Density, Habitat Use, and Ranging Patterns of Red Howler Monkeys in a Colombian Andean Forest

Authors: Gómez-Posada, Carolina, Martínez, Jesús, Giraldo, Paula, and Kattan, Gustavo H.

Source: Neotropical Primates, 14(1) : 2-10

Published By: Conservation International

URL: https://doi.org/10.1896/044.014.0102

Articles

DENSITY, HABITAT USE, AND RANGING PATTERNS OF RED HOWLER MONKEYS IN A COLOMBIAN ANDEAN FOREST

Carolina Gómez-Posada[1], Jesús Martínez[1,2,3], Paula Giraldo[1,2,4] and Gustavo H. Kattan[1]

[1] *Fundación EcoAndina/Wildlife Conservation Society Colombia Program, Cali, Colombia. AA. 25527, e-mail:<cgomez@wcs.org>, <gkattan@wcs.org>*
[2] *Departamento de Biología, Universidad del Valle, Cali, Colombia*
[3] *Present address: Universidad de Los Lagos, Osorno, Chile, e-mail: <jesusmartinezgz@gmail.com>*
[4] *Present address: Vrije University, Amsterdam, The Netherlands, e-mail: <palgira@yahoo.com>*

Abstract

We studied habitat use and ranging patterns of five red howler monkey troops for six months in a lower montane forest in the Colombian Andes. The study area is a mosaic of mature and secondary forest and non-commercial ash, pine and oak plantations that were established as part of a reforestation program. Home ranges (10 ± 3 ha) and daily distances traveled (554 ± 248 m) were similar to those reported for lowland habitats. Home range use differed between groups using mature forest versus secondary forest and plantations, reflecting structural differences between habitat types. We estimated a density of 0.72 individuals and 0.1 groups per hectare. This high density is related to the protected status of the study area and the howler monkeys' behavioral plasticity, which has allowed them to colonize new environments such as plantations.

Key Words: *Alouatta seniculus*, cloud forest, Colombia, density, home range, habitat use, mature and secondary forest, tree plantations

Resumen

Estudiamos los patrones de uso del espacio de cinco grupos de mono aullador rojo durante seis meses en un bosque montano bajo en los Andes de Colombia. El área de estudio es un mosaico de bosques maduros y de regeneración, y plantaciones no comerciales de urapán, pino y roble que fueron establecidas en un programa de reforestación. Las áreas de actividad (10 ± 3 ha) y las distancias recorridas diariamente (554 ± 248 m) fueron similares a las reportadas para poblaciones de tierras bajas. Los patrones de uso del área de actividad difirieron entre los grupos que usaban bosque maduro y los que usaban combinación de bosque secundario y plantaciones, lo cual refleja las diferencias estructurales entre los tipos de hábitat. Estimamos una densidad de 0.72 individuos y 0.1 grupos por ha. Esta alta densidad está relacionada con el estado de protección del área y con la plasticidad conductual de estos monos, que les ha permitido colonizar nuevos ambientes como las plantaciones.

Palabras Clave: *Alouatta seniculus*, bosque nublado, Colombia, densidad, área de dominio vital, uso de habitat, bosque maduro y secundario, plantaciones de árboles

Introduction

Home ranges and population densities of animals vary in relation to factors such as body size, diet, habitat type, social system, and human disturbance (Milton and May, 1976; Crockett and Eisenberg, 1987; Peres, 1997; Chapman and Balcomb, 1998). In general, for energetic reasons, animals of large body size require larger home ranges and have lower population densities than smaller animals within the same trophic level (Fleagle, 1999; MacNab, 2002). Population density is also modulated by habitat productivity and position in the trophic pyramid for a particular species (Eisenberg, 1980; Fleagle, 1999; MacNab, 2002). In addition, for animals like primates that live in groups, population density depends on home range, troop size and the degree to which ranges of different troops overlap (Eisenberg, 1980; Crockett and Eisenberg, 1987).

The red howler monkey (*Alouatta seniculus*) is one of the largest Neotropical primates, with females reaching up to 6.3 kg and males 7.5 kg (Defler, 2003). Home ranges of red howlers vary between 7 and 25 ha (Crockett and Eisenberg, 1987), but may reach up to 182 ha (Palacios and Rodríguez, 2001). Small home ranges have been associated with the highly folivorous diet and sedentary habits of howler monkeys, but may also vary on the basis of interspecific interactions (Milton, 1980; Gaulin and Gaulin, 1982; Braza *et al.*, 1983; Crockett and Eisenberg, 1987). Depending on habitat and group composition, among other factors, population densities of red howlers vary widely, with a mean of 34–55 ind/km^2, but densities as high as 150 ind/km^2 have been reported in some habitats (Crockett and Eisenberg, 1987; Chapman and Balcomb, 1998).

Throughout its broad distribution in northwestern South America, the red howler is found from lowland rain forest, gallery forest, and dry woodlands to montane forest. In the Colombian Andes it ranges up to 2400 m and occasionally up to 3200 m (Hernández-Camacho and Cooper, 1976; Defler, 2003). Montane populations of red howlers in the Colombian Andes are threatened by habitat destruction and fragmentation. Few tracts of continuous forest still exist in the Central and Western Cordilleras (Kattan and Álvarez-López, 1996), and many howler populations are isolated in small fragments, sometimes as small as 10 ha (Gómez-Posada *et al.*, 2005). Protecting and managing these populations requires an understanding of patterns of spatial and habitat use and population densities.

Humid montane forest differs from lowland rain forest in having lower productivity (correlated with a decrease in temperature) and lower plant diversity, especially when above 1500 m (Gentry, 1992; Cavelier, 2001). Thus, population densities of howlers may be expected to be lower in montane forest than in the lowlands. Relatively low densities have been reported for two sites in the Colombian Andes (Gaulin and Gaulin, 1982 = *ca.* 15 ind/km^2; Morales-Jiménez, 2002 = 31.3 ind/km^2), but patterns of habitat and space use and population densities have not been rigorously documented. In this study, we present data obtained over six months on population density and space use of five red howler troops in a cloud forest in the Central Cordillera of the Colombian Andes. Our study site is a mosaic of habitat types, including old-growth and secondary forest, and monodominant patches of both exotic and native trees that were established in a reforestation program. Our study area is within an extensive, continuous forest (several thousand hectares) and our data provide baseline information for a more extensive study documenting responses of red howlers to fragmentation (Gómez-Posada, unpublished data).

Study Area

The study was conducted at Otún Quimbaya Flora and Fauna Sanctuary (Otún Quimbaya), a 489 ha protected area located on the western slope of the Central Cordillera of the Colombian Andes, east of the city of Pereira. The study area ranges between 1800 and 2100 m. Otún Quimbaya is contiguous with Ucumarí Regional Park, encompassing 3980 ha. Both areas protect the Otún River drainage between elevations of 1750 and 2600 m. The study area lies in the very humid lower montane forest life zone of the Holdridge classification system (Londoño, 1994). Mean annual rainfall is 2712 mm (El Cedral weather station, Cenicafé, 1995–2001), with a bimodal pattern. Rainy periods occur in April–June and September–November. There is a mild dry season in December–February, and a stronger one in July–August (Aguilar and Rangel, 1994). In 2001 total precipitation was 2117.8 mm. Mean annual temperature is 15°C.

Native forest in the Otún River drainage was largely cleared during the first half of the 20th century, for the establishment of cattle pastures. Some old-growth forest fragments remained, mainly in deep canyons, although hardwoods were extracted from most of the region. In the 1960s a reforestation program was initiated by local authorities with the objective of stabilizing soils and stopping erosion in the watershed. Some patches were planted with exotic Chinese ash (*Fraxinus chinensis*) and cypress (*Cupressus lusitanica*), and with native Andean oak (*Quercus humboldtii*). Most of the area currently included in Otún Quimbaya, however, was abandoned to natural regeneration, with seeds provided by native forest remnants.

Currently, the Otún drainage is 80% forested, with a mosaic of old-growth forest, secondary forest of different ages, and interspersed patches of monospecific tree plantations. As these plantations were established for reforestation purposes, they were not managed and are presently invaded by native vegetation, particularly in the understory and edges (Durán and Kattan, 2005). The canopy remains monodominant, though. Presently the Otún Quimbaya area is covered by a mosaic of old-growth and secondary forest on the mountainsides, and strips of ash plantations on the valley floor, along the river. Oak and cypress plantations occur in small patches near the river, neighboring ash stands. A narrow dirt road cuts across the park and the ash plantations.

Methods

Between July and December 2001 we identified all red howler monkey troops in 113 ha of Otún Quimbaya, which included native forest of different ages, and ash, cypress and oak patches. We selected five groups (labeled C-G) for intensive observation. Each of these troops was followed for a maximum of three days per month. Daily travel routes involved going from a sleeping tree in the morning at 0630–0800, through a series of feeding trees throughout the day, to a different sleeping tree in the afternoon at 1600–1700. We identified individuals by age and sex following Defler (1981) and Soini (1992).

During observation periods, we recorded data on activity patterns and diet (Martinez, 2003; Giraldo *et al.,* submitted). To evaluate habitat use, we followed each troop, taking note of its location and habitat type every half hour. We superimposed a ¼ ha grid over a map of the study area, and plotted all troop locations to obtain frequencies of use of each ¼ ha quadrant within their home ranges (NRC, 1981). To quantify patterns of habitat use, we added all records in quadrants in each habitat type for each group, and used a χ^2 test to compare habitat use among groups. To establish whether quadrant use frequency distributions differed from random (Poisson), we used a χ^2 test. This distribution is zero-truncated because in theory some cells will remain unused (Robinson, 1986; Di Bitetti, 2001). We used a Spearman rank correlation coefficient to correlate the number of feeding and sleeping trees in each quadrant and the quadrant's frequency of use. We pooled troops in two categories according to the main habitat type they used (two troops in old-growth forest versus three troops in secondary forest/plantations), and used a Mann Whitney U test to compare the number of quadrants used per day, and the mean number of records per quadrant between the two habitat types. To test whether groups used habitat types in proportion to their availability, we compared the frequency of use of each habitat with its area within the home range with a χ^2 test.

We estimated the home range size of each troop as the number of ¼ ha quadrants used at least once (NRC, 1981). Home range overlap was calculated using the formula O = HR*D/GS, where O is overlap, HR is mean home range, D is population density and GS is mean group size. This index reveals the number of troops that can overlap at any point within the study area (Terborgh, 1983; DiBitetti, 2001). We correlated home range size and group size with a Spearman rank correlation coefficient. Daily distance traveled was defined as the distance covered by a group from one sleeping tree to the next (NRC, 1981). We joined all half-hour location points of each group with straight lines to obtain the distance traveled in a day. Daily distances traveled by different groups were compared with a Kruskal-Wallis test. The number of trees visited by groups in old-growth forest versus secondary forest/plantation was compared with a Mann-Whitney U test.

Results

Eleven red howler monkey troops with a total of 82 individuals inhabited the 113 ha study area (Table 1, Fig. 1), for a density of 72.6 ind/km^2 and 9.73 groups/km^2. We observed other groups outside the core study area, and solitary adult males throughout the study area. Red howler troops were stable throughout the study period (Table 1). Mean group size was 7.3 individuals (DS=2.5, range 3–10) and increased to 7.5 after an infant was born and a subadult male joined group G. Groups were composed of one adult male, one to three adult females, one or two subadults and one to four juveniles and infants. Sex ratio was biased toward females (1:0.6) and the ratio of adult females to immature individuals (juveniles and infants) was 1:1.2.

Habitat use. The five more intensely studied troops used different habitat types in different proportions (χ^2 = 1351.6, df = 8, $p < 0.01$; Table 2). Cypress plantations were used as corridors between forest patches and as sleeping trees, but were used infrequently during the day. Sometimes when howlers were foraging in secondary forest, where few large trees were available, they moved to cypress patches for diurnal resting periods. Oak stands also were only used as routes between ash stands and forest patches. Ash stands had some dispersed *Cecropia* and *Ficus* trees that were used as sleeping and feeding trees. Howlers also fed on immature ash fruits and used big ash trees as sleeping trees (Giraldo *et al.,* submitted).

Home range use was not random, as howlers used some quadrants more than expected (Fig. 2). The more inten-

Table 1. Size and composition of 11 red howler monkey troops at Otún Quimbaya Flora and Fauna Sanctuary, Central Andes of Colombia.

Group	Adult		Subadult		Juvenile		Infant	Unknown	Total
	M*	F*	M	F	M	F			
A	1	1	2	1	1				6
B	1	3			1		2	3	10
C	1	2				1	1		5
D	1	3	1	1	1	1	2		10
E	1	2	1	1	1		2		8
F	2	2	1	1	2		2		10
G	1	2	1	1		1	2		8
H								10	10
I								7	7
J	1	2	1			1			5
K	1	1						1	3
Total	10	18	7	5	6	4	11	21	82
Mean	1.1	2.0	1.2	1.0	1.2	1.0	1.8		7.5

* M: males; F: females

sively used quadrants, corresponding to dormitories, latrines, and feeding trees (r = 0.63, $p < 0.01$), did not form a core area but were dispersed throughout the home range. The number of sleeping and feeding trees per quadrant was lower for the three groups that mainly used plantations and secondary forest than for the two troops using mature forest (Z = 2.2, n = 143 and 63, p = 0.02) (Table 3). Home range use was different between groups using mature forest and groups using secondary forest and plantations. The latter usually used one or two quadrants intensively for several days, feeding and sleeping in the same area. After crops were exhausted in these feeding trees, monkeys moved throughout their home range in a haphazard way until finding a new feeding tree. In contrast, troops in mature forest used several quadrants each day, moving between feeding trees, sleeping trees, and latrines, traversing their home ranges in three or four days. The mean number of quadrants visited per day was similar for mature forest and

Table 2. Home range composition by habitat type, and proportion of observations in each habitat type, for five red howler monkey troops in Central Andes of Colombia.

Group	Habitat Type						N
	Mature Forest		Secondary Forest		Plantation		
	% home range	% obs.	% home range	% obs.	% home range	% obs.	
C	90.9	97.2	9.1	2.8*			246
D			58.9	63.3	41.1	36.7	297
E			31.4	17.3*	68.6	82.7*	272
F	17.3*	24.0	57.7	52.7	25.0	23.3	146
G	100	100					267

* Significant difference between observed and expected frequencies ($p < 0.05$, χ^2 test)

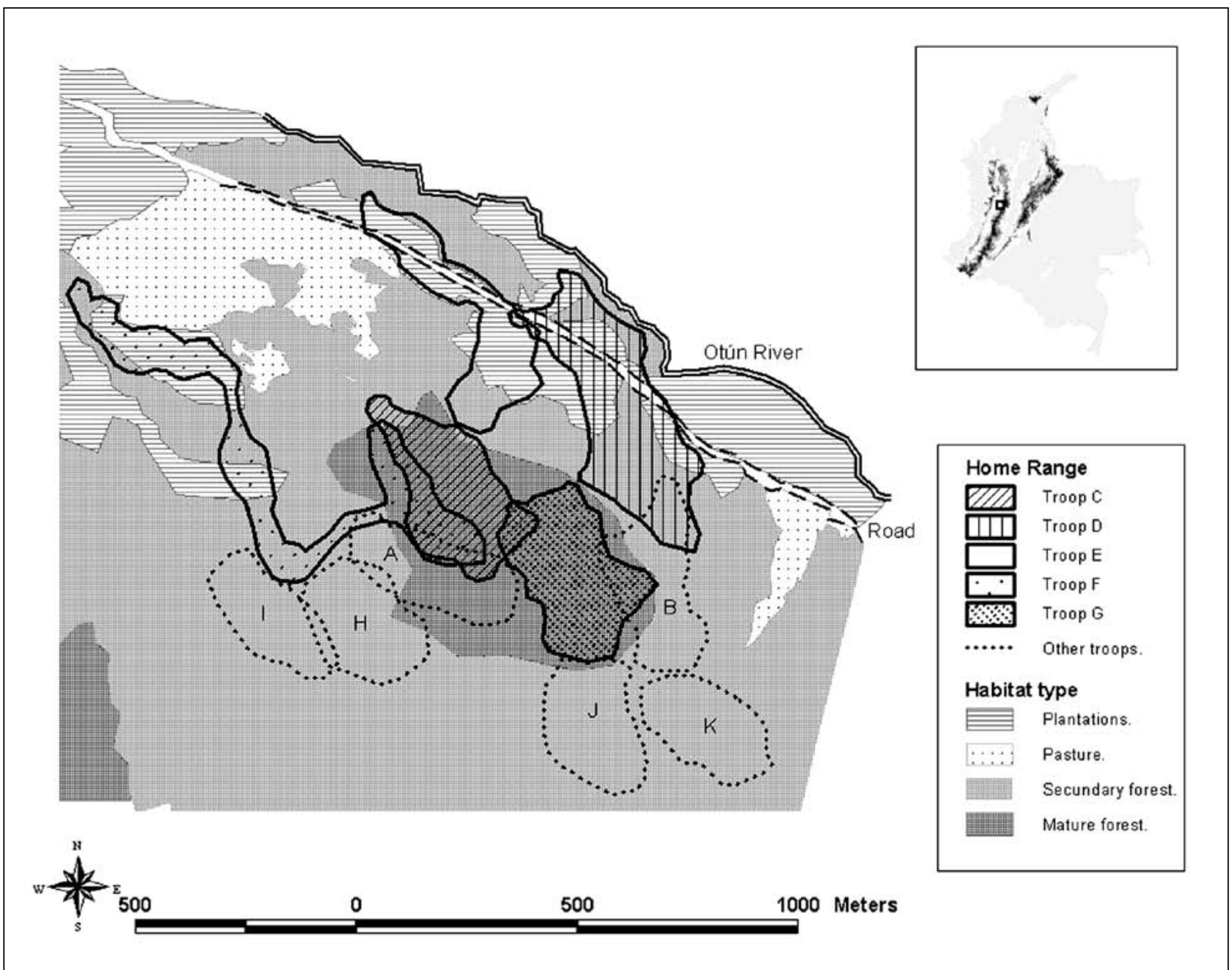

Figure 1. Map of Otún Quimbaya Flora and Fauna Sanctuary, Central Cordillera, Colombian Andes, showing habitat types and home ranges of red howler groups.

for secondary forest/plantation groups (U = 88, n = 17 and 12, $p = 0.5$; Table 3), but coefficients of variation were larger for the latter. The percent use of each quadrant was larger for mature forest troops (Z = 1.9, n = 143 and 63, $p = 0.05$) (Table 3).

Home range and daily distance traveled

Home ranges of the five troops varied between 7.5 and 14 ha, with a mean ± SD of 10.2 ± 3.03 ha (Table 4, Fig. 2). Bigger groups showed a tendency to have larger home ranges ($r_s = 0.87$, n = 5, $p = 0.05$). Groups C and G had small, compact home ranges 7.8 ± 0.4, with an area/perimeter ratio of 48:1, while the other groups had larger (11.9 ± 2.8) and elongated home ranges, with an area/perimeter ratio of 35:1 (Table 4, Fig. 2). Home ranges of the five troops were contiguous and had an overlap index of 0.98 (i. e., any point within the study area was used by 0.98 groups). Unused areas between home ranges were early second growth forest, which lacks the structure and resources required by howlers (Fig. 1). On average, each group shared 20.9% ± 12.9% of its home range with other groups. When groups met at feeding trees, they engaged in vocal displays and usually the smaller group retreated.

Daily distance traveled varied between 317.5 m (group D) and 1321.2 (group E), with a mean of 553.9 ± 247.9 (Table 4). Mean daily distance was similar among groups (H = 4.38, df = 4, $p = 0.3$). However, the coefficient of variation for groups using mature forest was much smaller (28%) than for groups using secondary forest/plantation (53%). This reflected different patterns of habitat use. When trees in plantations produced fruit, howlers exploited them intensively, remaining near this tree for one or more days. After the crop was exhausted, they traveled throughout the home range in search of fruiting trees. In mature forest, in contrast, howlers fed from several trees each day and traveled through their home range in three or four days. The number of feeding trees visited per day was lower for secondary forest/plantation groups (5.7 ± 1.6) than for mature forest groups (9.1 ± 4.4) (U = 54, n = 17 and 12, $p = 0.05$).

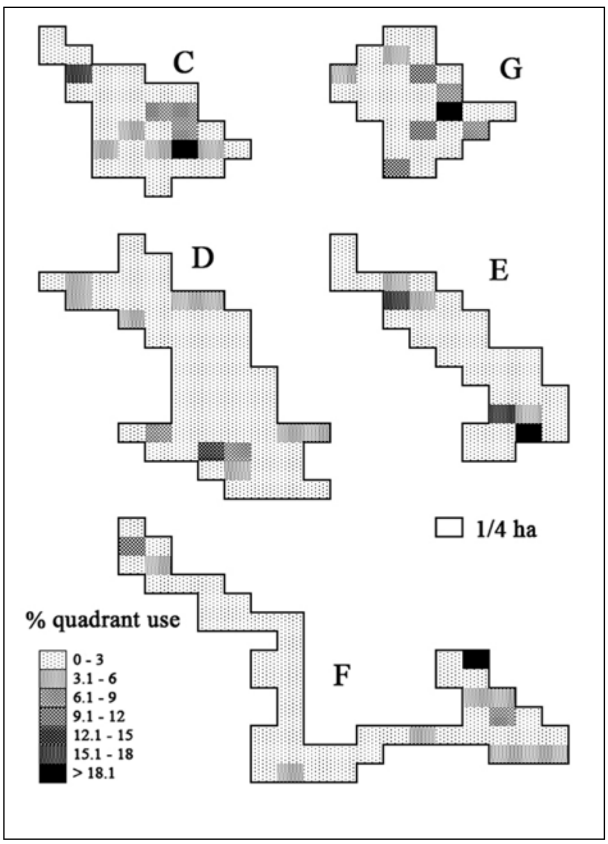

Figure 2. Intensity of use of quadrants in home ranges of five groups of howler monkey at Otún Quimbaya. Frequency distribution of quadrant use was significantly different from Poisson in all cases (group C: $\chi^2 = 1389.7$, df = 31, $p < 0.01$; group D: $\chi^2 = 590.9$, df = 55, $p < 0.01$; group E: $\chi^2 = 1977.1$, df = 34, $p < 0.01$; group F: $\chi^2 = 98$, df = 51, $p < 0.01$; group G: $\chi^2 = 3963$, df = 29, $p < 0.01$).

Discussion

Group sizes of red howler monkeys observed at Otún Quimbaya are within the range of 2–16 individuals (mean = 6–9) usually reported for this species (Neville, 1972; Izawa, 1988, 1997; Soini, 1992; Chapman and Balcomb, 1998; Defler, 2003). Group composition is also typical, with a slightly higher proportion of adult females to adult males (Defler, 1981), reflecting the red howler's social organization: one dominant male, one to four adult females and their offspring, and zero to three subadults (Izawa, 1988, 1997; Soini, 1992; Crockett, 1996). The ratio of adult females to immature (juveniles and infants) may give an idea of population health (Heltne *et al.*, 1976). A high ratio may indicate a declining population, and a low ratio may indicate an expanding population. At Otún Quimbaya we found 1.2 immature individuals for each adult female, suggesting a growing population (Defler, 1981).

Red howler monkeys usually have densities of 34–55 ind/km² (Defler, 1981; Freese *et al.*, 1982; Braza *et al.*, 1983; Terborgh, 1983; Soini, 1992; Chapman and Balcomb, 1998), but may vary from 4 to 150 (Neville, 1972; Klein and Klein, 1976; Rudran, 1979; Freese *et al.*, 1982; Crock-

Table 3. Number of feeding and sleeping trees per quadrant, number of quadrants visited per day and percent use of each quadrant (mean ± SD, CV), for five red howler troops using two habitat types in the Central Andes of Colombia.

	No. Trees	No. Quadrants	% Use
Mature forest (groups C and G)	2.0 ± 2.5	9.6 ± 3.5, 36.3	3.2 ± 5.0, 157.8
Secondary forest and plantation (groups D, E and F)	0.9 ± 1.3 p = 0.02	11.7 ± 6.9, 60 p > 0.05	2.1 ± 3.7, 178.5 p = 0.05

Table 4. Home range and daily distance traveled (x ± SD, n) for five red howler monkey troops at Otún Quimbaya Flora and Fauna Sanctuary, Central Andes of Colombia.

Group	Home range (ha)	Distance (m)	No. hours of observation	No. days of observation
C	8.0	526.7 ± 150.4, 6	119.4	18
D	14.0	412.2 ± 120.2, 6	136.4	19
E	8.7	661.3 ± 341.1, 9	132.0	15
F	13.0	660.0 ± 481.9, 2	52.1	9
G	7.5	528.3 ± 154.6, 6	117.4	15
Mean	10.2	553.9 ± 247.9, 29		

ett and Eisenberg, 1987; Rylands and Keuroghlian, 1988; Palacios and Rodríguez, 2001). Population densities of red howler monkeys vary depending on factors such as habitat characteristics (e. g., plant diversity and abundance, forest productivity and structure; Freese *et al.*, 1982; Crockett, 1985) and habitat heterogeneity and seasonality (Peres, 1997). Competition with other frugivorous species or with other primates may keep densities low (Klein and Klein, 1976; Defler, 1981; Palacios and Rodríguez, 2001). Much variability in red howler populations is related to their recent history, such as human disturbance (habitat alteration and fragmentation, hunting), fruit crop failure, and disease (Freese *et al.*, 1982; Crockett, 1985; Rylands and Keuroghlian, 1988; Peres, 1990; Sussman and Phillips-Conroy, 1995; Chapman and Balcomb, 1998).

The density of 72.6 ind/km^2 at Otún Quimbaya corresponded to the upper part of the range. The red howler is the largest frugivore in our study area and is in sympatry with only one other primate species, the night monkey (*Aotus lemurinus*). Howler monkey populations at our site were likely greatly reduced when this forest was exploited in the early- to mid-20th century (Londoño, 1994). Forest protection and restoration have presumably allowed howler populations to recover in the last 40 years. Flexibility in habitat use has allowed howlers to exploit new habitats such as ash plantations, and they are not limited to mature forest (Estrada and Coates-Estrada, 1996; Fedigan *et al.*, 1998; Fedigan and Jack, 2001). At Hato Masaguaral in Venezuela, for example, densities over 70 ind/km^2 have been reported (Neville, 1972; Rudran, 1979; Crockett and Eisenberg, 1987). Population size at this site has increased in part in response to forest recovery (Crockett and Eisenberg, 1987; Crockett, 1996). Fedigan and Jack (2001) found that in 28 years since the creation of Santa Rosa National Park in Costa Rica, the population of black howler monkey (*Alouatta palliata*) has increased seven-fold, due to protection and increase in forest cover.

Habitat use

Howler monkeys at Otún Quimbaya used the different habitat types in proportion to their availability, as has also been found in the lowlands, where howlers are reported as habitat generalists (Neville, 1972; Soini, 1982; Stevenson *et al.*, 1991; Palacios and Rodríguez, 2001). In our six-month study we observed low intra- and interspecific synchrony in fruit and new leaf production, and no absolute fruit scarcity for howlers (Giraldo *et al.*, submitted). Tropical montane forests do not present drastic periods of fruit scarcity, in contrast to the lowlands (Giraldo, 1990; Ataroff, 2001; Cavelier *et al.*, 2001). Quadrant use by monkeys at our site was dictated by the presence of feeding trees. Probably for this reason, there was no core area in the home range and quadrant use was not random.

Differences in structure and composition among habitat types at Otún Quimbaya generated differences in habitat use by howlers. In mature forest, the canopy is heterogeneous and densities of feeding and sleeping trees are high. Howlers used feeding trees for a short time and moved among them, traversing their entire home range in a few days, as occurs in lowland forest (Stevenson *et al.*, 1991; Izawa, 1997). Plantations, in contrast, are more homogeneous (monodominant canopy) and resource trees are more dispersed. Thus, howlers spent several days at one or two fruiting trees until exhausting the fruit crop, and then moved to another tree, which could be located in a far quadrant of their home range. This resulted in some quadrants being used intensively, whereas others were used only as movement routes. Groups living in plantations also had a less diverse diet than mature forest groups (Giraldo *et al.*, submitted). It is unlikely that monkeys could survive in plantations without neighboring tracts of native forest, and without having dispersed *Ficus* and *Cecropia* trees within the plantation (Giraldo *et al.*, submitted). The Moraceae are very important for howler survival in isolated forest patches, and in disturbed and second-growth forest (Rylands and Keuroghlian, 1988; Schwartzkopf and Rylands, 1989; Estrada and Coates-Estrada, 1996; Fedigan *et al.*, 1998).

Home range and daily distance traveled

Red howler home ranges vary widely, but tend to be small (6–30 ha). Home ranges at our site were similar to those reported for lowland forest (Neville, 1972; Defler, 1981; Crockett and Eisenberg, 1987; Soini, 1992; Izawa, 1997). Small home ranges in howler monkeys reflect their high use of leaves, a low-quality nutritional resource that is abundant and widely distributed (Milton, 1980; Gaulin and Gaulin, 1982; Braza *et al.*, 1983). A study in the Central range of the Colombian Andes at 2300 m of elevation (Gaulin and Gaulin, 1982), about 300 km south of our study area, reported a home range of 22 ha and a density *ca.* 15 ind/km^2 for a red howler group in a mature forest. At this site howlers are at the limit of their elevational range, and are sympatric with *Cebus apella*, a very active frugivore-insectivore that could represent strong competition for howlers.

A previous study at Otún Quimbaya (Morales-Jiménez, 2003) reported a home range of 14.5 ha for a troop in mature forest and 21.2 ha for a troop in ash plantation. This author suggested that the larger home range of the plantation troop was due to lower resource availability, as found in our study (Giraldo *et al.*, submitted). The plantation troop studied by Morales-Jiménez (2003) coincides with our troops D and E, which could suggest that a new group formed in this area. Fedigan and Jack (2001) found that population increase of mantled howler monkey at Santa Rosa National Park in Costa Rica was due to new group formation as forest recovered. Mantled howlers rapidly colonized secondary forest as trees reached a sufficient diameter at breast height to support their weight.

Home ranges of howler monkeys may decrease when population densities increase (Crockett and Eisenberg, 1987). For example, at La Macarena, Colombia (67 ha, 17–30 ind./km^2; Stevenson, *et al.*, 1991, 2000) and Caparú, Colombia (182 ha, 4 ind./km^2; Palacios and Rodríguez, 2001), densities are low and home ranges large. In contrast the opposite is observed at Hato Masaguaral in Venezuela (7–10 ha, 83–118 ind/km^2; Crockett and Eisenberg, 1987) and Otún Quimbaya (10.2 ha, 72.6 ind./km^2; this study). Home ranges of troops using mature forest at Otún Quimbaya were compact and small, whereas they were elongated and larger for plantation troops. This reflects structural and compositional differences between habitat types, as well as patch shape. In plantations the forest canopy is homogeneous and more discontinuous, and feeding trees and sleeping trees are more dispersed. In addition, plantations are in strips along the river and the road. Groups D and E could cross the road only at certain points where tree canopies provided a bridge. Thus, movement routes for plantation troops sometimes were long and linear. In mature forest, in contrast, movement routes were more tortuous and uniform, covering similar distances each day.

Daily travel routes of howlers are usually around 500–600 m in lowland habitats (Neville, 1972; Rudran, 1979; Stevenson *et al.*, 1991). Howler troops tend to be stable and use the same routes repeatedly. For example, in ten years of following a troop at La Macarena, Colombia, Izawa (1997) observed little changes in travel routes. Mean daily movements at Otún Quimbaya (317–1321 m/day) were similar, with variations related to habitat structure.

Home ranges and space requirements of montane red howler monkeys observed in this study are similar to those reported for lowland forest populations. The relatively high population density estimated for Otún Quimbaya is related to the recent history of protection and forest recovery in the area. Plasticity in habitat use has helped the howler population to recover, as they have been able to use tree plantations that offer some resources. Patterns of movement and home range use, however, differ between habitat types (mature forest vs. secondary forest and plantations). These differences are related to differences in resource distribution and availability in the different habitats.

Acknowledgments

We thank the National Parks Unit and the staff at Otún Quimbaya for logistical support and for permits. Thanks to Carolina Murcia and fellow researchers at WCS Colombia/EcoAndina for continued support and discussion of ideas, and to Leonor Valenzuela for help with the map. Financial support was provided by a grant from the John D. and Catherine T. MacArthur Foundation.

References

Aguilar, M. and Rangel, J. O. 1994. Clima del Parque Regional Natural Ucumari y sectores aledaños. In: *Ucumari, Un Caso Típico de la Diversidad Biótica Andina,* J. O. Rangel (ed.), pp.39–56. Corporación Autónoma Regional de Risaralda, Pereira.

Ataroff, M. 2001. Venezuela. In: *Bosques Nublados del Neotropico,* M. Kappelle and A. Brown (eds.), pp.397–442. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia.

Braza, F., Álvarez, F. and Azcarate, T. 1983. Feeding habits of the red howler monkeys (*Alouatta seniculus*) in the Llanos of Venezuela. *Mammalia* 47: 205–214.

Cavelier, J., Lizcano, D. and Pulido, M. 2001. Colombia. In: *Bosques Nublados del Neotropico,* M. Kappelle and A. Brown (eds.), pp.443 – 496. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia.

Chapman, C. and Balcomb, S. 1998. Population characteristics of howlers: Ecological conditions or group history. *Int. J. Primatol.* 19: 385 – 403.

Crockett, C. 1985. Population studies of red howler monkeys (*Alouatta seniculus*). *Nat. Geo. Res./Spring* 1:264–273.

Crockett, C. 1996. The relation between red howler monkey (*Alouatta seniculus*) troop size and population growth in two habitats. In: *Adaptive Radiation of Neotropical Primates,* M. A. Norconk, A. L. Rosenberg and P. A. Garber (eds.), pp.489–510. Plenum Press, New York.

Crockett, C. and Eisenberg, J. 1987. Howlers: Variations in group size and demography. In: *Primate Societies,* B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham and T. Struhsaker (eds.), pp.54–68. The University of Chicago Press, Chicago.

Defler, T. 1981. The density of *Alouatta seniculus* in the eastern llanos of Colombia. *Primates* 22: 564–569.

Defler, T. 2003. *Primates de Colombia*. Serie de Guías Tropicales 4. Conservación Internacional, Bogotá.

Di Bitetti, M. 2001. Home range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *J. Zoo. Lond.*: 253: 33–45.

Durán, S. and Kattan, G. 2005. Test of the utility of exotic tree plantations for understory birds and food resources in the Colombian Andes. *Biotropica* 37: 129–135.

Eisenberg, J. 1980. The density and biomass of tropical mammals. In: *Conservation Biology*, M. E. Soule and B. A. Wilcox (eds.), pp.35–55. Sinauer Associates, Massachusetts.

Estrada, A. and Coates-Estrada, R. 1996. Tropical rainforest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *Int. J. Primatol.* 17: 759–783.

Fleagle, J. G. 1999. *Primate Adaptation and Evolution*. Second edition. Academic Press, San Diego.

Fedigan, L. and Jack, K. 2001. Neotropical primates in a regenerating Costa Rica dry forest: A comparison of howler and capuchin population patterns. *Int. J. Primatol.* 22: 689–713.

Fedigan, L. M., Rose, L. M. and Morera, R. 1998. Growth of mantled howler in a regenerating Costa Rican dry forest. *Int. J. Primatol.* 19: 405–432.

Freese, C., Heltne, P. G., Castro, N. and Whitesides, G. 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *Int. J. Primatol.* 3: 53–90.

Gaulin, S. and Gaulin, C. 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest, Colombia. *Int. J. Primatol.* 3: 1–32.

Gentry, A. H. 1992. Diversity and floristic composition of Andean forests of Peru and adjacent countries: Implications for their conservation. *Mem. Mus. Hist. Nat. U. N. M. S. M.* 21: 11–29.

Giraldo, J. E. 1990. Estudio fenológico de una comunidad vegetal en bosque montano húmedo de la cordillera Occidental. *Cespedesia* XVI–XVII: 53–76.

Giraldo, P., Gómez-Posada, C., Martínez, J. and Kattan, G. Submitted. Resource use and seed dispersal by red howler monkey (*Alouatta seniculus*) in Andean forest. *Neotropical Primates.*

Gómez-Posada, C., Roncancio, N. and Hincapié, P. 2005. Evaluación de las poblaciones de mono aullador rojo (*Alouatta seniculus:* Primates) en fragmentos de bosque en el Valle del Cauca. Unpublished report, Corporación Regional del Valle del Cauca, Cali.

Heltne, P. G., Turner, D. C. and Scott Jr., N. C. 1976. Comparison of census on *Alouatta palliata* from Costa Rica and Panamá. In: *Neotropical Primates: Field Studies and Conservation,* R. Thorington and P. G. Heltne (eds.), pp.10–19. National Academy of Sciences, Washington DC.

Hernandez-Camacho, J. and Cooper, R. 1976. The nonhuman primates of Colombia. In: *Neotropical Primates: Field Studies and Conservation*, R. Thorington and P. G. Heltne (eds.), pp.35–69. National Academy of Sciences, Washington DC.

Izawa, K. 1988. Preliminary reports on social changes in red howlers (*Alouatta seniculus*). *Field Stud. New World Monkeys La Macarena Colombia* 1: 29–33.

Izawa, K. 1997. Stability of the home range of red howler monkeys. *Field Stud. Fauna Flora La Macarena Colombia* 11: 41–46.

Kattan, G. and Álvarez-López, H. 1996. Preservation and management of biodiversity in fragmented landscape in the Colombian Andes. In: *Forest Patches in Tropical Landscapes,* J. Schelhas and R. Greenberg (eds.), pp.3–18. Island Press, Washington DC.

Klein, L. and Klein, D. J. 1976. Neotropical primates: Aspects of habitat usage, population density and regional distribution in la Macarena, Colombia. In: *Neotropical Primates: Field Studies and Conservation,* R. Thorington and P. G. Heltne (eds.), pp.70–78. National Academy of Sciences, Washington DC.

Londoño, E. 1994. Parque Regional Natural Ucumarí: Un vistazo histórico. In: *Ucumari, Un Caso Típico de la Diversidad Biótica Andina,* J. O. Rangel (ed.), pp.13–24. Corporación Autónoma Regional de Risaralda, Pereira.

Martínez, J. 2003. Densidad poblacional, rango vital y patrón de actividad del mono aullador *Alouatta seniculus* (Primates: Cebidae) en el Santuario de flora y fauna Otún Quimbaya, Risaralda. Tésis de grado, Universidad del Valle, Cali, Colombia.

McNab, B. K. 2002. *The Physiological Ecology of Vertebrates: A View from Energetics.* Cornell University Press, Ithaca and London.

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

Milton, K. and May, M. 1976. Body weight, diet, and home-range area in primates. *Nature* 259: 459–462.

Morales-Jiménez, A. L. 2002. Densidad de los monos aulladores (*Alouatta seniculus*) en un bosque subandino, Risaralda, Colombia. *Neotrop. Primates* 10: 141–144.

Morales-Jiménez, A. L. 2003. Área de acción de los monos aulladores (*Alouatta seniculus*) en un bosque nativo y uno reforestado, Risaralda (Colombia). In: *Primatología del Nuevo Mundo: Biología, Medicina, Manejo y Conservación,* V. Pereira, F. Nassar and A. Savage (eds.), pp.113–132. Centro de Primatología Araguatos, Bogotá.

National Research Council. 1981. *Techniques for the Study of Primate Population Ecology.* National Academy Press, Washington DC.

Neville, M. K. 1972. The population structure of red howler monkeys (*Alouatta seniculus*) in Trinidad and Venezuela. *Folia Primatol.* 17: 56–86.

Palacios, E. and Rodríguez, A. 2001. Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a southeastern Colombian rainforest. *Am. J. Primatol.* 55: 233–251.

Peres, C. 1990. Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* 54: 47–59.

Peres, C. 1997. Effects of habitat quality and hunting pressure on arboreal folivore densities in Neotropical forests: A case study of howler monkeys (*Alouatta* spp.). *Folia Primatol.* 69: 199–222.

Robinson, J. G. 1986. Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. *Smithsonian Contr. Zool.* 431: 1–60.

Rudran, R. 1979. The demography and social mobility of a red howler (*Alouatta seniculus*) population in Venezuela. In: *Vertebrate Ecology in the Northern Neotropics,* J. Eisenberg (ed.), pp.107–126. Smithsonian Institution Press, Washington DC.

Rylands, A. and Keuroghlian, A. 1988. Primate population in continuous forest and forest fragment in central Amazonia. *Acta Amazonica* 18: 291–307.

Schwarzkopf, L. and Rylands, A. 1989. Primate species richness in relation to habitat structure in Amazonian rainforest fragments. *Biol. Conserv.* 48: 1–12.

Soini, P. 1992. Ecología del coto mono (*Alouatta seniculus*, Cebidae) en el río Pacaya, reserva Pacaya–Samiria, Perú. *Folia Amazonica* 4: 103–118.

Stevenson, P., Quiñones, M. and Ahumada, J. 1991. Relación entre la abundancia de frutos y las estrategias alimenticias de cuatro especies de primates en el Río Duda, Macarena. Unpublished report, Fundación para la Promoción de la Investigación y la Tecnología, Banco de la República, Bogotá.

Stevenson, P., Quiñones, M. and Ahumada, J. 2000. Influence of fruit availability on ecological overlap among four Neotropical primates at Tinigua National Park, Colombia. *Biotropica* 32: 533–544.

Sussman, R. and Phillips-Conroy, J. 1995. A survey of the distribution and density of the primates of Guyana. *Int. J. Primatol.* 16: 761–791.

Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton University Press, New Jersey.