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## RESOURCE USE AND SEED DISPERSAL BY RED HOWLER MONKEYS (*ALOUATTA SENICULUS*) IN A COLOMBIAN ANDEAN FOREST

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### Abstract

As part of a study of responses by red howler monkeys (*Alouatta seniculus*) to forest fragmentation, we studied red howlers in an extensive forest including a habitat mosaic of old-growth forest, secondary forest of different ages, and non-commercial monospecific plantations of exotic Chinese ash (*Fraxinus chinensis*) and pines, to produce baseline information on resource use and their role as seed dispersers. We followed three troops for six months, encompassing a dry and a wet season; in total, they fed on 48 species of trees, including fruits, leaves and flowers, but each group relied on a limited set of species available within its home range, particularly in the Moraceae and Cecropiaceae. This contrasts with lowland forest, where howlers feed on a larger variety of species. We observed no season of generalized fruit scarcity, as is the case in the lowlands. However, localized fruit scarcities in howler home ranges occurred. Howlers fed on relatively small quantities of leaves when fruit was available, and became primarily folivorous when fruit was unavailable. Howlers transported a mean of 2.3 species of seeds per fecal sample, to a mean distance of 116 m from the parent tree. More importantly, howlers are transporting seeds to ash and pine plantations, helping to enrich these habitats.

**Key words:** Andes, Colombia, red howler monkey, frugivory, folivory, montane forest, cloud forest, seed dispersal, habitat restoration

### Resumen

Como parte de un estudio sobre la respuesta del mono aullador rojo a la fragmentación de bosques, estudiamos una población en un bosque extenso que incluía un mosaico de hábitats de bosques maduros, bosques de regeneración de distintas edades, y plantaciones monoespecíficas de urapán o fresno de la China (*Fraxinus chinensis*) y pinos, para producir información de base sobre patrones de uso de recursos y su papel como dispersores de semillas. Seguimos tres grupos de aulladores durante seis meses, que incluyen una estación seca y una húmeda. Los tres grupos se alimentaron de 48 especies de árboles, incluyendo frutos, hojas y en menor medida flores, pero cada grupo dependió de unas pocas especies de acuerdo a la disponibilidad de aquellas en su área de actividad, particularmente en el Moraceae y Cecropiaceae. Esto contrasta con los bosques de tierras bajas, donde esta especie se alimenta de una variedad de especies mucho mayor. No observamos una época de escasez generalizada de frutos, como sí ocurre en tierras bajas, sin embargo, sí observamos escasez localizada en las áreas de actividad de los grupos estudiados. Los aulladores siempre consumieron pequeñas cantidades de hojas cuando había frutos disponibles, y fueron principalmente folívoros cuando los frutos fueron escasos. Los aulladores dispersaron un promedio de 2.3 especies de semillas en sus heces, a una distancia promedio de 116 m del árbol parental. Lo más importante, sin embargo, es que están transportando semillas a las plantaciones de urapán y pino, ayudando a enriquecer estos hábitats.

**Palabras clave:** Andes, Colombia, mico aullador rojo, frugivoría folivoría, bosque montano, bosque nublado, dispersión de semillas, restauración de hábitat

### Introduction

The red howler monkey, *Alouatta seniculus*, is widely distributed in northern South America. It is found in the northern and western Amazon basin and east to the Guianas, and in the Andes from Colombia to Bolivia. Red howler monkeys occupy a variety of forest habitats, from lowland rain forest in the Amazon, to gallery forest and relatively open woodland in savannas, tropical dry forest,

and cloud forest (Hernández-Camacho and Cooper, 1976). They can also use secondary forest and survive in isolated patches (Rylands and Keuroghlian, 1988; Schwarzkopf and Rylands, 1989). In Colombia the red howler is distributed from sea level to 2,400 m a.s.l. and occasionally up to 3,200 m a.s.l. (Hernández-Camacho and Cooper, 1976; Defler, 2003). Howler monkeys (*Alouatta* spp.) have a folivorous-frugivorous diet, although they do not possess a highly specialized digestive tract to deal with leaves, nor

do they exhibit particularly low metabolic rates (Milton, 1998). As frugivores, howlers are recognized as important seed dispersers in tropical forest, because they have long intestinal retention times and they move seeds away from the parent trees (Julliot, 1996a; Yumoto *et al.*, 1999). Secondary dispersers may then scatter these seeds and contribute to their germination (Andresen, 1999, 2002).

The ecology of red howlers has been well studied in a variety of lowland forest types. However, there is only one detailed study available for Andean populations (Gaulin and Gaulin, 1982). This one-year study examined food habits of one group of howlers at a cloud forest in the Central range of the Colombian Andes, and reported consumption of fruits and leaves of 34 plant species. There are reasons to believe that aspects of the behavioral ecology of howlers may differ between lowland and montane forest. First, plant diversity decreases with elevation and species composition changes (Gentry, 1992; Cavelier *et al.*, 2001), so montane populations may have a different and more restricted choice of food species. Second, primary productivity decreases with elevation in correlation with a decrease in temperature. These factors may affect activity patterns and space and resource requirements of howlers.

Montane populations of red howler monkeys in Colombia are threatened by habitat destruction and fragmentation. Recent estimates indicate that over 70 percent of Andean forests have been transformed, and most of what remains is in isolated patches, particularly within the howlers' range in the inter-Andean valleys (Kattan and Alvarez-López, 1996; Cavelier *et al.*, 2001). Across Latin America, howler monkeys have not escaped the negative consequences of human-caused disturbances of natural habitats. Some populations of mantled howlers (*Alouatta palliata*) have gone locally extinct, and many populations of *Alouatta* spp. barely persist in isolated fragments, under conditions that put them at risk (Estrada and Coates-Estrada, 1988, 1996; Gómez-Posada, unpublished data). However, some studies suggest that howlers can persist in isolated forest patches, relying on a limited subset of plant food species in the families Moraceae and Cecropiaceae (Estrada and Coates-Estrada, 1986; Rylands and Keuroghlian, 1988; Schwartzkopf and Rylands, 1989; Estrada *et al.*, 1999).

Understanding the ecology of red howler monkeys and their role as seed dispersers in montane forest fragments is critical to the conservation of both the monkeys and their habitat. Here we present results of a six-month study of red howler monkey at Otún-Quimbaya Flora and Fauna Sanctuary, a cloud forest site in the Central Cordillera of the Colombian Andes. The study site is a restored forest, formed by a mosaic of remnant patches of old-growth forest, second-growth forest and non-commercial monospecific tree plantations that were established as part of a revegetation program. Our study area (489 ha) is part of a larger forested area (several thousand hectares) and is the largest remnant in the howlers' range on the western slope

of the Central Cordillera of the Colombian Andes. This study provides baseline data for a larger study, currently in progress, documenting patterns of habitat and resource use, and space requirements of red howler monkeys in forest fragments in the Colombian Andes (Gómez-Posada, unpublished).

## Study Area and Methods

The study was conducted at the Santuario de Fauna y Flora Otún-Quimbaya (04°43'N, 75°28'W), located on the western slope of the Central Cordillera of the Andes of Colombia, east of the city of Pereira. This reserve protects a mosaic of Andean forests of different regeneration ages, including patches of old-growth forest, and patches of different sizes of native Andean oak (*Quercus humboldtii*), exotic Chinese ash (*Fraxinus chinensis*) and conifers. These monospecific tree stands were planted in the 1960s as part of a revegetation and soil stabilization program initiated by the local utility authority to protect the Otún river drainage (Londoño, 1994). Tree plantations were abandoned to natural regeneration and presently have a high plant diversity, particularly in the understory (Durán and Kattan, 2005), although the canopy is dominated by the planted species. The Sanctuary encompasses 489 ha at elevations between 1,800 and 2,100 m a.s.l., but is contiguous with Ucumari Regional Park, which protects 3,980 ha of forest between elevations of 1,750 and 2,600 m a.s.l. Precipitation in the region is bimodal, with peaks of rain in April and October and an annual mean of 2,712 mm (Estación Meteorológica El Cedral, CENICAFE, 1995–2001), and the mean annual temperature is 15°C (Aguilar and Rangel, 1994). A mild dry season occurs in December–January and a stronger one in July–August, when monthly precipitation may be under 100 mm.

The study was carried out during July–December 2001, including a dry and a wet season. We identified 11 monkey troops (mean group size  $\pm$  SD =  $7.3 \pm 2.5$  individuals) in an area of 113 ha, and selected three groups (labeled C, D, and E; Table 1) for intensive observations (Giraldo, 2003; Martínez, 2003). Each group used a home range of  $10.2 \pm 3.3$  ha during the six-month study period (Gómez-Posada *et al.*, 2004). The home range of troop C (8 ha) was completely contained in mature forest. Troop D's home range (14 ha) was next to the river, in an area of secondary forest (old enough to have a developed canopy with interlocking tree crowns), Andean oak, ash and pine plantations. Troop E (8.7 ha) used mostly an ash plantation and a small area of secondary forest. We tried to follow each group for three to four consecutive days each month, making observations between 06:30 and 17:00. We obtained 6–9 observation hours per day, depending on weather; monkeys remained inactive during cold days. The harsh topography also made following troops difficult. We recorded diet every 15 min using a slow scan method (Altmann, 1974, adapted by Robinson, 1986); in each sample, we scanned the group for ten minutes, and for each monkey, we noted the first item

consumed. In each scan we noted the type of food eaten (leaves, mature or immature fruits, flowers), the troop's location, and the habitat type. The proportions of use of different food items were compared with a G contingency test (Zar, 1996). Voucher samples of plants were collected and identified at several national herbaria (see Rios *et al.*, 2004).

To estimate availability of resources used by howlers, we measured fruit and new leaf production in three 400 x 4 m transects (total area sampled = 4,800 m<sup>2</sup>) distributed in an area of about 100 ha where the study troops occurred. No previous studies have evaluated resource availability for montane populations of red howler monkeys so there were no criteria for deciding transect size. We chose to use fixed-width transects (Stevenson *et al.*, 1998; Hemingway and Overdoff, 1999) and the size of the transects was decided by taking into account the lower diversity and smaller spatial scale of montane forests, compared with lowland forests (Gentry, 1992; Cavelier *et al.*, 2001; Silverstone-Sopkin, pers. comm.). We included all trees over 15 m tall. We monitored these transects once per month to estimate new-leaf production (estimated as the proportion of the tree's canopy with young leaves) and number of ripe fruits in canopy trees. Fruits were directly counted in one tree branch and multiplied by the number of branches to extrapolate to the whole tree. We explored the correlation of monthly fruit and leaf availability with intensity of use (for each group) using Spearman's rank correlation coefficient (Zar, 1996).

To complement feeding observations and document seed dispersal, we collected feces from the forest floor and understory vegetation, as soon as monkeys defecated. Defecation in howlers was a group activity; usually the alpha male initiated a defecation bout and all members of the group followed. Samples were washed, dried and filtered to separate fiber and seeds, and we counted manually all seeds >5 mm and estimated numbers of seeds <5 mm by weighing samples of 100 seeds. To estimate dispersal distances from parent trees, we made *ad libitum* observations (Altmann, 1974) while following a troop for at least two continuous days; we recorded the time and place of consumption of fruits at a particular tree, and the site where seeds were defecated afterwards (making sure monkeys had not fed on another tree of the same species). Points were located on a map of the study area and dispersal distances

measured as a straight line. We included data only on defecations that occurred after 20 h of beginning observations of a troop feeding on a particular tree, to make sure that seeds originated from this particular tree. Twenty hours is the mean retention time estimated for red howlers by Julliot (1996a), Andresen (1999) and Yumoto *et al.* (1999).

## Results

### *Availability of resources*

In the three transects we recorded a total of 74 species of trees and a mean ( $\pm$ SD) of  $83.3 \pm 30$  individual trees per transect, representing about one third of the species of canopy trees in the study area (Rios *et al.*, 2004). Availability of new leaves was low during the six months of the study, but some species like *Ficus* spp., *Cecropia telealba* and some Clusiaceae produced new leaves all the time. In general, trees in this cloud forest were nondeciduous and at any particular moment had a low proportion of the crown (~5%) covered in new leaves. The only deciduous species were Andean oak and Chinese ash (leaves not consumed by howlers in this study). In July and August availability was high because of synchronized leafing in Andean oak (Fig. 1).

Both the total fruit availability and the number of species in fruit peaked in August and November (Fig. 1). The August peak was due to fruiting of *Garcinia* sp. and *Wettinia kalbreyeri*. In November the peak was produced by *Heliocarpus americanus* (which has a dry fruit not consumed by howler monkeys) and the palm *W. kalbreyeri*. In general, fruit production in the forest showed little synchronization, both intra- and interspecifically, and reflected fructification events of individual trees. This was the case of one individual tree of *Ficus killipii*, and one *Garcinia* sp., which produced fruit during two non-consecutive months; this particular *Ficus* tree was an important food item for troop E during this study (Appendix and see below).

### *Diet composition and food preferences*

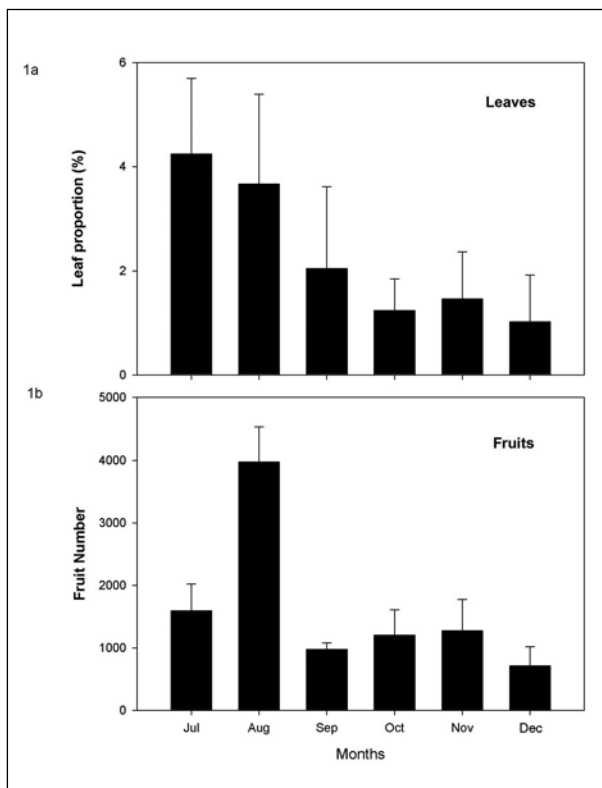
Although our aim was to follow each group for 3–4 days per month, the rough topography of the study area made it difficult to always locate and follow groups, in spite of intensive search efforts. Groups C and D were followed during five months and group E during four non-consecutive months. We obtained a total of 1,643 feeding records of fruits, leaves and flowers, in 388.3 hours of observation

**Table 1.** Size, composition and sampling effort (hours and days of observation) of three red howler monkey troops studied during six months in the Central Cordillera of the Colombian Andes (M = male, F = female).

Group	Adult		Subadult		Juvenile		Infant	Total	No. hours / No. days
	M	F	M	F	M	F			
C	1	2				1	1	5	119.4 / 18
D	1	3	1	1	1	1	2	10	136.4 / 19
E	1	2	1	1	1		2	8	132.0 / 15
<b>Total</b>	<b>3</b>	<b>7</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>5</b>	<b>23</b>	<b>388.3 / 52</b>

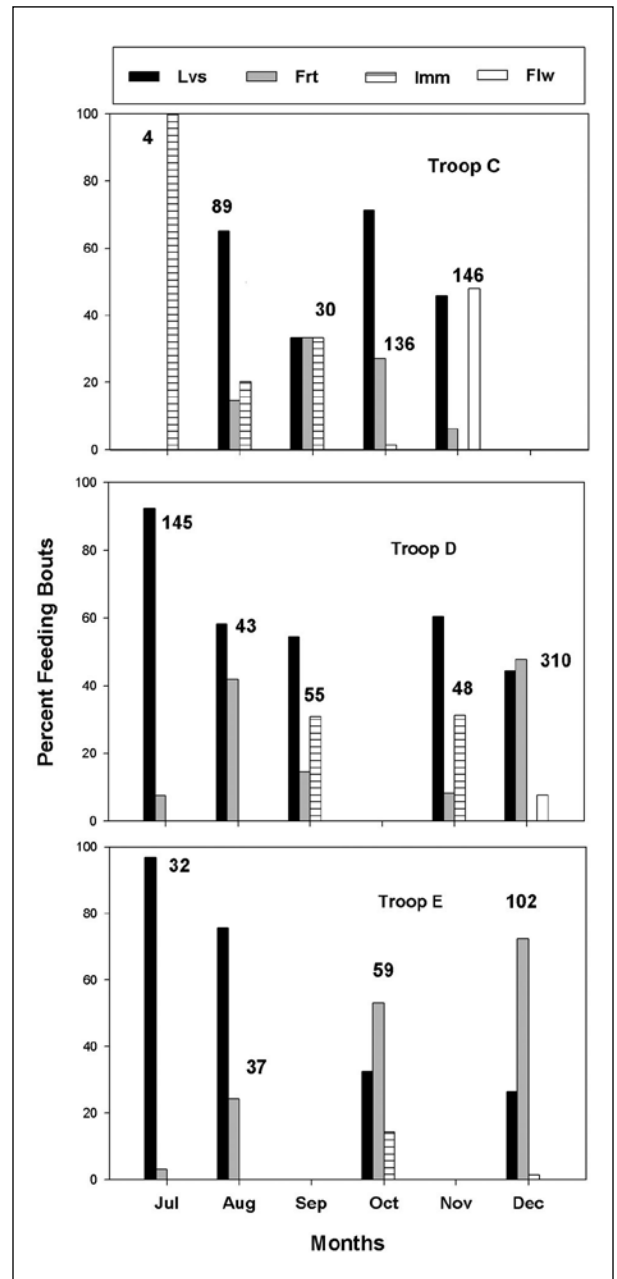
for the three howler groups in the six months of study. They fed on 48 species of plants, in some cases including fruits and leaves or fruits and flowers of the same species (Appendix). In addition, we once observed the adult male of group C feeding on tree bark, and a juvenile twice sucked and then dropped mouthfuls of moss obtained from a cypress tree.

The diet was mostly folivorous (49.2% of feeding records) and frugivorous (45.1%); flowers had a low representation in the diet (5.7%; Table 2). It was difficult to distinguish young and mature leaves through binoculars, particularly for species such as *Paullinia* sp., *Ficus* spp. and *Macarobium colombianum*, so we pooled all leaf-feeding records in one category. The most important plant families, with both fruits and leaves consumed, were the Moraceae (17 species with 45.7 percent of the total of 1,643 feeding records, including several species of *Ficus* representing 42.2 percent of feeding records) and Cecropiaceae (one species, *C. tealalba*, representing 17.2 percent of feeding records). The leaves of two other species, *Paullinia* sp. (Sapindaceae) and *Macarobium colombianum* (Leguminosae) also made up an important proportion of feeding records (Appendix). During their daily travel routes ( $553.9 \pm 247.9$  m; Gómez-Posada *et al.*, submitted), howlers always found at least one fruiting tree within their home range each month. Particularly important in this regard were *C. tealalba* and *Ficus* spp., which usually had one or more trees in fruit within



**Figure 1.** Resource availability for howler monkeys in the Cordillera Central of Colombia. Graph 1a shows the mean proportion per transect of tree canopy with new leaves, and graph 1b shows the mean number of fruits per transect ( $N = 3$  transects).

the study area. However, on any particular day howlers fed on a combination of fruits, leaves, and occasionally flowers, of several species. Monthly rates of consumption of the different food items varied widely (Fig. 2). This reflects intense and opportunistic feeding in particular trees when resources were available, as was the case with individual *F. killipii* and *Garcinia* sp. trees that produced fruit abundantly in non-consecutive months. There were significant differences among troops in diet composition ( $G = 328.7$ ,  $P < 0.01$ ; Table 2).



**Figure 2.** Diet composition of three groups of red howler monkeys in the Central Cordillera of the Colombian Andes. Bars show the proportion of feeding bouts of four items (Lvs = leaves, Frt = ripe fruits, Imm = unripe fruits and Flw = flowers) in observations made between July and December 2001. Numbers above bars indicate number of observations per month.

Troop C, with a home range in mature forest, fed on a total of 21 tree species and visited a mean of 5.4 (SD = 1.6) species per day. The most important items in the diet of this group were leaves of *Paullinia* sp. and *M. colombianum*, and leaves and fruits of *C. telealba* and two species of *Ficus*, in combination accounting for 65 percent of feeding records (Appendix). Another important species in this group's diet was *Otoba lehmannii*, which produced fruit continuously during this study, representing most of the immature fruit category (Fig. 2); however, howlers only took a small bite of the tissue of the area of insertion of the peduncle and dropped the rest of the fruit. In July we were able to follow this group for only one day, hence the small number of observations, all on *O. lehmannii* (Fig. 2). During November, this group fed heavily on flowers of *Macrolobium colombianum* (Fig. 2), which flowered synchronously throughout the forest.

Troop D, which had a mixture of ash and pine plantations and secondary forest in its home range, had a more varied diet. This troop fed on a total of 27 species, visiting a mean of 4.7 ( $\pm$  2.1) species per day. This group fed to some extent on immature fruits of Chinese ash (September and November; Fig. 2), but mostly relied on fruits and leaves of *Cecropia telealba* and several species of *Ficus* (Appendix). In July, little fruit was available within this group's home range, and monkeys relied heavily on leaves (mostly *Cecropia*; Fig. 2).

Finally, troop E had a home range mostly restricted to ash plantation, with some secondary forest. The diet of this group was limited to 12 species, with a mean of 4.4 ( $\pm$  1.9) species visited per day. However, three species represented 82.9 percent of feeding records (Appendix). This group relied heavily on leaves of a small number of trees, except during October and December, when it fed on fruits of a particular *Ficus killipii* tree for 58.4 percent of feeding records (Fig. 2). Other important items were *C. telealba* (fruits and leaves) and *Paullinia* sp. (leaves). This troop also fed to some extent on immature ash fruits in October (Fig. 2 and Appendix).

Only 27 of the 48 species eaten by the howlers were represented in the three transects. Several species that were important in the monkey's diet, such as *Ficus killipii* and *Paullinia* sp. (Appendix), were not found in transects. Some *Macrolobium colombianum* and *Garcinia* sp. trees

were present in transects, but these species fruited asynchronously throughout the study area. Howlers fed on these species, but not at the time when they were fruiting in transects; thus, we have no monthly estimate of fruit availability for these species, and could not calculate any preference index. There was no correlation between fruit and new leaf availability (Fig. 1) and consumption of these items by each group (Fig. 2;  $P > 0.3$  in all cases). However, leaf consumption in groups D and E decreased when fruit availability increased.

#### Seed dispersal

Each troop defecated two to four times daily, usually under a single tree. It was difficult to keep individual feces separate because they were scattered around when hitting vegetation under the tree, so we collected all feces from each group defecation bout, combined them into a single sample, and identified and counted numbers of seeds. Fecal samples contained a mean of 2.3 (SD = 1.04) species of seeds. We found a total of 9 species of intact seeds and 290,174 seeds in 60 samples. Seed size was highly variable, but most seeds (99.9%) were less than 5 mm long; this was the case with *C. telealba* (<3 mm), *Ficus* spp. (<0.8 mm) and *Miconia acuminifera* (<0.5 mm), which were the most abundant species in fecal samples (Table 3). The largest seeds found in feces were *Garcinia* sp. ( $33.8 \pm 0.54$  mm,  $N=20$ ) and *Allophylus mollis* ( $8.2 \pm 0.05$  mm,  $N=20$ ). Only five of the 9 seed species found in feces were observed in feeding records, while the other four species occurred in small numbers and we could not identify them. All seeds of *Ficus* spp. are very similar and we could not separate the different species, however, we observed consumption of fruits of at least five species of *Ficus* so the total number of species in the feces could be 13 or more. Dispersed seeds showed no evidence of parasitism, except for *A. mollis*, which had some seeds parasitized by a coleopteran larva. We obtained 33 direct dispersal distances from the feeding point in the parent tree to the defecation site (we could not obtain more dispersal distances because howlers sometimes fed on different trees of the same species in a single day and because we could not obtain 20 h of continuous following). In 14 cases, this distance was between 6 and 8 m (defecation under same tree). In the other 17 cases, mean dispersal distance was 116.1 m (SD = 92.1). Because howlers frequently visited the same feeding tree several times in a single day, it was not possible to determine retention times.

**Table 2.** Diet composition of three red howler monkey troops in the Andes of Colombia, measured as percent of feeding bouts observed.

Item Consumed	Troop			Three troops combined
	C	D	E	
Leaves	57.3	59.2	34.5	49.2
Ripe Fruits	17.0	31.4	60.6	39.2
Unripe Fruits	8.4	5.3	4.9	5.9
Flowers	17.3	4.0	0	5.7
N (feeding bouts)	405	601	637	1,643

**Table 3.** Number of seeds of nine species of plants found in 60 troop-composite fecal samples of three red howler monkey troops in the Andes of Colombia.

Plant species	Monkey troop		
	C	D	E
<i>Cecropia telealba</i>	54,545	56,587	58,276
<i>Ficus</i> spp.	5,461	4,870	100
<i>Miconia acuminifera</i>	43,076	38,986	28,085
<i>Allophylus mollis</i>	100	11	2
<i>Garcinia</i> sp.	7	0	0
<i>Dendropanax macrophyllus</i>	30	0	7
<i>Simplocus</i> sp.	2	11	0
Unidentified 1	8	0	0
Unidentified 2	2	8	0
<b>Total</b>	<b>103,231</b>	<b>100,473</b>	<b>86,471</b>

## Discussion

### *Resource availability and diet composition*

We observed three important differences between montane and lowland howler populations in their feeding ecology. First, during our six-month study, we observed no times of generalized fruit scarcity at the level of the entire forest, as is the case in lowland forest (Milton, 1980; Julliot, 1996a; Stevenson *et al.*, 2000; Palacios and Rodríguez, 2001). Instead, fruit was available in small but relatively constant amounts, although localized scarcities within the howlers' home ranges occurred (but our study included only six months, so we have no information on long-term patterns). Intra- and interspecific asynchrony in the phenology of cloud forest trees has been reported for other Andean sites (Ataroff, 2001; Cavelier *et al.*, 2001). Fruiting of many species, especially those important in the monkeys' diet (*Ficus*, *Cecropia*), tended to occur asynchronously. Howlers at our site usually combined fruit and leaves in their diet, although leaf use tended to decrease when fruits were available. They fed on the leaves of a wide variety of species, but each species was consumed in small amounts (as proportion of feeding bouts), although some species (*Paullinia* sp., *Ficus* spp. and *C. telealba*) produced new leaves all the time and were more continuously used (Appendix). The same general feeding pattern was reported by Gaulin and Gaulin (1982) for another site on the same mountain range. We did not observe consumption of oak leaves (*Quercus humboldtii*), as Gaulin and Gaulin (1982) did, even though home ranges of two groups included oak stands.

Second, the number of species of plants on which howlers fed was small, probably reflecting lower plant diversity compared to the lowlands. This is particularly true at our study site, which is a restored, secondary forest. We recorded a total of 48 species in their diet (fruits and leaves combined), but for one group this number was as low as 12 species in four months, and *Ficus* spp. and *C. telealba* represented more than 60 percent of the diet of the three

groups. The three groups fed on a total of 14 fruit species but these numbers may increase with longer study. The group studied by Gaulin and Gaulin (1982) in a mature forest fed on a total of 34 fruit species in one year; in contrast, studies on lowland populations usually report higher numbers. For example, a 2-year study of one troop of red howler monkeys in French Guiana reported a total of 195 species in the diet, including 97 species of fruits (Julliot and Sabatier, 1993). Two other studies in eastern Colombia reported 17 species of fruits consumed by one troop in 9 days (Yumoto *et al.*, 1999), and 43 species consumed in 12 months by one troop (Stevenson *et al.*, 2002). The third difference is in the size and color of fruits. Howler monkeys are reported to prefer large, yellow or orange-colored fruits (Janson, 1983; Julliot, 1996b). At our site, most fruits consumed by howlers were small (10–40 mm, except for *C. telealba*) and many were green or whitish (such as some *Ficus* spp. and *A. mollis*) or purple (*Miconia acuminifera*), and the only large and yellow fruit in their diet was *Garcinia* sp. Our study did not encompass a full year cycle, but few large and yellow or orange fruits in canopy trees are available at this cloud forest site (Rios *et al.*, 2004), and most were not consumed by howlers.

Availability of resources varied among the three groups, reflecting the heterogeneous nature of our study area. In particular, the group living in ash plantation had a restricted diet, and resorted to leaves when little fruit was available within its home range. Most resources used by troops in ash plantations are in neighboring secondary forest and a few native trees dispersed within the plantations. Our measures of monthly fruit and leaf availability did not correlate with consumption, but this could be a result of our transects not adequately representing resource availability and our study not covering a full year cycle. The observed intra- and interspecific asynchrony in fructification suggests that a better estimate of fruit availability in montane forest could be obtained by placing more but shorter transects dispersed throughout the study area and inside howler home ranges.

Monkeys at our study site depended heavily on a few species in the Moraceae, especially *Ficus* spp., and *Cecropia telealba*. This capacity to rely on a limited set of fruit species, in addition to folivory, allows howler monkeys to survive in small and degraded forest fragments, and in anthropogenic habitats (Rylands and Keuroghlian, 1988; Schwartzkopf and Rylands, 1989; Coates-Estrada, 1996; Estrada *et al.*, 1999, 2002; Gómez-Posada *et al.*, 2005). Throughout tropical America, the Moraceae (particularly *Ficus*, *Morus*, *Brosimum*, *Poulsenia* and *Pseudolmedia*) and Cecropiaceae have emerged as critical resources for different species of howlers, in particular in second-growth habitats (Gaulin and Gaulin, 1982; Milton, 1991; Julliot and Sabatier, 1993; Silver *et al.*, 1998; Estrada *et al.*, 1999, 2002; Gómez-Posada *et al.*, 2005).

#### Seed dispersal

Howler monkeys are important members of the seed-disperser guild in tropical forests, because of their abundance, biomass, flexibility of habitat use, and the sheer number of seeds they move within and between habitats (Estrada and Coates-Estrada, 1984; Julliot, 1996a; Silver *et al.*, 1998; Yumoto *et al.*, 1999). At our study site, howlers defecated intact seeds of at least nine species that were able to germinate (Giraldo, 2003). The number of dispersed seed species at our site, however, is small compared to lowland forest sites. For example, one group of howlers dispersed nine species in 9 days in eastern Colombia (Yumoto *et al.*, 1999) and one group in French Guiana dispersed 86 species in 2 years (Julliot, 1996a).

On the other hand, howlers were seed predators for three species at our site (*Fraxinus chinensis*, *Wettinia kalbreyeri* and *Otoba lehmannii*) because they ate unripe fruits. They also sometimes dropped the large seeds of *Garcinia* sp. under the parent tree after partially eating the fruit. Howler feces at our site always had seeds, usually of several species. Most seeds were small, and in preliminary tests many were removed by dung beetles (Giraldo and Gómez-Posada, unpublished data), so were less likely to be predated by rodents. Removal of seeds by secondary dispersers such as dung beetles contributes to increased seed survival (Estrada and Coates-Estrada, 1986; Andresen, 1999, 2002). Although many seeds were deposited under the parent tree, monkeys also moved seeds to different areas of their home ranges. Most importantly, they moved seeds between habitats, in particular to the ash plantation, enriching the ash plantation and catalyzing secondary succession.

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**Appendix.** Plant species eaten by three troops of howler monkey at Otún-Quimbaya Flora and Fauna Sanctuary, in the Central Andes of Colombia. Table shows the percentage of each species in the diet and the type of item consumed (F = mature fruits, I = immature fruits, L = leaves and R = flowers).

Family /Species	Troop C			Troop D			Troop E	
	%	Item		%	Item		%	Item
MORACEAE								
<i>Ficus killipii</i>						58.4	L, F	
<i>Ficus cuatrecasana</i>	5.7	L						
<i>Ficus tonduzii</i>	9.6	L, F						
<i>Ficus aff. hartwegii</i>				3.0	L			
<i>Ficus humboldtii</i>	2.7	L, F		3.7	L			
<i>Ficus</i> sp. 1				15.3	L, F			
<i>Ficus</i> sp. 2				10.5	F			
<i>Ficus</i> sp. 3				5.2	L			
<i>Ficus</i> sp. 4				2.2	L			
<i>Ficus</i> sp. 5				0.7	L			
<i>Ficus</i> sp. 6				0.5	L			
<i>Ficus</i> sp. 7				0.5	F			
<i>Sorocea</i> sp.				2.3	R			
<i>Morus insignis</i>						0.5	L	
<i>Pseudolmedia</i> sp.	3.7	L						
Moraceae sp. 1				0.8	L			
Moraceae sp. 2	4.9	L						
CECROPIACEAE								
<i>Cecropia telealba</i>	9.6	L, F		27.1	L, F	12.6	L, F	
SAPINDACEAE								
<i>Paullinia</i> sp.	22.0	L		3.7	L	11.9	L	
<i>Allophylus mollis</i>	1.0	F						
LEGUMINOSAE								
<i>Macrolobium colombianum</i>	18.3	L, R		3.7	L, R	4.1	L	
<i>Inga aff. oerstediana</i>				2.3	L			
OLEACEAE								
<i>Fraxinus chinensis</i>				5.3	I	4.9	I	
CLUSIACEAE								
<i>Garcinia</i> sp.	3.0	F						
<i>Chrysochlamys colombiana</i>						4.1	L	
<i>Chrysochlamys</i> sp.				0.8	L			
ROSACEAE								
<i>Prunus integrifolia</i>	1.7	L						
ARALIACEAE								
<i>Dendropanax macrophyllum</i>	0.3	L		0.8	L	0.2	L	
MYRISTICACEAE								
<i>Otoba lehmannii</i>	7.9	I						
ARECACEAE								
<i>Wettinia kalbreyeri</i>	0.5	I						
FLACOURTIACEAE								
<i>Casearia sylvestris</i>	1.0	L						

continued on next page

## Appendix, continued from previous page

Family /Species	Troop C			Troop D			Troop E	
	%	Item		%	Item		%	Item
MELASTOMATACEAE								
<i>Miconia acuminifera</i>				0.8	F			
SOLANACEAE								
<i>Solanum sycophanta</i>				2.0	L		0.2	L
TILIACEAE								
<i>Heliocarpus americanus</i>				0.8	L		0.3	L
Unidentified								
Sp. 1	3.7	L, F						
Sp. 2	1.5	L						
Sp. 3	1.0	L						
Sp. 4	1.0	L						
Sp. 5	0.5	L						
Sp. 6	0.5	L						
Sp. 7							3.0	L
Sp. 8							0.3	L
Sp. 9				4.3	L			
Sp. 10				1.3	L			
Sp. 11				1.0	L			
Sp. 12				0.7	L			
Sp. 13				0.3	L			
Sp. 14				0.3	L			
<b>Total Frequencies</b>	<b>405</b>			<b>601</b>			<b>637</b>	
<b>Total Species</b>	<b>21</b>			<b>27</b>			<b>12</b>	