

RESEARCH ARTICLE

Ranging Behavior and Foraging Ecology of Lowland Woolly Monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador

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In a year-long study, I investigated the ranging behavior of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a terra firma rainforest in Yasuní National Park, Ecuador, and examined the relationship between ranging, diet, food availability, and food patch use for this population. In Yasuní the total home range sizes for two social groups were 124 and 108 ha, which are much smaller than has been reported previously for *Lagothrix* elsewhere in its geographic distribution. The mean yearly day range estimates for these same groups were 1,792 m and 1,878 m, which are well within the range of variation previously reported. Ranging behavior was not correlated with the current habitat-wide abundance of ripe fruit, which comprises 76.3% of the yearly diet for this population, but was associated with one measure of likely insect prey abundance and with the availability of immature fruits, a minimal part of the diet. Specifically, one study group moved significantly greater distances during months of high likely insect prey abundance and when immature fruits were abundant. The second study group also traveled farther when likely insect prey abundance was high and when immature fruits were abundant, although the latter relationship only approached significance. This group also devoted significantly more of its daily activity budget to travel during these times. These results indicate that variation in ripe fruit abundance makes no meaningful contribution to explaining variation in ranging behavior for this population of woolly monkeys. Instead, the results raise the possibility that some aspects of the ranging behavior of frugivorous primates may be related to the availability of alternative food sources, such as animal prey, or to monitoring the phenological status of important fruit trees, rather than simply reflecting the degree of intragroup feeding competition. *Am. J. Primatol.* 59:47–66, 2003. © 2003 Wiley-Liss, Inc.

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## INTRODUCTION

In primates, home range size has been shown to correlate negatively with habitat quality (e.g., *Cercopithecus aethiops* [Struhsaker, 1967] and *Pan troglodytes* [Suzuki, 1969]). Home range size within a species also tends to increase with increasing group size [Dunbar, 1988], and a similar relationship between group biomass and range size has also been found to hold at the interspecific level [Milton & May, 1976; Clutton-Brock & Harvey, 1977]. Day range length likewise tends to scale with both group size and habitat quality: in many species, larger groups travel farther each day (e.g., *Cercocebus albigena* [Waser, 1977], *Theropithecus gelada* [Iwamoto & Dunbar, 1983], *Macaca fascicularis* [van Schaik et al., 1983], *Cebus olivaceus* [de Ruiter, 1986], and *Cebus apella* [Janson, 1988]), and day journeys tend to be longer for groups living in poorer habitats (e.g., *Cercopithecus aethiops* [Struhsaker, 1967]). In general, these relationships hold more strongly for frugivorous and omnivorous than for folivorous primates [Clutton-Brock & Harvey, 1977; Mace & Harvey, 1983; Dunbar, 1988; Janson & Goldsmith, 1995]. Together, these results strongly implicate group energy requirements, resource availability, and intragroup scramble competition over food as the critical factors affecting variation in primate ranging, both within and across species [Isbell, 1991; Janson, 1992; Janson & Goldsmith, 1995].

Despite the robust cross-species and within-species relationships found between ranging behavior and habitat quality, group size, and diet, general statements about these relationships within the same social group or the same local population over time are not so straightforward [Clutton-Brock, 1977b; Dunbar, 1988], and studies that have examined this issue have failed to find a consistent pattern. For example, while Marsh [1981] found that red colobus monkeys (*Procolobus badius*) ranged farther during months of decreased food availability, Raemakers [1980] found that gibbons (*Hylobates lar*) ranged far shorter distances when food was scarce, and Kaplin [2001] found no significant relationship between food availability and mean day range length in single groups of either blue monkeys (*Cercopithecus mitis*) or L'Hoest's monkeys (*Cercopithecus lhoesti*). These inconsistent results probably reflect the fact that animals can cope with resource scarcity (and with the increased feeding competition that it engenders) in many different ways, depending on individual and species-typical foraging strategies. Increased intragroup feeding competition under conditions of scarcity may lead animals to increase their individual foraging efforts, which might then be reflected in longer group day ranges, faster travel times, increased time allocation to moving, larger seasonal home ranges, and visits to more feeding patches by a group each day. Alternatively, animals could respond to scarcity without altering ranging behavior appreciably, by broadening their diet or by spending more time in each feeding patch in accord with simple predictions of optimal foraging theory. In such cases, ranging behavior might be correlated with other ecological variables, such as climatic conditions or the availability of alternative resources. Animals could also opt to minimize competition over scarce foods by spreading further apart from other group members or by forming separate foraging parties. Finally, they could actually reduce the effort devoted to subsistence—by ranging less, resting more, or

metabolizing reserves of fat or muscle—as a strategy for conserving energy until conditions improve.

In this work I describe the ranging behavior of woolly monkeys (*Lagothrix lagotricha poeppigii*) living in a terra firma forest in lowland Ecuador, at the far western edge of the species' geographic range, with the aim of exploring which of these various ecological strategies best characterizes this population. I begin by providing basic data on home range size, range overlap, intensity of range use, and day range length for three social groups of woolly monkeys. I then consider how ranging behavior covaries with ecological conditions, and examine whether day range length, time allocation to movement, and travel rate are associated with the seasonal availability of several different resource types (fruits, flowers, new leaves, and insect prey) or with other ecological variables (temperature and rainfall). I also consider how diet, resource availability, ranging patterns, and patch use decisions are related to one another, and I examine two simple predictions of optimal foraging models on how animals should respond to habitat-wide resource scarcity—specifically, that diet breadth and patch residence time should increase as resource availability decreases [Charnov, 1976; Stephens & Krebs, 1986]. Finally, I compare the ranging behavior of woolly monkeys in Yasuní to that of populations studied elsewhere, and discuss the implications of this study for understanding the comparative socioecology of woolly monkeys across the Amazon lowlands.

## **METHODS**

### **STUDY AREA**

This study was conducted in the western portion of the 900,000-ha Yasuní National Park in the Amazon region of Ecuador (75°28'E, 0°42'S). The study area consists largely of nonfloodable, primary tropical forest, and is located south of the Río Napo, 47 km along a road constructed through the park's northwestern corner in 1993 and 1994. During the study period (April 1995 to March 1996) rainfall averaged 273 mm per month and peaked twice, first at the onset of the study in May and June 1995 and again in March 1996. Rainfall was least during the three-month dry season from July to September 1995. Prior to the start of behavioral data collection, roughly 30 km of trails in the site were mapped using a hip chain, clinometer, and sighting compass, and were referenced to specific points along the road that were localized with a hand-held global positioning system. The locations of all feeding sources used by woolly monkeys during the course of the behavioral sampling were also mapped relative to the trail system. Trail map points and feeding source locations were converted into UTM coordinates to make an accurate map of the trail system.

### **STUDY SPECIES AND GROUP COMPOSITION**

Woolly monkeys were the most numerous and most frequently encountered of 10 resident primate species. At least five social groups, totaling close to 110 individuals, used various portions of the study site. These groups were all of typical composition, containing two to five adult males, several subadult males, nine to 11 reproductive age females, and four to six juveniles. Two of

these groups (those which ranged closest to the road) were the principal focus of this study. Group 1 varied in size from 25 individuals at the start of the study to 24 individuals by the end, due to the death of a subadult male, the disappearance of an adult male, and the birth of a female infant. Group 2 contained 23 individuals at both the start and end of the research period, with one adult female lost to hunting and one infant female born during the study. Further details concerning the composition of these two groups are provided in Di Fiore [1997] and Di Fiore and Rodman [2001]. A third group (group 3) was followed intermittently, and although an accurate group count was never obtained, I estimated that this group contained approximately 18 independently-locomoting animals.

## BEHAVIORAL DATA COLLECTION

From April 1995 to March 1996, I collected activity and ranging data on the two main study groups during two 5-day follows of each group each month. Each follow consisted of 2 days of instantaneous scan sampling and 3 days of focal sampling [Altmann, 1974]; however, in this work I limited my analyses to data collected on scan days during which ranging data were recorded systematically. Also, because of differences in habituation levels between the two groups, which limited data collection in group 2 early in the study, I restricted my analyses of that group's ranging behavior and activity patterns to the last 9 months of the study. A full 12 months of data were available for group 1.

During sampling, I collected scans at 10-min intervals between 0630 and 1730 hr. The scans lasted for 5 min and were followed by 5 min of inactivity until the next scan began. During a scan I recorded the age and sex class (or individual identity, if possible) and behavior of each individual seen during the scan period. Each animal was watched for 5 sec after being detected, and its predominant behavior during that interval was recorded. I tried to collect behavioral records on as many different animals as possible during a scan by changing positions frequently. However, group members were often spread out over an area of more than 1 ha, so only a fraction of the group could be sampled during any given scan (mean=4.76, SD=1.79, range=1 to 15, n=3731). Care was taken to avoid sampling the same individual more than once in a given scan, but the same individuals could be sampled in successive scans. This could potentially introduce bias if particular individuals were sampled more often than others, or if behavior in one scan was a clear predictor of behavior in a subsequent scan. However, there is no indication that particular individuals were more commonly sampled than others, and bout lengths for all but the longest feeding and resting bouts were typically far less than the 5-min interval between scans. The analyses herein are based on a total of 17,747 behavioral records collected during 2,165 scans on group 1 and 1,566 scans on group 2. I used these records to determine time budgets and monthly and yearly diets, as described below and elsewhere [Di Fiore, 1997; Di Fiore & Rodman, 2001].

During each scan I also recorded the location of the geographic center of the group relative to marked trails and feeding trees. I use these location records to assess a group's total home range size and overlap with adjacent groups, its average daily path length each month, and its average travel rate each month (which was calculated by dividing average daily path length each month by time spent moving). When possible, location records were collected even if activity data could not be collected during a given scan (e.g., if all group members were resting out of view) using other cues to the group's whereabouts, such as vocalizations or

branch movements. Additional location records, but no behavioral data, were collected by trained field assistants who would follow groups separately from me for periods of 1–5 days using the same location-sampling procedures. In all, 6,218 location records were recorded on a total of 134 observer-days over the course of the study (94 days recorded by me, and 40 by field assistants). Of these, a total of 2,759 location records were collected for group 1, 1,983 records for group 2, and 1,476 records for group 3. Assistants collected 13% of the total set of location records for group 1, 15% for group 2, and 71% for group 3. For months during which both assistants and I collected data on the same groups, analysis of variance (ANOVA) tests revealed no significant effect of observer on the distance a group was recorded as moving between consecutive location records.

## ECOLOGICAL SAMPLING

To obtain an estimate of the density, distribution, and abundance of plant resources available in the forest, five 1-ha belt transects, each consisting of 100 consecutive 10 m × 10 m blocks, were placed randomly throughout the study area. Within these transects, all trees >10 cm diameter at breast height (DBH) were tagged and identified by experts in the flora of the region to characterize the floristic composition of the forest. Fifty of the 10 m × 10 m blocks on each transect were then selected for phenological monitoring according to a stratified design in which two out of every four consecutive blocks were chosen at random as a phenology quadrat. Each month from April 1995 to March 1996, the crowns of 1,416–1,459 individual trees located in these 2.5 ha were inspected with binoculars, and the presence and abundance of new leaf flush, flowers, and fruits in either the crown itself or in any associated epiphytic plants were noted. The actual number of trees monitored varied slightly from month to month because a number of trees were lost due to inclement weather or natural death during the course of the study. New leaf abundance and flower abundance were scored as the proportion of the total tree crown bearing these phenophases; for immature and ripe fruits, the actual crop size (number of fruits) was estimated by making repeated counts of subsections of the crown and extrapolating from these to the full crown volume [Di Fiore, 1997]. All phenological data were collected by trained botanists and field assistants concurrently with my behavioral data collection regime.

For comparability to other studies of neotropical forest phenology [e.g., Peres, 1994], I initially characterized the monthly habitat-wide availability of new leaves, flowers, and both immature and ripe fruits as simply the proportion of monitored trees that bore each of these phenophases each month. However, because this crude index does not take into account differences in crown size or the proportion of a crown bearing either new leaves or flowers, or in actual crop size for crowns bearing immature or mature fruits, I calculated several additional indices to characterize the habitat-wide availability of these phenophases. For new leaves and flowers, I calculated an index based on the DBH, which correlates well with crown volume in the Yasuní forest [Di Fiore, 1997]. I first used the DBH to estimate the crown volume of each monitored tree using a regression equation determined previously [Di Fiore, 1997]. I then multiplied crown volume by the proportion of the crown comprising new leaves or flowers, summed these values across the set of monitored trees, and divided this sum by the total crown volume of trees monitored. For immature and mature fruits, I calculated indices based on actual fruit crop size. To do this, I

took the logarithm of the number of fruits estimated in each fruit-bearing crown, summed these log scores across the set of fruiting trees, and divided this by the total number of trees monitored that month.

The total set of trees monitored represented at least 185 different genera belonging to at least 56 families, but clearly not all of these genera were used as plant food resources by woolly monkeys. Therefore, in calculating habitat-wide availability for immature and ripe fruits, I limited the set of trees contributing to the index to only those 25 genera, from 18 different families, whose fruits contributed to at least 1% of the woolly monkey diet over the course of the study. This reduced the number of trees contributing to the two fruit indices each month to 482–490. As I was unable to determine the taxonomic identity of most leaves and flowers eaten by woolly monkeys during the study, I believed it was inappropriate to restrict the data set for these phenophases. Thus, for flowers I used the full set of trees monitored each month to construct the flower availability index. I did the same for new leaves but omitted trees from the family *Arecaceae* (palms), as woolly monkeys were never seen to eat palm leaves.

I was unable to directly measure seasonal variation in the abundance of animal prey, which for woolly monkeys are principally canopy invertebrates. However, if Yasuní is similar to other neotropical sites, then invertebrate abundance should peak shortly following the transition from the dry to the rainy season [Wolda, 1978a, b, 1982; Smythe, 1982; Robinson, 1986; Janson & Emmons, 1990]. Thus, climatological data on rainfall may provide a crude proxy measure of likely insect prey abundance. As an alternative measure of insect prey abundance, I used data collected in Manu National Park, Peru (71°22'W, 11°54'S), the closest (and, indeed, only) Amazonian site for which published data on seasonal changes in insect biomass are available [see Fig. 17.3 in Janson and Emmons, 1990]. In Manu, peak insect abundance coincides with the dry-to-wet season transition occurring in September–November [Janson & Emmons, 1990]. The 3-month dry season recorded in Yasuní during this study from July to September, and the transition to wetter conditions over the subsequent months, correspond closely to the climatological profile of Manu [Terborgh, 1990]; therefore, it seems appropriate to use these data as a crude approximation for conditions in Yasuní.

## ANALYSES

To calculate time budgets, all activity records were first assigned to one of seven mutually exclusive activity categories: EAT, FORAGE, MOVE, REST, SOCIAL REST, SOCIAL ACTIVITY, and OTHER NONSOCIAL [Di Fiore & Rodman, 2001]. MOVE was defined as changing positions within or between tree crowns, exclusive of that taking place while searching a substrate. To determine monthly time allocation to movement and other activity categories, I treated each scan (rather than each individual activity record within a scan) as an independent data point (following Clutton-Brock [1977a]). First I calculated the proportion of each scan that the various activity categories represented, and then averaged these proportions across scans. This method is recommended when variable numbers of individuals are seen per scan to reduce the chance of biasing estimates of time allocation toward overrepresentation of conspicuous, aggregate activities [Clutton-Brock, 1977a]. In order to correct for differences in the number of individual records collected during different months of the year and at different times of the day, I first calculated separate activity budgets for each hour of the

day and then averaged these hourly budgets within each month to construct monthly time budgets. Time budgets were calculated for groups 1 and 2 separately, but I did not calculate separate budgets for males vs. females or for adults vs. juveniles, since for each group these different sex and age classes were sampled very nearly in proportion to their representation in the population. For each group, the number of hours per day spent moving each month was then calculated from the monthly time budgets by multiplying the proportion of time spent moving by 10 hr (the time period over which day range length was calculated, as described below).

I determined the relative contribution of various items (ripe fruit, immature fruit, flowers, new leaves, other vegetative plant parts, and animal prey) to the monthly and yearly diets of groups 1 and 2 by calculating their simple proportional representation among the set of 3,673 individual activity records during which animals from these groups were observed eating. Note that for this calculation, multiple feeding records could come from the same group scan and are not entirely independent. Nonetheless, as this is the most commonly used method of determining primate diets in the literature, I used this method for comparability to other studies. I also determined the average number of feeding patches visited per hour each month for groups 1 and 2 by dividing the total number of patches visited by the total observation hours for each group during the month. I defined a patch as a discrete feeding site in which animals fed for at least 5 “monkey-minutes” and that was separated from other such sites by at least one tree crown; patches were generally single tree crowns or, more rarely, lianas that spanned several trees. Monkey-minutes in a patch is the time between when the first feeder entered the patch and the last feeder left the patch, multiplied by the average number of individuals feeding in the patch during that period. The number of monkey-minutes a group spent in a particular patch was calculated from counts of the number of feeding individuals taken at specified intervals between when the first feeders entered and the last feeders left a patch. These counts were performed quickly at the start of each 5-min group scan, before searching for additional group members to sample, and again at the end of the group scan after reconnoitering the group. For groups 1 and 2, I then calculated the average number of monkey-minutes each group spent per patch each month by dividing the total number of monkey-minutes recorded for that group during the month by the total number of patches in which the group fed.

Home range sizes and patterns of range use were evaluated by superimposing a 100 m × 100 m grid on top of a map of each group’s set of location records, and totaling all of the records that fell into each 1-ha cell of the grid. Other studies of *Lagothrix* ranging behavior have employed a variety of cell sizes in similar analyses of range use (0.25 ha [Stevenson et al., 1994], 1 ha [Defler, 1996], and 0.92 and 3.7 ha [Peres, 1996]). I chose to use a 1-ha cell size because the diffuse spatial configuration of woolly monkey groups argues strongly in favor of using cells of at least this size, as groups are invariably spread over an axis of >50 m and thus span more than one 0.25-ha quadrat.

Finally, day range lengths were determined for each group based on the point-to-point displacements between consecutive location records scored during group follows. Because follows sometimes lasted less than a full day, especially early in the study, and because they were not evenly distributed across either months of the year or hours of the day, I first calculated the average hourly range length for each group for each hour of the day within each month of the year. I then summed these hourly averages within months to construct average monthly day range lengths, and I derived yearly average day range lengths by computing

the grand mean of the set of monthly day ranges. Day range lengths were computed for the period between 0700 and 1700 hr only, because sampling prior to 0700 and after 1700 was limited. This procedure provided the largest comparable datasets for groups 1 and 2, and maximum comparability within groups across months. It is unlikely that this method greatly underestimates daily path length, since group movement before 0700 and after 1700 was generally limited.

**RESULTS**

**Home Range Size and Usage**

Group 1 was recorded in a total of 118 1-ha quadrats over the course of the study, group 2 used 102 quadrats, and group 3 was observed in 99 quadrats (Fig. 1). If we assume that the groups took the most direct route possible while traveling between any two successive scan points, group 1 must have traversed an additional two quadrats and group 2 an additional three quadrats in order to

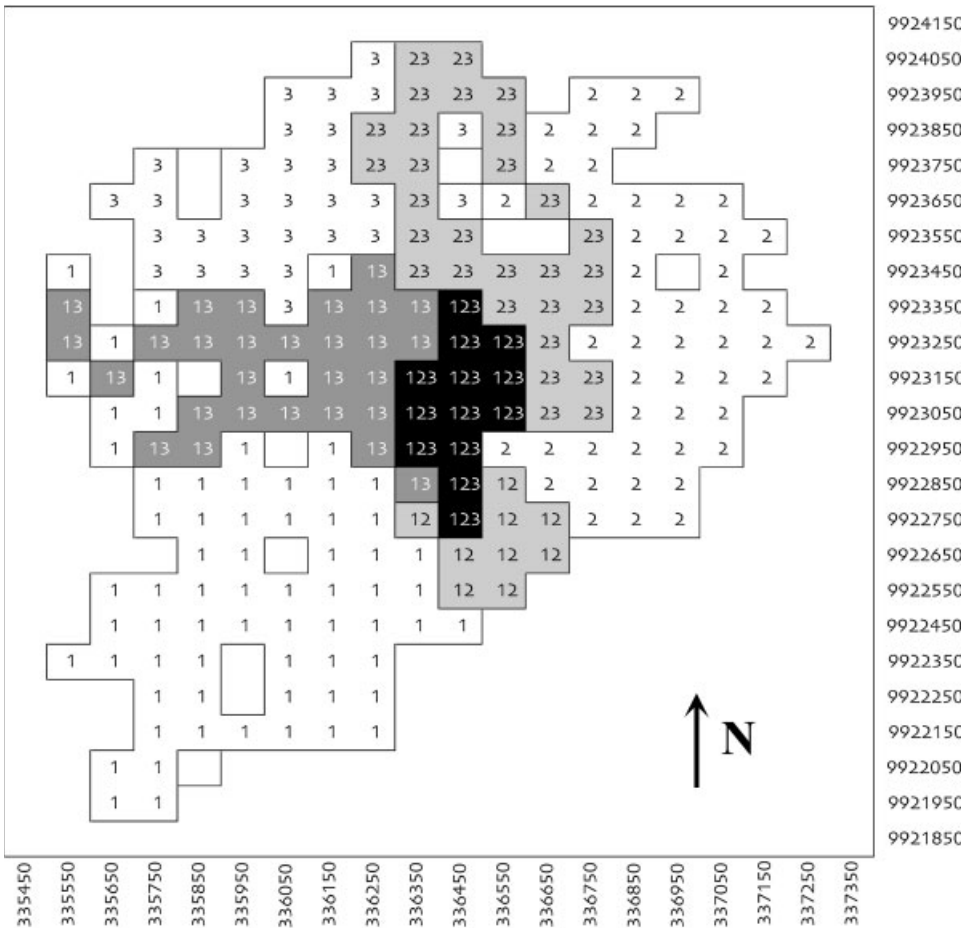


Fig. 1. Home ranges and range overlap between the three study groups. Cell size is 100 m × 100 m = 1 ha. Axes indicate the UTM coordinates for the center of the cell. Shading indicates cells wherein overlap between adjacent groups was noted. Numbers in cells indicates which groups were observed using that cell.

accommodate the observed distribution of used cells, although they were not recorded in those quadrats during any group scan. Including these quadrats, plus a handful of additional quadrats that were never seen to be used but that lie within the boundary of cells visited by a group, yield overall home range size estimates of 124 ha for group 1, 108 ha for group 2, and 105 ha for group 3. Plotting the cumulative number of quadrats entered over the course of the study yields a curve that approaches a clear asymptote for both groups 1 and 2, suggesting that these are accurate estimates of total home range size. A similar curve for group 3 was still increasing after 12 months, however, suggesting that the size of group 3's range was not fully determined.

Groups 1 and 2 used a 22-ha area in common, groups 2 and 3 overlapped in range by 42 ha, and groups 1 and 3 overlapped by 41 ha. A total of 13 ha were used in common by all three groups (Fig. 1). Group 1 shared a total of 56 ha, or 45% of its range, with adjacent groups: 50 ha with some combination of groups 2 and 3; 3 ha at the southwestern edge of its range with a fourth, unstudied social group; and an additional 3 ha at the northwestern margin of group 1's home range that were used either by group 3 or by a fifth, unstudied group. Group 2 shared a total of 51 ha, or 47% of its range, with its two neighbors (groups 1 and 3). Finally, although ranging data are incomplete for group 3, the sampled part of its range overlapped those of the two principal study groups by 70 ha (71%); undoubtedly, its range overlapped that of adjacent groups to the north and west as well.

Figure 2 shows a surface plot representing the intensity of home range use by the two principal study groups based upon the total number of location records falling within each 1-ha cell of the grid. The darker regions on the plot shows core areas of more intense range use within each group's range, as well as several large, minimally used areas that appear inside the range boundaries. For group 1, 25 1-ha quadrats accounted for roughly half (52%) of location records, and only 57 core hectares together account for over 80% of location sightings. For group 2, roughly half (48%) of the location records were noted in only 20 quadrats, and 44 core hectares contained 80% of the records. The most heavily used 1-ha cells in the habitat tended to be areas of high feeding tree density (Fig. 3) or ridgetops, while without exception, gaps in the groups' ranges comprised low-canopy, disturbed secondary forest with few large trees. Woolly monkeys entered these areas infrequently, preferring areas of tall, primary forest.

### **Day Range Length and Time Allocation to Ranging**

The estimated average day range length (0700–1700 hr) for group 1 over the 12 months of the study was 1,792 m ( $\pm 247$  SD); for group 2 over the last 9 months of the study it was 1,878 m ( $\pm 395$  SD). This latter figure is comparable to the estimated average day range length for group 1 over the same 9 months (1890 m  $\pm 180$  SD), and there was no significant difference between groups 1 and 2 in average monthly day range length during this time period (paired sign test,  $n=9$  months,  $P>0.99$ ). These estimates of day range length derived from combining data from partial day follows are very similar to the average length of 27 complete 0700–1700 hr follows (1866 m  $\pm 496$  SD) collected on the whole population (11 on group 1, 13 on group 2, and three on group 3) during the same time period. Across the year, average MOVE time was 36.6% for group 1 and 36.0% for group 2, and varied from 28.7% to 41.9% ( $\pm 1.3\%$  SE) across months for group 1, and from 29.8% to 42.1% ( $\pm 1.6\%$  SE) for group 2. Groups 1 and 2 separately showed a similar overall pattern of time allocation to moving across

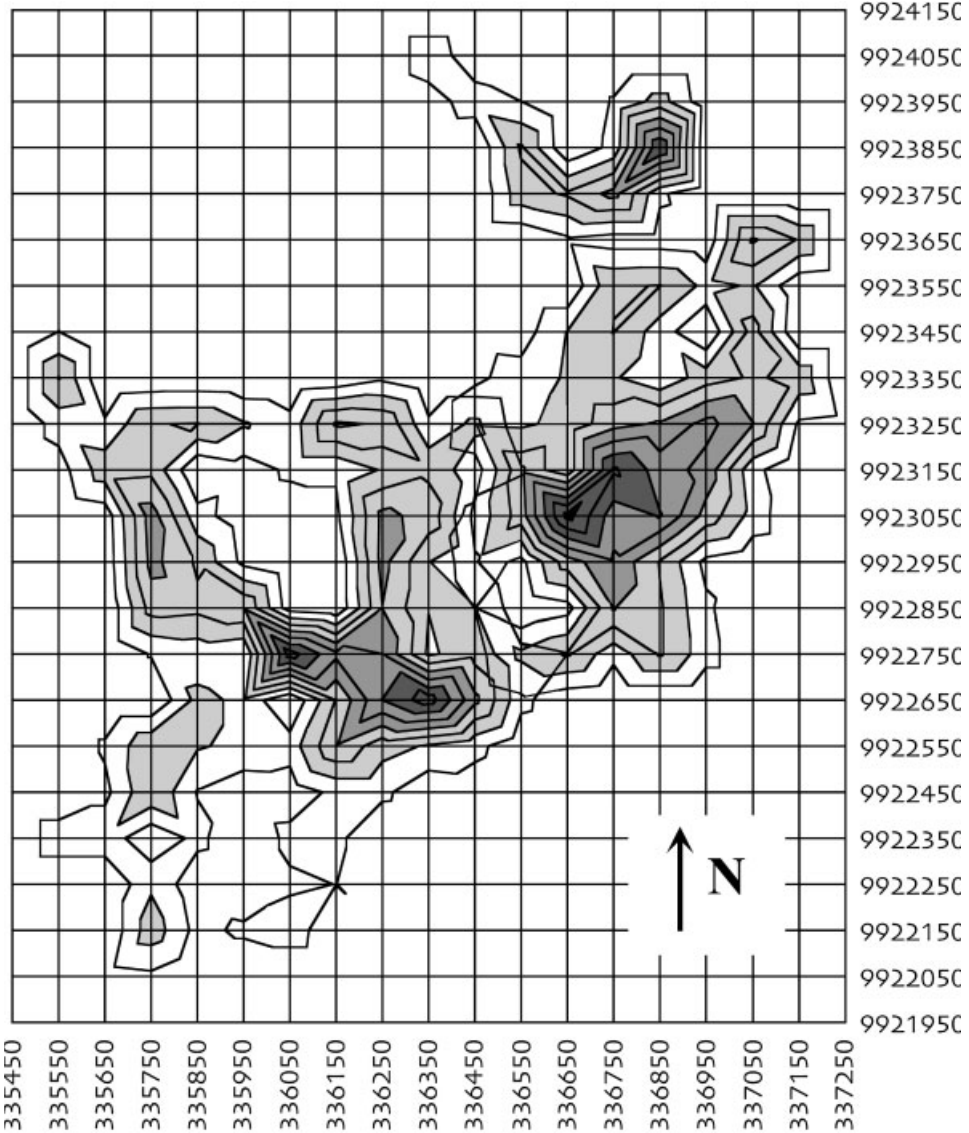


Fig. 2. Patterns of range use for groups 1 (lower left) and 2 (upper right), determined based on the number of location records scored for each 1-ha cell. Axes indicate the UTM coordinates. Shaded isoclines represent percentage of records (0–5%).

months, and the groups did not differ significantly either in monthly MOVE time or in monthly travel rate (paired sign tests,  $n=9$  months,  $P > 0.99$  for MOVE time,  $P > 0.50$  for travel rate).

**Ranging Behavior and Foraging Ecology**

*Ranging and Resource Availability.*

The monthly habitat-wide abundance of ripe and immature fruits, flowers, and new leaves varied over the course of the study (Fig. 4). Ripe fruit abundance

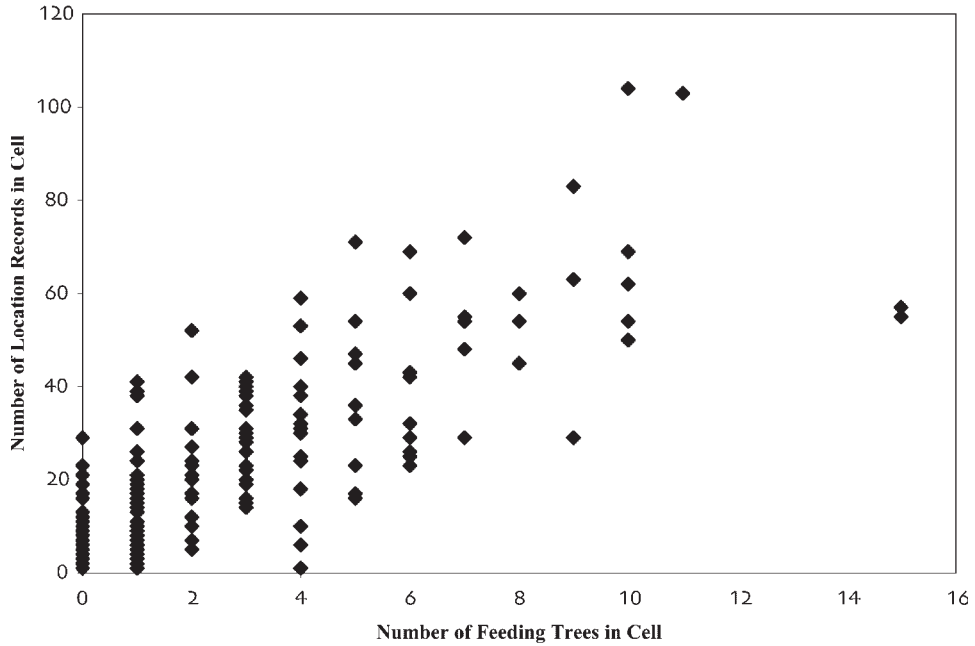


Fig. 3. Scatterplot of the number of location records scored for each 1-ha cell in the home ranges of groups 1 and 2 by the number of different feeding sources marked in those cells ( $r_s=0.758$ ,  $n=198$  cells total,  $P<0.001$ ).

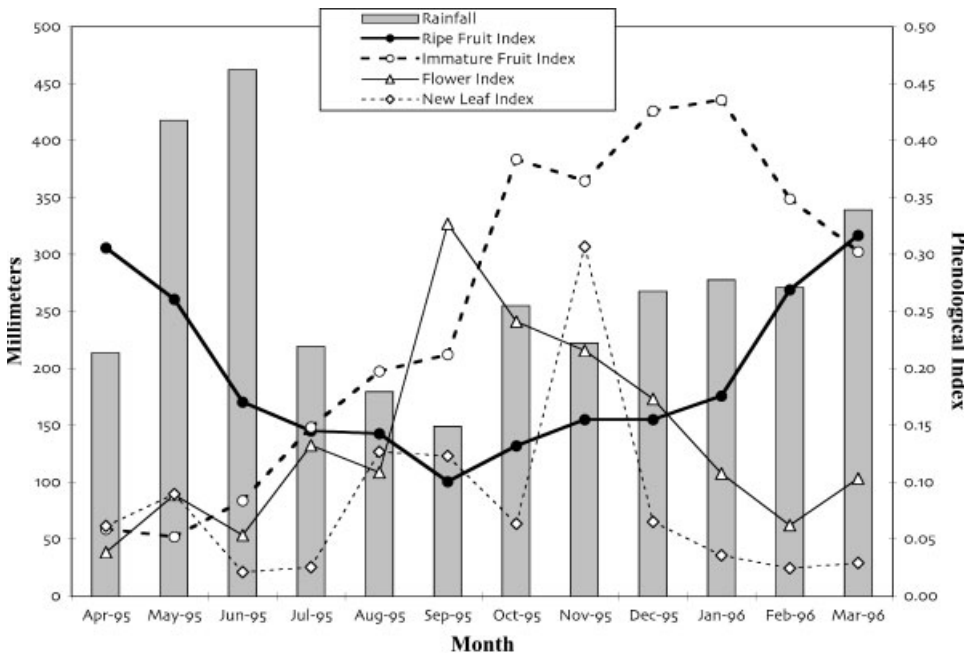


Fig. 4. Rainfall and phenological patterns for new leaves, flowers, and immature and ripe fruits over the course of the study. The calculated value for the flower index is multiplied by 8, and the leaf index is multiplied by 4 to accommodate them on the same axis as the indices for immature and ripe fruits.

was high during April 1995, declined to a low from July to September 1995, and rose again starting in October 1995. Not surprisingly, the peak in the abundance of immature fruit preceded that of the peak in ripe fruit. An identical pattern is seen if the entire set of phenology trees monitored, rather than the smaller subset of trees from genera contributing to at least 1% of the yearly fruit diet, are used to calculate the ripe and immature fruit abundance indices; in fact, the crop size-based indices calculated from the limited and full phenology data sets are highly correlated (Spearman rank correlation:  $r_s=0.791$ ,  $n=12$ ,  $P<0.01$  for ripe fruits;  $r_s=0.973$ ,  $n=12$ ,  $P<0.001$  for immature fruits). The crop size-based indices were also highly correlated with more traditional indices calculated as the simple proportion of monitored trees bearing a particular phenophase, both for the data set limited to genera contributing to at least 1% of the diet ( $r_s=0.940$ ,  $n=12$ ,  $P<0.002$  for ripe fruits;  $r_s=0.989$ ,  $n=12$ ,  $P<0.001$  for immature fruits) and for the full set of trees ( $r_s=0.929$ ,  $n=12$ ,  $P<0.002$  for ripe fruits;  $r_s=0.967$ ,  $n=12$ ,  $P<0.001$  for immature fruits). Flower abundance peaked during the dry-to-wet season transition in September and October of 1995, while new leaf abundance peaked in August and September, in the late dry season (and showed an anomalous peak in November based entirely on a single enormous tree that flushed an entire crown of new leaves that month).

Day range length, MOVE time, and travel rate were not significantly related to either rainfall or temperature, or to the monthly habitat-wide abundance of new leaves, flowers, or ripe fruits (Table I). However, when compared to the habitat-wide abundance of immature fruits, day range lengths for groups 1 and 2, MOVE time for group 2, and travel rate for group 1 all show large, positive  $r_s$  values, several of which are significant at the  $P<0.05$  level (Table I).

The final column in Table I indicates the relationship between ranging behavior and an index of same-month likely insect abundance in Yasuni based on data from Manu National Park, Peru. Significant, positive correlation coefficients are found between same-month likely insect abundance and the estimates of day range length for both groups 1 and 2. There are also significant, positive associations between likely insect abundance and MOVE time for group 2, and between insect abundance and travel rate for group 1. Together these results suggest the possibility that ranging behavior may be more immediately tied to foraging for insect prey than to foraging for plant resources, which is consistent with previously reported results [Di Fiore & Rodman, 2001] and with other researchers' suggestions concerning the importance of insect prey in the foraging ecology of frugivorous woolly monkeys [Stevenson, 1992; Stevenson et al., 1994].

#### *Diet, Ranging, Resource Availability, and Patch Use.*

Ripe fruits constituted 76.3% ( $\pm 8.3$  SD) of the overall woolly monkey diet across the year, comprising 60–91% of the monthly diets of both groups 1 and 2; for both groups, the consumption of immature fruit was negligible. Animal prey was the next most important food type in the diet, averaging 10.5% ( $\pm 5.0$  SD) for group 1 and 8.8% ( $\pm 4.1$  SD) for group 2, and comprising 3.5–17.7% of the diet of each of these groups each month. To evaluate the influence of diet on ranging behavior, I examined the relationship between the monthly proportion of ripe fruit and animal prey in the diet and the three variables describing ranging patterns. Day range length, MOVE time, and travel rate were not related to the proportions of either ripe fruits or animal prey in the diet of either group 1 or group 2 each month.

TABLE I. Spearman Rank Correlation Coefficients Between Ranging Variables, Habitat-Wide Indices of Resource Availability, and Climate Variables

Ranging variable	Ripe fruit crop index	Immature fruit crop index	Flower index	New leaf index	Rainfall	Temp	Same-month likely insect abundance (Manu National Park)
Group 1 move time	-0.490	0.182	0.413	0.287	0.014	-0.014	0.105
Group 2 move time	-0.117	0.733 <sup>a</sup>	0.317	0.417	0.067	-0.250	0.850 <sup>a,c</sup>
Group 1 day range	-0.224	0.727 <sup>a</sup>	0.524 <sup>b</sup>	0.287	-0.119	0.091	0.713 <sup>a</sup>
Group 2 day range	-0.150	0.650 <sup>b</sup>	0.150	0.217	0.100	-0.250	0.717 <sup>a</sup>
Group 1 travel rate	0.077	0.587 <sup>b</sup>	0.189	0.063	-0.112	0.077	0.636 <sup>a</sup>
Group 2 travel rate	0.117	0.217	-0.383	-0.383	0.367	-0.250	0.200

N=12 for Group 1 cells, N=9 for Group 2 cells; all tests are 2-tailed.

<sup>a</sup>P < 0.05, <sup>b</sup>P < 0.10.

<sup>c</sup>P value remains < 0.10 if the Bonferonni correction for multiple tests on the same variable is applied [Sokal & Rohlf, 1981].

To examine the relationship between diet and resource availability, I compared both the proportion of fruit and animal prey in the diet, one measure of dietary diversity (the number of different genera of fruits consumed each month) to the habitat-wide availability of ripe fruits for both groups 1 and 2. For group 1, the proportion of fruit in the diet was significantly positively correlated with ripe fruit availability ( $r_s=0.657$ ,  $n=12$ ,  $P<0.05$ ); this relationship was not seen for group 2 ( $r_s=0.283$ ,  $n=9$ ;  $P=0.43$ ). There was no significant relationship in either group between dietary diversity and ripe fruit availability (group 1:  $r_s=0.299$ ,  $n=12$ ,  $P=0.321$ ; group 2:  $r_s=0.517$ ,  $n=9$ ,  $P=0.144$ ), but for both groups the correlation coefficient was positive. Consumption of animal prey was positively rather than negatively related to ripe fruit availability for both groups 1 and 2 (group 1:  $r_s=0.392$ ,  $n=12$ ,  $P=0.194$ ; group 2:  $r_s=0.633$ ,  $n=9$ ,  $P=0.073$ ). Although these relationships did not reach significance at the  $P<0.05$  level, they do suggest that woolly monkeys did not simply turn to insects as an alternative resource during periods of fruit scarcity, but rather incorporated them into the diet more during periods of fruit abundance.

Finally, I tested whether woolly monkeys visited more feeding patches per day and/or spent more monkey-minutes in those patches during months of lower resource abundance, as would be expected if they were following a strategy of increasing foraging effort during this time. Contrary to the first part of this prediction, the number of patches visited per day was positively rather than negatively related to ripe fruit abundance for both groups, although not significantly (group 1:  $r_s=0.497$ ,  $n=12$ ,  $P=0.100$ ; group 2:  $r_s=0.450$ ,  $n=9$ ,  $P=0.203$ ). Moreover, contrary to prediction, the mean number of monkey-minutes spent in a patch was unrelated to ripe fruit abundance for group 1 ( $r_s=-0.007$ ,  $n=12$ ,  $P=0.982$ ), although it did show a weak (but nonsignificant) negative relationship with ripe fruit abundance for group 2 ( $r_s=-0.367$ ,  $n=9$ ,  $P=0.300$ ).

## DISCUSSION

### Relationship Between Range Use and Foraging Ecology in Woolly Monkeys

During periods of lower habitat-wide fruit abundance in this study, highly frugivorous woolly monkeys did not increase their day range length, allocate additional time to moving, or increase their travel rate (the composite of these two variables), any one of which might have allowed them to visit additional food sources each day. There is thus no indication that woolly monkeys devoted additional effort to finding additional fruit patches by ranging farther or traveling more when fruit was less abundant, as has been reported for other primates [Clutton-Brock & Harvey, 1977; Isbell, 1991; Janson & Goldsmith, 1995]. In fact, both study groups tended to visit fewer rather than more patches per day when fruit was less abundant, although the relationship between these variables was not significant for either group. Taken together, these results indicate that woolly monkeys in Yasuní do not increase their foraging efforts, as indexed through ranging behavior, during periods of lower habitat-wide fruit abundance, and other lines of evidence suggest the same pattern. For example, Di Fiore and Rodman [2001] found that the total amount of time that woolly monkeys devoted to subsistence activity (i.e., time spent eating plus time spent foraging for animal prey) was significantly and positively, rather than negatively, correlated with the

abundance of ripe fruit in the habitat across this same study period, while time spent resting was significantly negatively related to ripe fruit abundance. In other words, that study revealed that foraging effort gauged as time devoted to subsistence (rather than as time or energy devoted to ranging, as is considered here) was least and resting time was greatest when the habitat-wide availability of ripe fruits was lowest, implying that woolly monkeys may cope with periods of lower fruit abundance in the short-term by reducing rather than increasing their overall foraging efforts.

Superimposed on this result is the possible influence of likely prey abundance. In this study, woolly monkeys foraged more for insect and other animal prey when fruits were most abundant, and, depending on the group, they ranged farther, spent more time moving, moved faster, or performed some combination of these behaviors when one measure of likely insect abundance was greatest. Thus, ranging behavior may, in part, be driven by the abundance of insect prey. This idea is consistent with the fact that animal prey appears to be a preferred dietary item [Di Fiore, 1997]. Obviously, this idea warrants further testing once data on seasonal changes in insect abundance in Yasuní itself, rather than proxy data from Manu, are available. This observation suggests that in addition to following a short-term energy conservation strategy when ripe fruits are least abundant, as has been suggested elsewhere [Di Fiore & Rodman, 2001], woolly monkeys may also pursue an energy-maximizing strategy [sensu Schoener, 1971]—or perhaps more accurately, a protein-maximizing strategy—when it is possible, devoting additional foraging effort to resources such as insects and other animal prey when ripe fruits are abundant and basic metabolic needs are easily met or when the abundance of potential prey is high. This strategy may be important for laying in fat reserves that can be mobilized when overall fruit availability is low [Di Fiore & Rodman, 2001].

Obviously, this argument would be strengthened if it could be demonstrated that the period of lowest resource abundance revealed in this study was also a period of true scarcity (i.e., fruit abundance was so low that not finding or not consuming enough fruit had clear fitness consequences). This might be done by documenting the presence of ketones, a by-product of fat metabolism, in the urine of animals at that period of time, as Knott [1996] has demonstrated for other primates; such a study is currently in progress in Yasuní. However, the fact that woolly monkey body weight fluctuates considerably over the course of the year [Peres, 1996], to the point where local hunters express a preference for hunting woolly monkeys when they are fatted, does lend indirect support to the idea that periods of low ripe fruit abundance are indeed lean times.

Finally, it is intriguing to consider the significance of the strong, positive relationship seen between ranging variables and the habitat-wide abundance of immature fruits, which constitute a negligible part of the woolly monkey diet. The fact that both study groups of woolly monkeys ranged farther, and that one spent more time moving and the other moved faster, when immature fruits were prevalent raises the possibility that their ranging decisions may, in part, be tied to efforts to monitor the phenological status of important fruit resources, rather than simply reflecting the results of intragroup feeding competition.

### **Variation in Woolly Monkey Range Use and Spatial Requirements**

As Defler [1996] and Peres [1996] have noted, there is considerable variation among woolly monkey populations in ranging patterns, and the results of this

TABLE II. Ranging Parameters for Various *Lagothrix lagothricha* Populations

Taxon	Study site	Group size	Home range (ha)	Group biomass (kg) <sup>a</sup>	Space used (ha/kg)	Space used (ha/ind)	Overlap	Mean day range (m)	Max day range (m)	D <sup>b</sup>	Source <sup>c</sup>
<i>L. l. poeppigii</i>	Yasumí, Ecuador	25 to 24	124	94	1.32	5.2	45%	1792 <sup>d</sup>	2738	2.85	1
<i>L. l. poeppigii</i>	Yasumí, Ecuador	23	108	98	1.10	4.7	47%	1878 <sup>d</sup>	2859	3.20	1
<i>L. l. poeppigii</i>	Río Pacaya, Peru	17 to 23	350	112	3.13	20.6	-	540 <sup>e</sup>	950 <sup>e</sup>	-	2
<i>L. l. poeppigii</i>	Río Manu, Peru	14	400+	105	≥ 3.81	≥ 28.6	-	-	-	-	3
<i>L. l. poeppigii</i>	Río Manu, Peru	10	250+	75	≥ 3.33	≥ 25.0	-	-	-	-	3
<i>L. l. lugens</i>	Tinigua, Colombia	17 to 19	169	96	1.76	9.9	100%	1633	1853 <sup>f</sup>	2.23	4
<i>L. l. lagothricha</i>	Río Peneya, Colombia	42 to 43	1100	260	4.23	26.2	-	-	-	-	5
<i>L. l. lagothricha</i>	Río Peneya, Colombia	13	350	86	4.07	26.9	65-100%	-	-	-	6
<i>L. l. lagothricha</i>	Río Peneya, Colombia	45	450	245	1.84	10.0	50-100%	-	-	-	6
<i>L. l. lagothricha</i>	Caparu, Colombia	24	748	123	6.08	31.2	90-100%	2280	3582	1.48	7
<i>L. l. cana</i>	Río Urucu, Brazil	44 to 49	1021+	270	≥ 3.78	≥ 23.2	-	-	-	-	8

<sup>a</sup>Calculation of biomass for Yasumí groups based on composition of study groups [Di Fiore & Rodman, 2001] and weights noted in Lu [1999]; remainder of group biomass estimates taken from Peres [1996].

<sup>b</sup>Defensibility Index [Mitani & Rodman, 1979] calculated as Mean Day Range Length/Home Range Diameter.

<sup>c</sup>1. This study; 2. Soini [1986]; 3. Ramirez [1980]; 4. Stevenson, et al. [1994]; 5. Izawa [1976]; 6. Nishimura [1990]; 7. Defler [1996]; 8. Peres [1996].

<sup>d</sup>Calculated for period from 0700 to 1700 only.

<sup>e</sup>Day range value for straight line displacement between sleeping sites.

<sup>f</sup>Max day range value is for the largest of four trimester means.

study only broaden the range of variations observed. Home range sizes for woolly monkey groups in Yasuní are the smallest reported for this species anywhere in its geographic distribution, and are only one-eighth to one-tenth the size of the largest recorded *Lagothrix* home ranges (Table II). Moreover, the spatial requirements of the Yasuní population, calculated either in terms of home range area per individual [following Defler, 1996] or per kilogram of group biomass [following Peres, 1996] are two-thirds to one-sixth of those found for other sites (Table II).

The reasons underlying the nearly 10-fold variation seen in home range size and more than sixfold variation found in spatial requirements per individual are not yet understood, but part of the explanation may lie in the marked differences in body size and group composition (and thus in total group biomass) among the four currently recognised subspecies of lowland woolly monkeys. *Lagothrix lagotricha lagotricha* and *L. l. cana*, the two larger-bodied subspecies, tend both to live in larger groups and to utilize much larger home ranges than the two smaller subspecies, *L. l. lugens* and *L. l. poeppigii*. Using the data in Table II to effect a crude comparison of mean group biomass for *L. l. lagotricha* + *L. l. cana* vs. *L. l. lugens* + *L. l. poeppigii* reveals that groups of the former pair of taxa have more than twice the biomass of the latter (196.8 vs. 96.7 kg/group). However, group biomass explains only 54% of the variance in home range size in a simple linear regression of log (home range size) on log (group biomass), and both the Yasuní groups and the Tinigua population of woolly monkeys fall far below this regression line, indicating that home range size in these populations is still far smaller than expected given group metabolic needs. Part of the remaining variability in woolly monkey home range size may have to do with gross differences in overall habitat quality, perhaps as indexed by soil fertility [Defler, 1996]. Specifically, Defler [1996] has noted that the whitewater soils of Tinigua (where home range size is smaller than at all other sites except Yasuní) are likely to be far richer than those at Caparú (where home range size is 4.4 times greater than at Tinigua), and are also presumably richer than at other lowland sites, such as Urucu, further east in the Amazon basin. The same may be true for soils in Yasuní, given its closer proximity to the Andean foothills. However, until soil samples from additional sites are analyzed, this remains a plausible, but untested, hypothesis.

In contrast to the small size of their home ranges relative to other populations of *Lagothrix*, average day range lengths for woolly monkey groups in Yasuní were well within the range of variation seen across sites (Table II). Moreover, for the three populations for which both home range size and day range length have been reported, the average daily travel distance is greater than the diameter of the yearly home range (and much greater than the diameter of the smaller subset of the home range that woolly monkeys use each month), which suggests that territorial defense might be possible in at least these three populations [Mitani & Rodman, 1979; Lowen & Dunbar, 1994]. However, woolly monkeys have never been reported to defend exclusive portions of their home ranges. The question of why we do not see territoriality in this species remains open, but perhaps one answer lies in the fact that insects and other animal prey do not constitute economically defendable resources; these resources may either renew too rapidly or occur in such unpredictable and ephemeral patches that they cannot be defended effectively. The combination of relatively long day ranges with small home ranges (particularly in the two smaller-bodied subspecies), and the absence of territorial defense, lends additional support to the idea that ranging behavior in at least some populations of *Lagothrix* is associated with

animal prey foraging (and perhaps with fruit tree monitoring) rather than reflecting the result of intragroup or between-group feeding competition.

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