lagothrix lagotricha*, social organization, diet

### INTRODUCTION

Woolly monkeys (*Lagothrix spp.*) are among the least studied genera of New World monkeys under natural conditions. They are members of the subfamily Atelinae comprising the spider monkeys (*Ateles spp.*) and woolly spider monkeys (*Brachyteles arachnoides*) [Napier & Napier, 1967]. The genus includes two species, *L. flavicauda* and *L. lagotricha*. The latter is widespread in the Amazon basin and consists of four allopatric subspecies: *L.l. lagotricha*, *L.l. poeppiggi*, *L.l. cana*,

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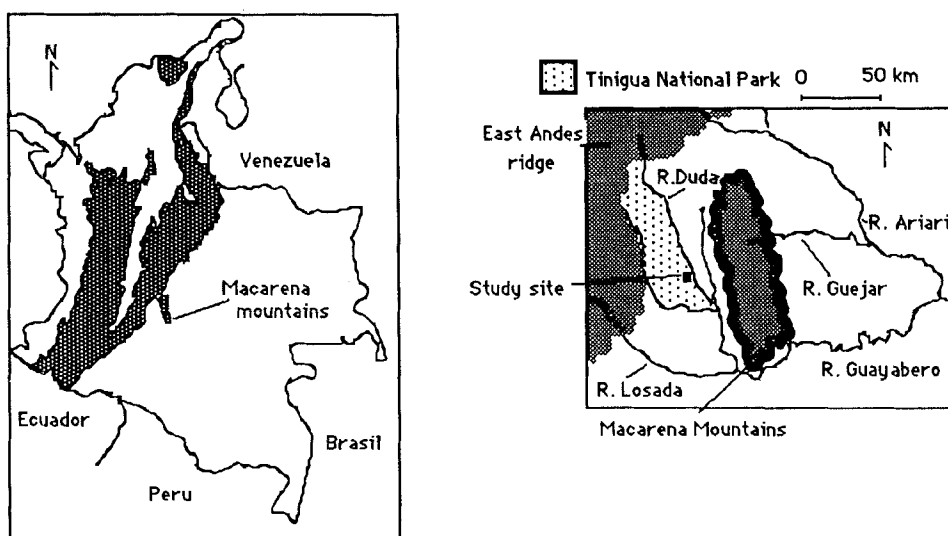


Fig. 1. The geographical location of the study area in Colombia.

and *L.l. lugens* [Fooden, 1963]. Short-term studies [Kavanagh & Dresdale, 1975; Izawa, 1976; Ramirez, 1980] have shown that woolly monkeys live in heterosexual groups composed of 10–45 individuals. Home range size varies among groups and localities, but usually ranges from 250 to 760 ha [Nishimura & Izawa, 1975; Deffler, 1987]. Woolly monkeys usually prefer tall mature forest with continuous canopy [Soini, 1990]. Whole groups move as units, although they are frequently found in subgroups that maintain auditory contact [Deffler, 1989]. They feed primarily on fruits, although leaves and insects are an important component of their diet [Izawa, 1975; Milton & Nessimian, 1984; Soini, 1990]. In a 6-month pilot study of woolly monkeys in La Macarena, Colombia, quantitative information on the diet composition was collected where fruits comprised 78% of the diet, arthropods 12%, leaves 9%, and other items 1% [Stevenson, 1992].

The most detailed sociological information on woolly monkeys comes from a series of studies by Nishimura [1986, 1988, 1990]. He found that males are dominant over females, each male in the group can copulate with an estrous female, and it seems that nulliparous females disperse from their natal groups.

In this paper we present new ecological information for *Lagothrix lagotricha lugens* (henceforth *Lagothrix lagotricha*). Our study integrates data on habitat use, activity, and diet to correlate specific behaviors, feeding strategies, and the social structure of this species with variations in fruit abundance throughout 1 year.

## STUDY AREA

This study took place in tropical rain forest on the eastern border of Tinigua National Park west of La Macarena mountains ( $2^{\circ} 40'$  north and  $74^{\circ} 10'$  west, 350 m over sea level) at the base camp "Colombia" on the right margin of Río Duda, Departamento del Meta, Colombia (Fig. 1). The region is characterized by a high seasonality in rainfall, with a dry period from December to March and a rainy period through the rest of the year ( $> 100$  mm per month). According to 20-year records obtained from Instituto Colombiano de Hidrología, Meteorología y Adecuación de Tierras (HIMAT), the average rainfall and temperature are 2,400 mm

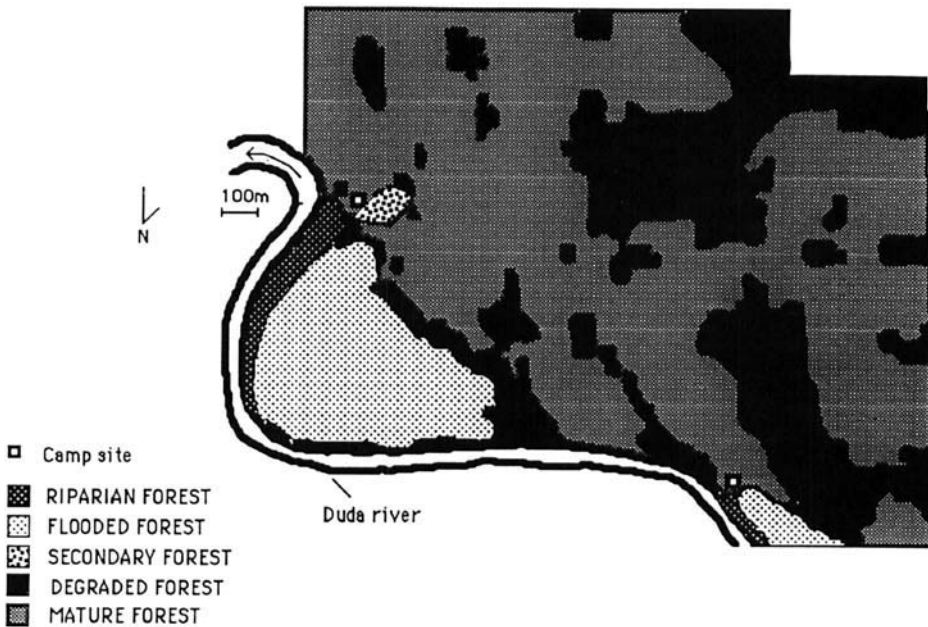


Fig. 2. Distribution of the vegetation types in the study area, according to the authors' experience. Base camp is shown on the left side.

and 25°C. During our study period year (March 1990–February 1991) total rainfall was 2,604 mm with May and June being the wettest months (430 and 428 mm) and January and February the driest (0 and 46 mm). The dry period spanned only these 2 months for this particular year. The topography of the area undulates with rolling hills dissected by brooklets, and flooded areas near river margins. Based on Hirabuki [1990] the vegetation types in the area were grouped in three easily recognized categories:

1. *Mature forest*, localized on hill ridges, with trees of 20–25 m in height, and a continuous canopy with emergent trees reaching 30 m. This forest type supports the highest diversity of tree species.
2. *Open-degraded forest*, localized on erosion fronts, small valleys and brooklets. This forest presents a high variety of vines, lianas, and bamboo with a few trees of 20 to 25 m in height, resulting in a discontinuous canopy and a thick understory.
3. *Flooded forest*, localized to flatlands formed by the river and characterized by a discontinuous canopy dominated by *Ficus spp.*, *Inga spp.*, and *Cecropia sp.* with an understory covered mostly by “platanillos” (*Heliconia spp.*).

We constructed a vegetation map of the study area (426 ha) by superimposing a 50 × 50 m grid on a trail map and assigning a particular forest type to each cell based on our best knowledge of the terrain. The most common vegetation type was mature forest (53%) followed by open degraded forest (34%) and flooded forest (11%). The remaining 2% was composed of riparian forest and a secondary human disturbed forest. Riparian forest is localized in recently formed sand shores, covered mostly by graminoids, *Tessaria integrifolia* and young *Cecropia* trees (Fig. 2).

Seven species of monkeys are common in this area: *Lagothrix lagotricha* (woolly monkey, churucu, mono barrigudo), *Cebus apella* (capuchin, maicero), *Ateles belzebuth* (spider monkey, marimba), *Alouatta seniculus* (howler monkey, aullador), *Saimiri sciureus* (squirrel monkey, mono ardilla), *Callicebus cupreus* (titi monkey), and *Aotus sp.* (night monkey). Woolly monkeys are the most abundant species in terms of biomass and density (Stevenson, in preparation).

## METHODS

### Socioecological Data

Data on activity and diet, habitat use, and social interactions of individual woolly monkeys were collected using a combination of instantaneous and focal animal sampling [Altmann, 1974] comprising 48 h of observation per month for a total of 624 h throughout the duration of the study. Focal and instantaneous samples were evenly distributed across all hours of the day and for all age/sex classes (12 h of focal sampling and 72 instantaneous samples per class per month, see below). Observations were concentrated on a single group (CR-12). Individuals were identified using natural marks on the genitals (characteristic spot patterns on clitoris and penis), face (distinctive facial shapes and expressions), and body size. In addition, some adult males had one or more broken fingers which do not bend, aiding as identification signals. All individuals in the group were identified since July 1990.

**Activity.** During focal samples, instantaneous samples were taken 10 min apart, recording the type of activity the focal animal was performing. Activities were classified in the following categories: moving, feeding on fruit, feeding on vegetative parts (leaves, stems, petioles, roots, and flowers), feeding on arthropods (larvae and adult arthropods), and feeding on other items (termitaria soil and vertebrate prey). Resting and other behaviors (reproductive, affiliative, and agonistic interactions) were also recorded. Two hundred eighty-eight instantaneous samples were taken each month, evenly distributed between adult males, adult non-lactating females, adult lactating females, and juveniles. In order to compare age/sex classes, the data was grouped into 3-month periods (March–May, June–August, September–November, December–February), and G tests (tests of independence) were made to check for differences between age/sex classes in activity patterns for each period. Since the Gs of different parts of the independence table add up to the total G for the whole table in the case of non-independence between age/sex class and activity, it was possible to detect which age/sex classes were causing the rejection of the null hypothesis. Additionally, G-tests were also made to the total data to examine differences in activity patterns between age/sex classes on an annual basis.

**Fruit and leaves diet.** Whenever the focal animal was feeding on fruit or vegetative parts of plants, the number of minutes spent feeding, the plant species, and whether the fruit was mature or immature were recorded.

**Habitat use.** The focal animal's location and the observed vegetation type were recorded every 30 min from 6:00 to 18:00 h. Trails, marked every 50 m, were used to determine the exact location of the focal animal on a map with a superimposed 50 × 50 m grid.

**Intra and interspecific agonistic interactions.** Each time the group or subgroup of a focal animal encountered another group of the same or different species of monkey, the presence or absence of agonistic interactions such as chasing and grabbing were recorded. Additionally, the context of the interaction (e.g., within a fruiting tree) was noted. Agonistic interactions within members of the same group were also recorded, registering the age and sex of the participants, directionality of

the behavior (who attacked whom), and the context. Data were pooled for the whole year and a chi-square test performed, to evaluate differences between age/sex classes in the number of agonistic interactions received and directed.

### Fruit Abundance

Variations in fruit abundance during the year of study were estimated using two different methods: fruit traps and phenological transects. A total of 300 fruit traps (800 cm<sup>2</sup> each) were distributed with equal density in the three types of vegetation formations in proportion to the area covered by each formation (150 in broad-leaf forest, 100 in open-degraded forest, and 50 in flooded forest). The contents of the traps were collected twice a month, separating fruits and seeds from leaves, stems, flowers, and animal material. Samples were dried in an oven for 6 h at about 80°C and weighed in an electronic balance. Fruit abundance was calculated biweekly and separately for each forest type in kilograms of dry fruit per hectare per day.

Phenological transects were carried out also twice a month along trails where the traps were located. The length of the transects varied according to the abundance of each forest type (2,784 m in mature forest, 1,885 m in open-degraded forest, and 929 m in flooded forest), and the width was 2 m (1 m at each side of the trail). Fruit abundance was quantified by the basal area [ $\pi$  (Diameter at Breast Height/2)<sup>2</sup>] of every fruiting tree which projected its crown above the transect. Basal area has been shown to be positively correlated with fruit production [Leighton & Leighton, 1982]. Since most of the trees bore fruit for more than one consecutive biweekly period, fruit production for each period was calculated a posteriori as the sum of the fractions of the basal areas of all the trees fruiting during that period, according to a triangular fruit production pattern for each tree. This is justified as follows: Fruit production for each individual tree was not assumed constant through time, but to increase linearly up to the median fruit period and then to decrease linearly (triangular distribution). Several tropical tree species have shown this approximate fruit production pattern [Howe, 1982]. The basal area of each tree was then divided according to such distribution. For example, if a tree of basal area 100 cm<sup>2</sup> fruited during three consecutive biweekly periods, fruit production during the first, second, and third period was 22.2, 55.5, and 22.2 cm<sup>2</sup>, respectively (which adds up to 100), instead of being 33, 33, and 33 cm<sup>2</sup> (which assumes constant fruit production through time). By following such procedure we avoided overestimation of fruit production by very big trees with long fruiting periods. For more details see Stevenson et al. (in preparation). Only plants which bear animal dispersed and ripe fruit were considered.

## RESULTS

### Study Group

A total of six groups of *Lagothrix* were found in the study area. These did not have exclusive home ranges. For example, CR-12 home range overlapped completely with CR-2. A group does not necessarily defend the whole range it utilizes, but seems to temporarily defend some areas of it by means of agonistic behaviors. However, neighboring groups tend to avoid one another. Some groups seem to dominate others; for example groups CR-12 and CR-2 seemed to be the strongest in the area during the study. Agonistic encounters in which chasing between individuals was observed, occurred seven times between these groups. In most of the cases the biggest group (CR-2) would win the encounter, displacing CR-12. Adult males were more active during the agonistic encounters, and the strongest aggressions observed occurred toward females.

TABLE I. Composition of Some Woolly Monkey Groups Present in the Study Area\*

Group	♂	♀	♂S	♀S	J	I	Total	Source
CR-1	4	5	0	2	2	1	14	Personal observation (1988)
CR-1	4	6	1	0	5	3	19	Nishimura (personal communication, 1990)
CR-2	8	10	0	4	5	2	≈33	Izawa & Nishimura [1988]
CR-12	4	5	1	1	2	4	17	Personal observation (1990)
CR-12	4	7	2	0	6	2	21	Personal observation (1991)
CR-D	4	4	1	1	3	1	≈14	Personal observation (1990)
CR-Z	5	7	2	0	5	2	≈21	Personal observation (1991)

\*♂ = adult males; ♀ = adult females; S = subadults; J = juveniles; I = infants.

Group size in Tinigua varied between 14 individuals (group CR-D) to approximately 30 in group CR-2 (Table I). In July 1990 the study group (CR-12) was comprised of 17 individuals: 4 adult males, 5 adult females, 1 subadult male, 1 subadult female, 1 juvenile male, 1 juvenile female, 2 infant males, and 2 infant females. Changes in size and composition of the group were due to two births (a male and a female in September 1990 and February 1991, respectively), one emigration (a subadult female in November 1990), and three immigrations (1 adult female in December, and an adult female with a dependent juvenile female in June 1991) (Fig. 3).

### Fruit Production

Fruit production varied through the year and both methods used to estimate it (traps and phenology) showed the same basic pattern. The number of trees recorded in the phenological transects was significantly correlated with both the production of fruit in the traps and the basal area of the trees in phenological transects ( $r^2 = .32$ ,  $P = .003$  and  $r^2 = .55$ ,  $P = .02$ , respectively). The number of trees bearing mature fruit (Fig. 4) seemed to be the less biased estimate of fruit abundance (Stevenson et al., in preparation).

There was a peak of production at the beginning of the rainy season with a gradual decrease to a minimum by the end of the season. A second increase in fruit production occurred in the dry period. The mature forest produced more fruit than the other types of forest, and its pattern of fruiting was very similar to that of the open-degraded forest. In contrast, fruit production in the flooded forest peaked toward the middle of the rainy season when the other forest types showed a decrease in fruit supply.

### Habitat Use

Woolly monkeys preferred mature forest (82%) to open-degraded forest (11%) and flooded forest (5%) (approximately 80% of the data corresponds to group CR-12). Although this type of forest covers most of the study area, woolly monkeys use it more than expected from random use ( $X^2 = 34.4$ ,  $P < 0.01$ ). There were significant differences in the frequencies of use of mature forest across the year ( $G = 24.2$ ,  $P < 0.05$ ) due mostly to an increase in the use of open-degraded forest during the period of fruit scarcity (Fig. 5). An increase in the use of flooded forest was observed in July; actually the highest fruit production in this forest occurred between May and July.

Based on 2 years following the study group, we calculated the size of its home range as approximately 169 ha. Different parts of the home range were used more

NAME	SEX	JUL	AGU	SEP	OCT	NOV	DEC	JAN	FEB	MAR/	JUN
PELE	♂	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
CARECA	♂	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
ZICO	♂	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
TOSTAO	♂	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
FALCAO	♂s	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
NELINHO	J♂-♂s	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
AMPARO	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
MADONA	♀	+++++	+++++	B	+++++	+++++	+++++	+++++	+++++	+++++	+++++
BO	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
GLORIA	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
PIA S.	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
LATOYA	♀s	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
PAOLO I.	i-J♂	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
GABRIELLA	i-J♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
BASINGER	i-J♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
AMARILDO	i-J♂	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
MENCHA	J♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
MAURO G.	i♂	+++++	+++++	B	+++++	+++++	+++++	+++++	+++++	+++++	+++++
NIDIA	i♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
NILSEN	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
JULIA	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
JANE	♀	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++

Fig. 3. Members of the woolly monkey study group (CR-12) from July 1990 to June 1991. ♂ = male, ♀ = female, J = juvenile, i = infant, s = subadult. D = desertion from the group, J = joining the group, B = birth.

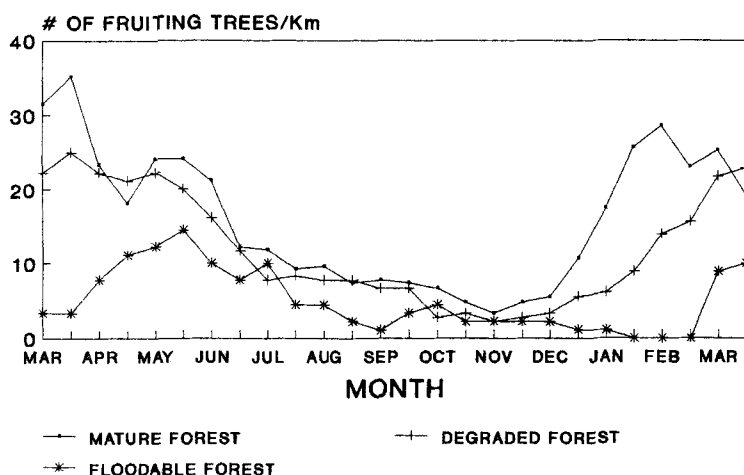


Fig. 4. Fruit production of the area during the study based on the number of fruiting trees per km of phenological transects. Abundance for each forest type is presented.

heavily depending on the location of fruiting trees (Fig. 6). More than 90% of the cells recorded at least seven times were heavily used for fruit feeding.

Daily traveling distances of the group were estimated based on days in which the monkeys were followed for a minimum of 12 h (including adjacent days). Average traveling distance was 1,633 m with a standard deviation of 435 m. Traveling distance was significantly shorter during September until November, when fruit was scarce (mean = 1,210 m, s.d. = 243 m), than during months with high fruit abundance (mean = 1,691–1,853 m;  $F = 5.82$ ,  $P < 0.01$ ) (Table II).

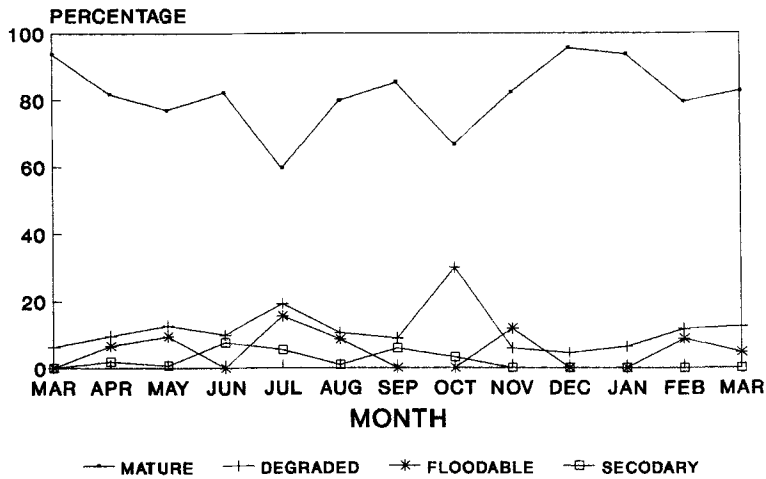


Fig. 5. Percentages of utilization of each forest type across the year by woolly monkeys.

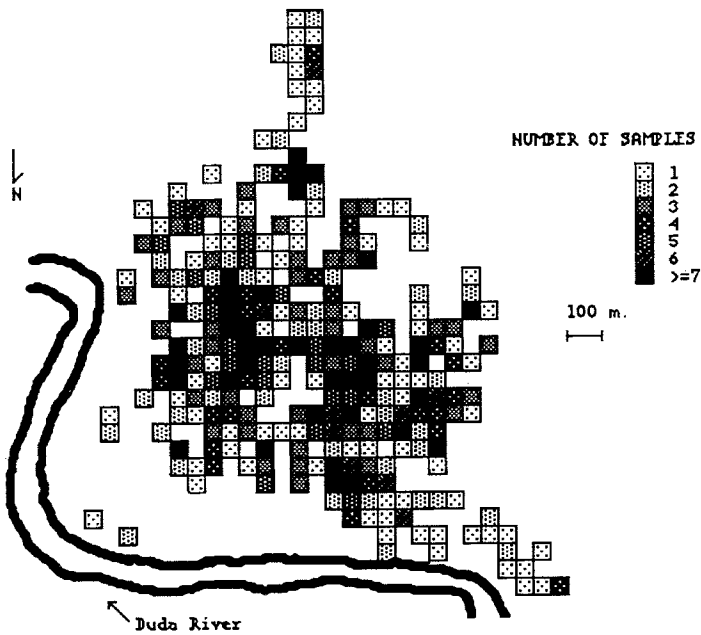


Fig. 6. Use frequencies of the study group home range, based on instantaneous samples each 30 min during the study.

### Activity

The study group spent 24% of the instantaneous samples moving, 36% resting, 36% feeding, and 4% in other activities, combining all samples throughout the study year ( $n = 3,456$ ). Combining all age/sex classes, the proportion of samples in each activity varied significantly from month to month ( $G = 129.6$ ,  $P < 0.05$ ).



TABLE II. Daily Distances Traveled by Focal Woolly Monkeys in 12 h of Continuous Sampling (including adjacent days)\*

Trimester	March/May	June/August	September/November	December/ February	Total
AVG	1,853	1,691	1,210	1,796	1,633
SD	109	365	243	344	435
N	6	11	10	14	31

\*AVG = trimestral averages; SD = standard deviations; N = number of data.

During months of fruit scarcity (especially November), woolly monkeys spent only a small proportion of their time moving and interacting socially, and most of it resting (Fig. 7). Significant positive correlations were found between the number of trees bearing ripe fruit and the number of samples moving for each month, and the number of trees bearing ripe fruit and the number of samples in other activities for each month ( $r^2 = .62$ ,  $P = .001$  [moving] and  $r^2 = .53$ ,  $P = .01$  [other]). Although the proportion of fruit, leaves, and arthropods in the diet changed drastically between months, individuals showed little variation in the percentage of time spent feeding between months ( $G = 21.1$ ,  $P > 0.05$ ).

The proportion of samples of each activity varied significantly on a daily basis (Fig. 8). In general, moving and feeding were predominant during early morning and afternoon with resting concentrated in the midday. This general pattern deviated slightly at different times of the year. For example, in May 1990, with cooler and rainy days, the resting peaks at midday were less pronounced and feeding and moving were more evenly distributed throughout the day. In months of fruit scarcity the sleeping periods started earlier (between 16:00–17:00 h) than in months of fruit abundance (18:00 h).

On an annual basis, individuals of different age/sex classes did not differ significantly in their activity patterns (Table III) except in the scarcity period (T3) when males and lactating females rested much more than non-lactating females and juveniles ( $G = 22.6$ ,  $P < 0.05$ ), and juveniles spent more time interacting socially and playing than other age/sex classes ( $G = 15.3$ ,  $P < 0.05$ ). Lactating females seemed to spend more time feeding than other classes, although these differences were not statistically significant. This activity, as well as moving, showed less variation than resting and social activities.

## Diet

Woolly monkeys consumed mostly fruits (60% of all samples), followed by arthropods (23%), leaves, stems, roots, and flowers (17%), and other items (soil from termitaria nest, fungi, a frog) (1%). Diet composition within these broad categories varied significantly between months ( $G = 238$ ,  $P < 0.05$ ). During periods of fruit scarcity, individuals spent less time feeding on fruit (37 and 41% in October and September). During these months the diet has a high component of vegetative plant parts, reaching levels as high as 50% (Fig. 9). A significant negative correlation was found between the number of samples eating vegetative parts and the number of trees bearing ripe fruit in phenological transects each month ( $r^2 = .45$ ,  $P = .01$ ).

Arthropods were the second most important food category in the woolly monkey's diet (23% of all samples). Although most of the times these items were not identified, occasional observations suggest that they consisted mostly of Coleoptera and Lepidoptera larvae, adult Orthoptera, Diptera, and Arachnidae. Ants and mantids were also eaten. Individuals foraged for arthropods in green leaves

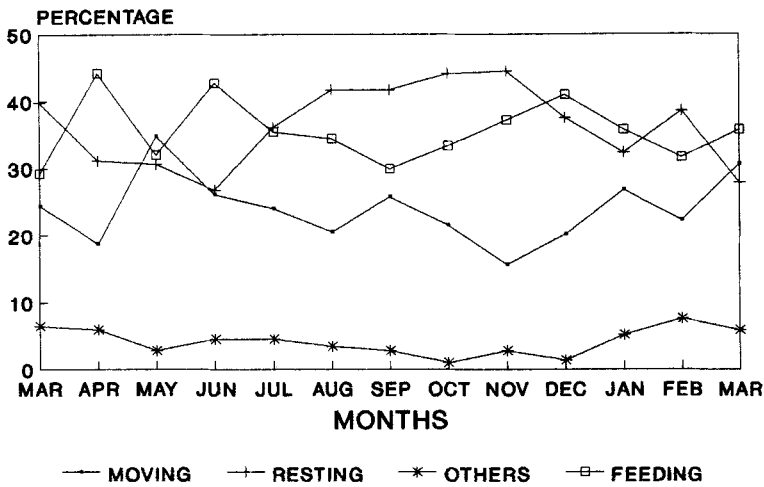


Fig. 7. Variation in the percentages of each activity carried out by woolly monkeys across the study, based on instantaneous samples each 10 min ( $N = 288$  for each month).

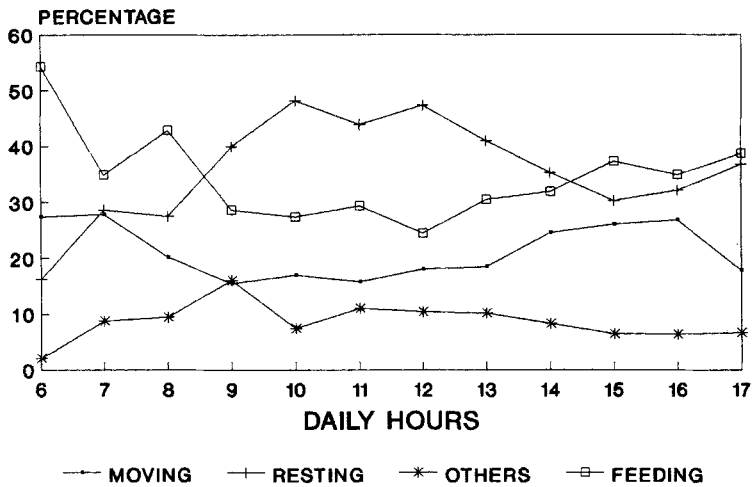


Fig. 8. Variation in the percentages of each activity performed by woolly monkeys across the day, combining all data ( $N = 312$  for each h).

(52%), dry leaves (25%), palm leaves (14%), inside rotten branches (4%), spiderwebs (2%), tree trunks (2%), and the surface of branches (2%). A significant positive correlation was found between the number of samples in which arthropods were consumed and the number of trees with fruit ( $r^2 = .40$ ,  $P = 0.02$ ). This result suggests that variation in the availability of insects eaten by woolly monkeys is coupled with fruit production.

The vegetative parts of plants most frequently consumed were young tree leaves (53% of the time), followed by young vine leaves (29%), flowers (10%), and epiphytes (7%). Variations in the intake of these items across the whole year are shown in Figure 10. In general, vegetative parts and flowers were mostly con-

TABLE III. Percentages of Samplings Recorded in Each Activity for Different Age/Sex Classes\*

	Moving	Resting	Other	Feeding
T1				
♂	24	42	3	30
♀/i	20	40	2	39
♀	32	27	5	36
J	27	26	10	36
T2				
♂	22	38	4	35
♀/i	24	33	2	41
♀	24	35	5	37
J	24	32	6	38
T3				
♂	16	53	4	27
♀/i	19	44	1	35
♀	25	41	2	32
J	24	35	2	39
T4				
♂	21	43	2	34
♀/i	26	34	2	38
♀	24	34	6	36
J	21	33	9	36
Total				
♂	22	43	4	31
♀/i	23	38	2	38
♀	26	33	4	36
J	24	31	7	37

\*♂ = adult males; ♀/i = lactating females; ♀ = adult females; J = juveniles and subadults of both sexes. Results are grouped by trimesters (T1-4).

sumed during months when fruit was scarce. Variations in the consumption of tree leaves, vine leaves, and epiphytes show the same pattern, but vine leaves were mostly eaten during October while tree leaves were eaten during November.

Young leaves were mostly eaten from only a few species: *Brosimum alicastrum* (23%), *Monstera dilacerata* (6%), *Machaerium sp.* (3%), *Henrietella sylvestris* (3%), and *Jacaratia digitata* (3%). Several vine species of the family Bignoniaceae were also important sources of leaves (i.e., *Xylophragma seemanniana*), but most of these were not identified. Only 5% of the time spent feeding on leaves was spent feeding on mature leaves, and these came mostly from *H. sylvestris* and *J. digitata*. Flowers were eaten mostly from *Astrocaryum chambira*.

Table IV lists the top 20 species of fruit consumed by woolly monkeys based on the number of minutes spent by focal individuals eating each species. The species most heavily used was *Gustavia hexapetala* (Lecithydaceae), which started fruiting at the beginning of the fruit abundance period. Two species followed, *Spondias venulosa* and *Spondias mombin*, which were important in the last phase of the period of high fruit production. Other important genera were *Brosimum spp.*, *Pouroma spp.*, *Ficus spp.*, *Inga spp.*, and *Garcinia sp.* Table V lists the families of plants that contributed to the fruit diet of *Lagothrix* in order of importance. The most important family was Moraceae which contributed 28 species (including Cecropiaceae) followed by Anacardiaceae (3 species) and Lecithydaceae (1 species).

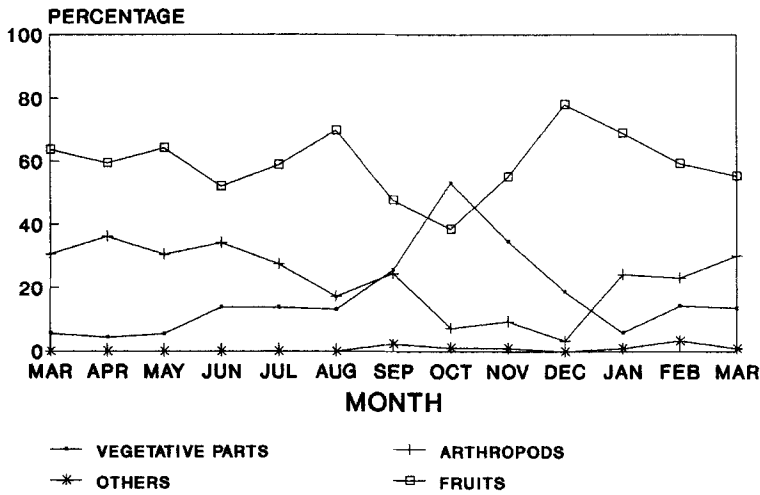


Fig. 9. Variation in the percentages of feeding on different items in the woolly monkeys' diet during the study period (based on instantaneous samples).

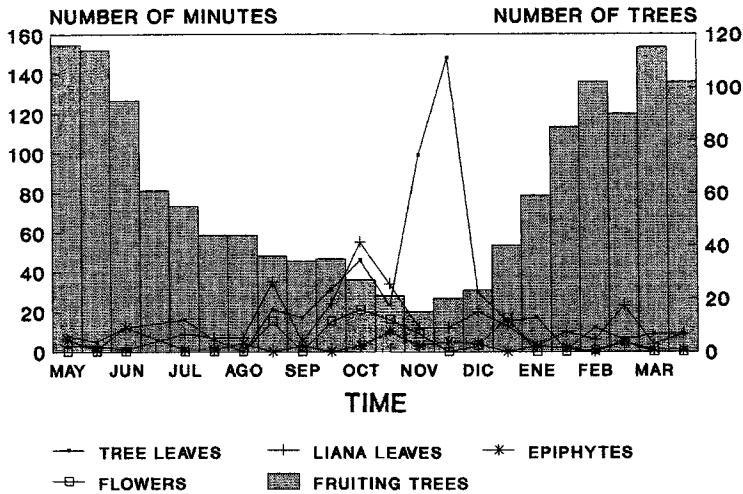


Fig. 10. Variations in feeding time on vegetative parts of plants and flowers during the study period by woolly monkeys (based on the number of minutes observed). The bars represent fruit abundance (total number of fruiting trees in the phenological transects).

Other important families were Burseraceae, Sapotaceae, Melastomataceae, and Guttiferae.

Woolly monkeys consumed mostly ripe fruit (82% of the species), but they also fed on a variety of unripe fruits and devoted more time to eating it during the last weeks of the fruit scarcity period (Fig. 11). Across all fruit species, 14% were consumed, both ripe and occasionally unripe, and only 4% were consumed unripe and/or seed preyed. There was no significant correlation between the number of instantaneous samples feeding on fruit and the number of trees bearing ripe fruit each month ( $r^2 = .22$ ,  $P = .12$ ), because during fruit scarcity woolly monkeys

**TABLE IV. The Most Important Fruit Species Consumed by Woolly Monkeys**

No. of minutes consumed	Species	Family
954	<i>Gustavia hexapetala</i>	Lecithydaceae
715	<i>Spondias venulosa</i>	Anacardiaceae
653	<i>Spondias mombin</i>	Anacardiaceae
217	<i>Brosimum alicastrum</i>	Moraceae
183	<i>Pouroma bicolor</i>	Cecropiaceae
173	<i>Protium cf. crenatum</i>	Burseraceae
172	<i>Inga cf. coruscans</i>	Mimosaseae
153	<i>Ficus perforata</i>	Moraceae
134	<i>Brosimum guianense</i>	Moraceae
131	<i>Garcinia macrophylla</i>	Guttiferae
125	<i>Crepidospermum rhoifolium</i>	Burseraceae
117	<i>Sarcalus brasiliensis</i>	Sapotaceae
99	<i>Doliocarpus dentata</i>	Dilleniaceae
97	<i>Ficus cf. piresiana</i>	Moraceae
92	<i>Protium cf. apiculatum</i>	Burseraceae
90	<i>Enterolobium schomburgkii</i>	Mimosaseae
83	<i>Inga alba</i>	Mimosaseae
81	<i>Henrietella sp.</i>	Melastomataceae
80	<i>Ficus spenophylla</i>	Moraceae
67	<i>Jacaratia digitata</i>	Caricaceae

**TABLE V. The Most Important Plant Families Used for Fruit Consumption by Woolly Monkeys**

Family	No. of minutes consumed	%	No. of species used
Moraceae	1,502	23	28
Anacardiaceae	1,384	21	3
Lecithydaceae	954	14	1
Burseraceae	487	7	6
Mimoseseae	483	7	15
Sapotaceae	196	3	7
Melastomataceae	185	3	8
Guttiferae	131	2	2
Cesalpinaceae	128	2	3
Rubiaceae	125	2	2
Annonaceae	101	2	5
Dilleniaceae	99	1	1
Arecaceae	97	1	4
Polygonacea	87	1	3
Caricaceae	67	1	1
Tiliaceae	56	1	1
Meliaceae	46	1	3
Celastraceae	43	1	3
Euphorbiaceae	39	1	1
Lauraceae	37	1	3

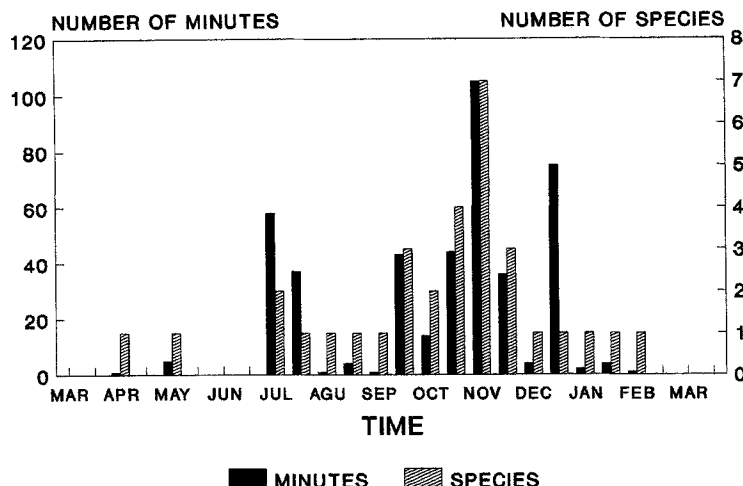


Fig. 11. Number of minutes and species used by woolly monkeys to feed on unripe fruit at different periods of the study year.

compensate fruit feeding with unripe fruit. In fact, there was a significant negative correlation between the number of minutes spent feeding on unripe fruit and the number of trees bearing ripe fruit ( $r^2 = .43$ ,  $P < .001$ ).

On an annual basis, there were no significant differences in diet composition of different age/sex classes ( $G = 17.5$ ,  $P > .05$ , Table VI). However, non-lactating females and juveniles showed a higher consumption of arthropods during the third 3-month period comprising September to November (T3, fruit scarcity period). Lactating females also tended to feed more on fruits and leaves and less on arthropods, although this pattern was not statistically significant.

### Intragroup Agonistic Interactions

Table VII summarizes the agonistic interactions between members of the same group according to the age/sex class of the interactants. Attacks were neither performed nor received equally by all age/sex classes ( $\chi^2 = 119$ ,  $P < 0.01$ ,  $\chi^2 = 660$ ,  $P < 0.01$ ). Males were the most aggressive and least attacked, while juveniles and non-lactating adult females showed the reverse pattern. Lactating females were attacked less by males than were non-lactating females (Table VII). More than half of the agonistic interactions were observed while the monkeys were feeding on fruit (55%). Additionally, the total number of agonistic interactions and the number of interactions that occurred while feeding on fruit were highest in periods of fruit abundance (Total: Trimester-1 = 39, T-2 = 30, T-3 = 36, and T-4 = 62). This could be explained by less time available for encounters, or by resource separation during periods of fruit scarcity.

### DISCUSSION

Although the size of the study group falls within the observed ranges for *Lagothrix*, its home range size is much smaller than that reported for other groups (Table VIII). Daily traveling distance is also shorter compared to other groups in other areas but not in all cases (Table VIII). Woolly monkeys used mature forest more heavily than other kinds of vegetation types in the area. This pattern of

**TABLE VI. Percentage of Feeding Samplings on the Different Categories Included in the Diet of Woolly Monkeys for Each Age/Sex Class\***

	Vegetative parts	Arthropods	Fruits
<b>T1</b>			
♂	3	38	59
♀/i	5	23	72
♀	7	39	54
J	1	35	64
<b>T2</b>			
♂	12	30	58
♀/i	15	20	65
h	14	30	56
J	14	27	59
<b>T3</b>			
♂	39	7	54
♀/i	53	4	43
♀	30	24	46
J	33	16	51
<b>T4</b>			
♂	14	15	70
♀/i	9	16	75
♀	13	13	74
J	18	21	62
<b>Total</b>			
♂	16	24	59
♀/i	19	18	64
♀	16	27	57
J	17	25	58

\*♂ = adult male, ♀/i = lactating females; ♀ = adult females; J = juveniles and subadults. Results are grouped by trimesters (T 1-4).

variation in habitat use was coupled with spatial variation in the number and type of fruiting trees. Defler [1989] obtained a similar pattern for woolly monkeys living in the river Apaporis, Colombia.

Besides the present study and a previous one in the same locality (Stevenson, in preparation), there is virtually no information on activity budgets of woolly monkeys. Patterns of activity throughout the day were similar in both studies, with feeding and moving concentrated mostly during the morning and afternoon hours, and resting peaks at midday. This pattern is common to many species of primates and may be determined partially by energetic requirements after the long period of nocturnal inactivity and to facilitate thermoregulation during the hot midday hours [Van Roosmalen, 1985; Oates, 1987]. Changes in activity patterns such as increased resting time in periods of fruit scarcity were coupled with important changes in diet composition, namely an increase in the intake of leaves, flowers, and unripe fruit. This whole pattern of variation in activity budget and diet is consistent with the inverse relationship between the proportion of leaves in the diet of a species and the time it spends moving, reported in several other primate species [Clutton-Brock & Harvey, 1977].

Stevenson [1992] found different estimates in diet composition at this site. He

TABLE VII. Number and Direction of Intragroup Agonistic Interactions Observed Between Different Age/Sex Classes\*

Aggressor	Context	Aggressee									Total
		♂	♂s	♀/i	♀	♀s	J♂	J♀	Ja	a	
♂	fr	0	3	9	5	1	2	6	5	6	37
	ot	2	6	12	15	1	10	5	0	1	52
♂s	fr	0	0	0	4	0	0	1	4	0	9
	ot	0	0	2	3	0	0	0	0	0	5
♀/i	fr	0	0	1	1	0	0	5	4	0	11
	ot	0	0	1	3	0	2	2	0	0	8
♀	fr	0	0	2	1	0	1	2	0	0	6
	ot	0	0	0	1	0	0	1	2	0	4
♀s	fr	0	0	0	0	0	0	0	0	0	0
	ot	0	0	0	0	0	0	0	0	0	0
J♂	fr	0	0	0	1	0	0	1	0	1	3
	ot	0	0	0	7	0	0	0	0	0	7
J♀	fr	0	0	0	0	0	0	0	0	0	0
	ot	0	0	0	0	0	0	0	0	0	0
a	fr	0	1	3	0	0	2	1	7	23	37
	ot	0	0	0	1	0	1	1	2	2	7
Total	fr	0	4	15	12	1	5	16	20	30	103
	ot	2	6	15	30	1	13	9	4	3	83
		2	10	30	42	2	18	25	24	33	186

\*♂ = adult males; ♂s = subadult males; ♀/i = lactating females; ♀ = adult females; ♀s = subadult females; J♂ = male juveniles; J♀ = female juveniles; Ja = unknown sex juveniles; a = unknown class. Aggressions are separated into fruit feeding contexts (fr) and other contexts (ot).

TABLE VIII. Home Range Size for Woolly Monkey Groups at Different Study Sites

Locality	Group size	Home range size (ha)	Source
Caquetá (Colombia)	13	350	Nishimura [1990]
	45	450	
Manú National Park (Perú)	10	250	Ramirez [1980]
	14	400	
Rio Pacaya (Perú)	13	400	Soini [1990]
NW Amazonas (Colombia)	23	760	Defler [1989]
Macarena (Colombia)	19	169	This study

found higher estimates of fruit feeding time (78% vs. 60%) and lower estimates for leaves (9% vs. 17%) and arthropods consumption (12% vs. 23%). The differences are explained mainly because his study period only covered 6 months of fruit abundance. The lower arthropod consumption in his work could be also related with differences in the methods used (time spent vs. instantaneous samples in this study).

The high proportion of arthropods in the diet of *L. lagotricha* is rather unusual when compared with the importance of this item in related species of similar size such as *Brachyteles* and *Ateles* [Klein, 1972; Milton, 1984; Strier, 1991; Van Roosmalen, 1985]. We postulate that the exploitation of this niche may be coupled with a higher cohesiveness in the social structure of this species compared to the closely related spider monkeys (*Ateles spp.*). In more frugivorous species such as spider



monkeys, searching for food in small groups is advantageous from the individual's point of view, because it minimizes intraspecific competition in fruiting trees [Klein, 1972; Symington, 1988]. In the case of *Lagothrix*, feeding on arthropods can buffer the negative effects of being displaced from fruit-feeding places in a patch. This idea is supported by the fact that submissive age/sex classes, such as juveniles and non-lactating females, spend more time feeding on insects than more dominant classes (males and lactating females).

## CONCLUSIONS

1. Woolly monkeys spent most of their time in mature forest where fruit availability is higher than in open-degraded or flooded forests.
2. Changes in habitat use observed were coupled with changes in fruit supply across vegetation types.
3. Woolly monkeys spent 24% of point samples moving, 36% resting, 36% feeding, and 4% on other activities, but these proportions varied across the year depending on fruit availability.
4. The diet consisted mostly of fruits (60%), arthropods (23%), vegetative parts and flowers (17%), and other items (1%), but also varied across the year.
5. Non-lactating females and juveniles spent more time eating insects than adult males and lactating females, probably because females and juveniles are excluded from fruiting trees by adult and subadult males.
6. The high proportion of arthropods in the diet is proposed as a mechanism influencing the cohesiveness of woolly monkey groups.

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