

## Primate Population Densities in Three Nutrient-Poor Amazonian Terra Firme Forests of South-Eastern Colombia

Erwin Palacios<sup>a</sup> Carlos A. Peres<sup>b</sup>

<sup>a</sup> Conservation International Colombia, Bogotá, Colombia; <sup>b</sup> School of Environmental Sciences, University of East Anglia, Norwich, UK

---

### Key Words

Primate biomass · Colombian Amazonia · Oligotrophic forests · Protected areas

---

### Abstract

We censused primate populations at three non-hunted 'terra firme' forests of south-eastern Colombian Amazonia. The aggregate biomass densities of diurnal primates at all sites were amongst the lowest recorded for any non-hunted forest in western Amazonia and elsewhere in the Neotropics. Densities of red howler monkeys were low, as is typical in Amazonian terra firme forests far removed from white-water rivers, and densities of woolly monkeys were 1.5–3.5 times lower than those estimated for this species in central-western Brazilian Amazonia. Densities of small to mid-sized primates except for brown capuchins (*Cebus apella*) and white-faced capuchins (*Cebus albifrons*) were similar to those of other oligotrophic Amazonian forest sites. Our results are in agreement with other studies showing that terra firme forests of lowland Amazonia typically sustain a low biomass density of primates and other mid-sized to large vertebrates. Large reserves are therefore required to assure the viability of primate populations in oligotrophic systems. Given the escalating negative impacts of human habitat disturbance and hunting in Colombian Amazonia, we urge that a baseline sampling protocol to quantify the abundance and distribution of the harvest-sensitive vertebrate fauna be established within protected areas and the large indigenous reserves so that conservation efforts can be defined and implemented.

---

Copyright © 2005 S. Karger AG, Basel

---

**KARGER**

Fax +41 61 306 12 34  
E-Mail [karger@karger.ch](mailto:karger@karger.ch)  
[www.karger.com](http://www.karger.com)

©2005 S. Karger AG, Basel  
0015–5713/05/0763–0135\$22.00/0

Accessible online at:  
[www.karger.com/fpr](http://www.karger.com/fpr)

---

Erwin Palacios, Conservation International Colombia  
Apartado Aéreo 12114  
Bogotá D.C. (Colombia)  
Tel./Fax +571 3452852 54 63  
E-Mail [epalacios@conservation.org](mailto:epalacios@conservation.org)

## Introduction

Primates are one of the hallmarks of the Amazonian vertebrate fauna. They comprise between 25 and 40% of the aggregate frugivore biomass in Neotropical forests [Eisenberg and Thorington, 1973; Eisenberg et al., 1979; Terborgh, 1983], represent a large proportion of the mammal species richness [Terborgh, 1983; Peres, 1999a] and play key roles in the forest dynamics, especially as seed dispersers and predators [Terborgh, 1990; Chapman and Chapman, 1995; Norconk et al., 1998; Peres and van Roosmalen, 2002]. They are, however, increasingly threatened by anthropogenic habitat disturbance and from hunting [Chapman and Peres, 2001].

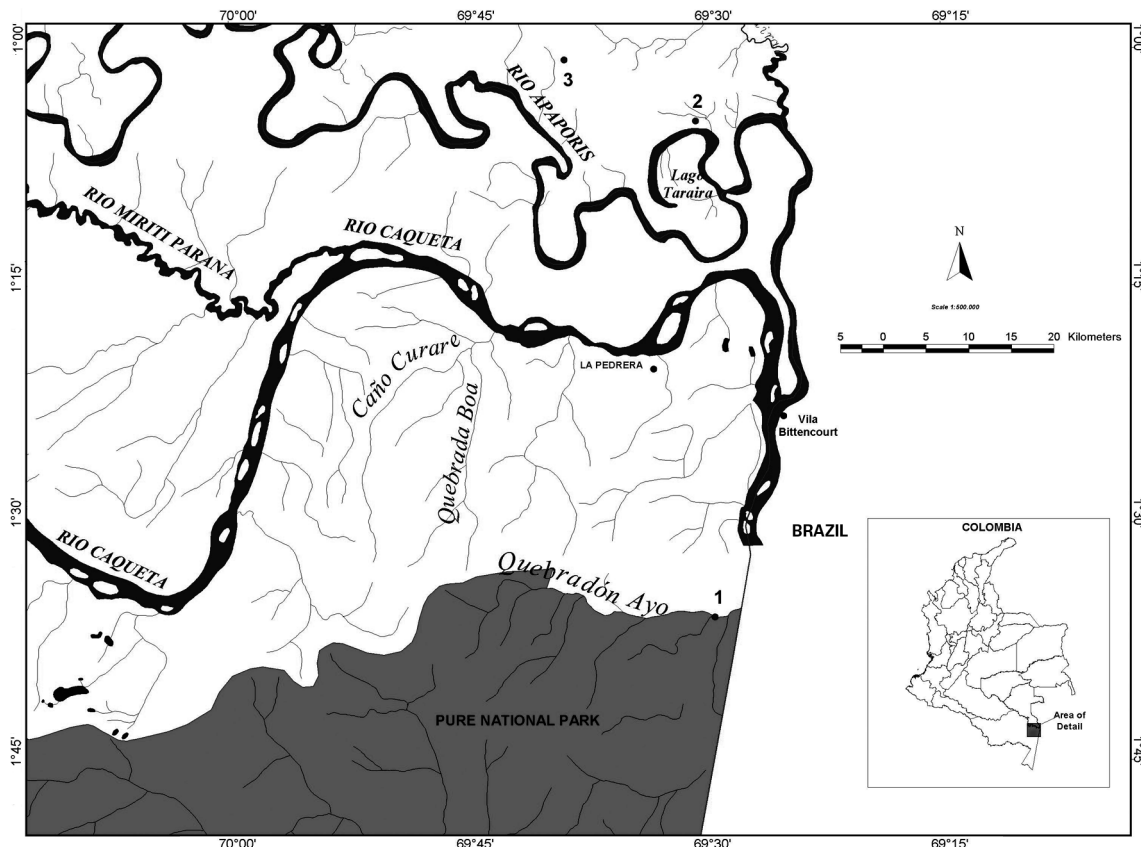
Previous studies on primate species richness and abundance in lowland Amazonia have shown that forest productivity is a key factor regulating primate biomass. Unflooded (hereafter 'terra firme'), oligotrophic forests, for example, harbour lower primate densities than the nutrient-rich, seasonally flooded forests along white-water rivers [Peres, 1997a, b, 1999b]. Bottom-up mechanisms regulating forest vertebrate populations, such as nutrient-dependent resource availability, influence the size of primate populations that a given area can sustain and should therefore be an important consideration in reserve design. The implications are that oligotrophic forest systems require larger reserves to maintain viable vertebrate populations than nutrient-rich forest systems.

Data on primate abundance and distribution are, therefore, required to support conservation planning in the Colombian Amazon area. Information on its primate population densities is, however, almost entirely lacking (but see Stevenson [1996], Defler [2001, 2003a, b]), as most primatological studies in this region have focused on the ecology of a particular species [Stevenson, 1992, 1998; Defler, 2001; Defler and Defler, 1996; Palacios, 1997, 2003; Palacios et al., 1997; Palacios and Rodríguez, 2001]. Here we describe the primate community structure at three terra firme forest sites of south-eastern Colombia. This study is part of an ongoing effort to document population densities of large vertebrates throughout this region. We present population density and biomass estimates, and discuss them in relation to other Amazonian forest sites surveyed to date.

## Methods

### *Sampling Sites*

Surveys were conducted at three terra firme forest sites of eastern Colombian Amazonia (fig. 1). The first was 10 km upriver from the mouth of the Quebradón el Ayo (1°35' S, 69°30' W), a small clear-water tributary of the Rio Caquetá (the Rio Japurá in Brazil), Department of Amazonas (fig. 1). The Ayo headwaters lie about 35 km upstream from our camp site and are at the northern boundary of the recently established Puré National Park. Heavy rainfall during the wet season (April–July) can cause unexpected flash floods of up to 4 m over 1–2 days. At this time, the high water level of the Rio Caquetá affects the Ayo discharge, temporarily inundating forest levees south of the stream. The nearest villages – La Pedrera, Colombia (~600 inhabitants), and Vila Bittencourt, Brazil (~400 inhabitants) – are 30 km north and 23 km north-east of the study area, respectively. Although Brazilians occasionally fish the Ayo along the extensive meanders of the lower reaches of the stream near the Rio Caquetá, hunting rarely takes place and is restricted to two clay saltlicks some 10 km south-west of the survey site. We met no hunters or fishers, and heard no gunshots, along the Ayo during the three field campaigns (2001–2003) of approximately 25 days each.



**Fig. 1.** Location of the three terra firme forest sites surveyed in the lower Rio Caquetá and Apaporis basins, south-eastern Colombian Amazonia: (1) Quebradón el Ayo, (2) Caparú Biological Station and (3) Caño Pintadillo. The shaded area on the border of Brazil indicates the boundaries of the recently decreed 988,980 ha Puré National Park.

The second survey site was 6 km upstream from the mouth of the Caño Pintadillo (1°02' S, 69°39' W), a clear-water creek flowing from the Serranía de Taraira to the Río Apaporis, a second-order black-water tributary of the Rio Caquetá. This area was in the Yaigójé-Apaporis Indigenous Reserve (or *resguardo*), and the nearest indigenous settlement was located about 25 km to the west along the opposite flank of the Serranía de Taraira. To our knowledge, there had been no hunting in the census area (confirmed by interviews with indigenous people and local field assistants). The only signs of human activity were two old fishing camps 1.5 km from the bank of the Apaporis and some fallen logs along the stream showing old chain-saw scars. Some 16 years ago, the Pintadillo was travelled by gold miners (*garimpeiros*) on their way to the Serranía de Taraira in search of a goldmine that was never found [E. Yucuna, pers. commun.].

The third site was the Caparú Biological Station (1°05' S, 69°31' W) in the Indigenous Conservation Area of the Yaigójé-Apaporis Reserve and on the northern margin of Taraira Lake, an oxbow of the Río Apaporis. Subsistence hunting was sporadic, but generally prevented by the protected status granted to this area by local indigenous authorities and the continuous presence of researchers at the station since 1983.

## Line-Transect Surveys

The line-transect is a two-dimensional sampling method [Burnham et al., 1980], which provides comparable population density estimates across both sites and species. We conducted censuses during April-May 2001 at the Quebradón el Ayo, March-April 2002 at Caño Pintadillo and November-December 2002 at Caparú. At each site, two transects of 5 km in length were cut and subsequently marked with flagging tape every 50 m. They were left to 'rest' for 1 day prior to censusing. The trails were walked simultaneously by two independent observers [Peres, 1997a, b], between 6.30 and 11.45 h as well as between 13.45 and 16.45 h (average speed of approx. 1.25 km/h), with brief stops (20 s) every 100 m to minimize background noise. Censuses were not carried out in the rain. To ensure spatial independence of observations, starting points of the trails were always more than 400 m apart from each other, and an angle greater than 90° was formed between any pair of trails. Observers walked slightly faster on return walks (approx. 1.6 km/h), but this did not affect detection probabilities. One-way cumulative census distances at Ayo, Pintadillo and Caparú were 200.7, 275 and 335 km, respectively. Return census effort (50.0 km at Ayo, 175.0 km at Pintadillo and 225 km at Caparú) provided additional sightings that contributed to the detection models. These detection events were considered independent from those in the morning, as a rest period of 2–2.5 h at the end of the trails allowed animals to redistribute themselves, and assured not seeing the same groups in the same places.

For most primate species, the detection probability in the morning is not very different from that in the afternoon, and analysing data from return censuses are only problematic for diurnal primate species (for example callitrichids) retiring to their sleeping site (or becoming less detectable) before 17.00 h [Peres, 1999a, b]. As return census walks never ended later than 16.45 h, it is unlikely that detection events of callitrichids present at one (Ayo) of the surveyed sites (*Cebuella pygmaea* and *Saguinus fuscicollis*) were missed because they become less detectable in the late afternoon.

At every encounter with primates we recorded the species, group size and height in the forest, location along transect, perpendicular distance from the transect to the first animal detected and the mean group spread. A maximum of 15 min was allocated to observations following each encounter which, in most cases, was sufficient to obtain a reliable group count.

## Population Density Estimates

Transect data were analysed with the DISTANCE software [Laake et al., 1993]. Group density estimates were obtained using either the hazard rate or half-normal models with a cosine adjustment [Buckland et al., 1993], on the basis of ungrouped perpendicular distances from transect to the first animal sighted. Detection events of animals heard, but far from the transect, were not included in the analysis. Whenever necessary we truncated 5% of the outlying perpendicular data and pooled data across different sites for those species with a small number of detection events, in order to strengthen the site-specific density estimates. For some species with an insufficient sample size, density estimates (D) were calculated using:

$$D = ND/L \ 2(ESW),$$

where D = group density (groups per square kilometre), ND = number of sightings for each species, L = cumulative transect length walked in each site, ESW = effective strip width, defined as the largest perpendicular distance observed for each species, but excluding obvious outliers.

This was the case for the white-fronted capuchin (*Cebus albifrons*), the squirrel monkey (*Saimiri sciureus*), the red howler (*Alouatta seniculus*) and the black-headed uakari (*Cacajao melanocephalus*), recorded 3 or less times at each site. For species living in large, uncohesive groups – for example, the woolly monkey (*Lagothrix lagothricha*), and *C.*

**Table 1.** Population density and biomass estimates for primate species censused in three Colombian Amazonian terra firme forests

Species	Ayo				Pintadillo				Caparú										
	MGS	n	SR	GD groups/ km <sup>2</sup>	ID ind./ km <sup>2</sup>	B kg/ km <sup>2</sup>	MGS	n	SR	GD groups/ km <sup>2</sup>	ID ind./ km <sup>2</sup>	B kg/ km <sup>2</sup>	MGS	n	SR	GD groups/ km <sup>2</sup>	ID ind./ km <sup>2</sup>	B kg/ km <sup>2</sup>	
<i>Saguinus fuscicollis</i>	5.6	16	0.64	3.02	16.9	5.24	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
<i>Callicebus torquatus</i>	2.6	7	0.35	2.63	6.8	6.52	2.8	10	0.22	1.71	4.8	4.6	3.1	28	0.5	3.1	9.6	9.2	9.2
<i>Saimiri sciureus</i>	18	1	0.05	0.63	11.3	8.47	10	3	0.1	0.54	5.4	4.05	18.1	10	0.18	0.17	3.1	3.1	9.6
<i>Cebus apella</i>	7.2	11	0.55	4.24	30.4	70.8	5.3	22	0.5	3.85	20.4	47.5	7	56	1	4.42	30.9	71.9	71.9
<i>Cebus albifrons</i>	10	1	0.05	0.25	2.5	5.4	9	3	0.07	0.02	1.8	3.9	9.3	6	0.1	0.39	3.6	7.8	7.8
<i>Pithecia monachus</i>	4	18	0.9	2.8	11	19.36	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
<i>Cacajao melanocephalus</i>	NC	NC	NC	NC	NC	NC	40	1	0.04	0.036	1.44	3.64	P	P	P	P	4.1 <sup>a</sup>	10.2	10.2
<i>Alouatta seniculus</i>	5	1	0.05	0.21	1.05	5.46	0	0	0	0	0	0	P	P	P	P	4 <sup>b</sup>	20.8	20.8
<i>Lagothrix lagothricha</i>	12.7	19	0.76	0.54	6.9	48.3	18.7	12	0.27	0.19	3.6	25.2	15.3	40	0.72	0.43	6.6	46.2	46.2
Total		74		14.3	86.9	169.5	51		6.35	37.4	88.9		140		8.51	61.9	175.7		

MGS = Mean group size; n = number of independent detection events for each species; SR = sighting rate; number of animals seen per 10 km walked; B = biomass; NC = the species does not occur at the site; P = the species occurs at the site but was not detected during actual census walks.

<sup>a</sup> Data from Defler [2001].

<sup>b</sup> Data from Palacios and Rodriguez [2001].

*melanocephalus* – which can spread out over hundreds of metres in the forest (occasionally >1 km), we further added one third of the mean group spread to the ESW estimated by DISTANCE in order to avoid high density estimates [Peres, 1997a]. Mean group sizes, derived from reliable group counts, were then multiplied by group density estimates in order to obtain mean population densities at each site. Crude population biomass densities were calculated using the mean body weight of a given species, defined as 80% of the average adult body weight of males and females of each species [Peres, 1993].

## Results

### *Primate Abundance and Biomass*

The aggregate population densities of diurnal primates at Pintadillo, Caparú and the Ayo were 37.4, 61.9 and 86.9 individuals km<sup>-2</sup>, respectively. A similar pattern was obtained for whole groups; the overall group density at the Ayo was more than double that at Pintadillo, and almost twice that at Caparú (table 1). With 2 exceptions (*L. lagothericha*, *S. sciureus*), the highest densities were recorded at Caparú, with the most pronounced differences between this site and Pintadillo. The density of woolly monkeys at Caparú was essentially the same as at the Ayo (6.6 vs. 6.9 individuals km<sup>-2</sup>), and squirrel monkeys were remarkably rare (3.1 individuals km<sup>-2</sup>). Densities of brown capuchins (*Cebus apella*) at Caparú and the Ayo were similar and about 30% higher than at Pintadillo. Estimated densities of *C. apella* were 1.8–3.8 times higher than the second most abundant species at any site. Howler monkeys were never seen or heard at Pintadillo. However, at least two groups were heard on a few mornings at the Ayo, but only one group was detected during censuses. We failed to hear or see any group of this species during the survey period, but a previous census and a study on habituated groups [Palacios, 1997, 2000] indicate that howler monkeys rarely vocalize at Caparú.

The total primate biomass estimated for the three sites was remarkably low for non-hunted Amazonian forests (Ayo: 170 kg km<sup>-2</sup>; Pintadillo: 89 kg km<sup>-2</sup>; Caparú: 176 kg km<sup>-2</sup>). The mean biomass for the three sites was only 145 kg km<sup>-2</sup>, representing 39.4, 20.7 and 47% of the total vertebrate biomass censused at each of these sites [Palacios, 2002; E. Palacios, unpubl. data].

## Discussion

### *Primate Abundance in Nutrient-Poor Forests*

The lower Rio Apaporis and Caquetá region of north-western Amazonia have a mean annual rainfall of 3,836 ± 486 mm (n = 11 years [Defler and Defler, 1996]) and are within one of the wettest areas of the entire Amazon basin. High rainfall has been related to low-productivity plant communities [Kay et al., 1997; Peres and Janson, 1999; Janson and Chapman, 1999]. Soils in this region are also notoriously poor in nutrients with a low to very low fertility and low exchange capacity for positive ions [IGAC, 1997, 1999; Defler, 2003; E. Palacios, unpubl. data]. Low primate biomass densities at these three oligotrophic Colombian sites would therefore appear to reflect limited resource availability, a pattern typical of terra firme forests throughout lowland Amazonia because of their geochemical characteristics and severe nutrient constraints [Irion, 1978]. An illustration of such low produc-

tivity in south-eastern Colombian Amazonia is provided by the extremely large home range (182 ha) used by a habituated group of red howler monkeys at Caparú Biological Station (lower Apaporis River), some 25 km south of the Pintadillo site [Palacios and Rodríguez, 2001]. This is the largest home range size ever documented in free-living howlers from over 65 studies of the ranging behaviour of the genus *Alouatta* from southern Mexico to northern Argentina [Peres, 1997a]. Woolly monkeys (*L. lagothericha*) and black-headed uakaries (*C. melanocephalus*) at Caparú also use very large home ranges [Defler, 1996, 2001].

The aggregate population density and biomass of diurnal primates at these forest sites are amongst the lowest ever recorded for non-hunted forests in Amazonia and throughout the Neotropics. The biomass estimate for Pintadillo was marginally higher than that recorded at a PDBFF Reserve, north of Manaus, Brazil (81 kg km<sup>-2</sup> [Rylands and Keuroghlian, 1988]), and slightly lower than that recorded for the Island of Maracá, Roraima, Brazil (105 kg km<sup>-2</sup> [Mendes-Pontes, 1994]), which represent some of the lowest primate biomass estimates for non-hunted Neotropical forests [Peres, 1999b]. The primate biomass at Pintadillo may have been slightly underestimated because red howlers were not observed during the surveys, although they were most likely present. Even if we assume that howler monkeys at Pintadillo are equally abundant as those at Caparú Biological Station (4 individuals km<sup>-2</sup> [Palacios and Rodríguez, 2001], which shares similar climatic and edaphic conditions [IGAC, 1999], the total primate biomass would be only 110 kg km<sup>-2</sup>, which is still extremely low for a non-hunted Amazonian forest. On the assumption that howlers are largely restricted to the margins of lakes and rivers, Defler [2003] reported an ecological density at Caparú for these riparian and lake edge habitats of 15 individuals km<sup>-2</sup>. Red howlers are considered to be habitat specialists during at least part of the year, making intensive use of the seasonally flooded Igapó forest during times of fruit scarcity [Palacios and Rodríguez, 2001]. A few widely scattered groups of howler monkeys can also be found in the unflooded forest matrix on high ground, as far as 1.4 km from river banks or lake edges. Density estimates based entirely on censuses restricted to lake and river edges may therefore be inappropriate in this case and are likely to provide an inflated group density estimate inconsistent with the distribution of this species at this site.

Our failure to detect red howlers at Pintadillo also illustrates the rarity of this species in Amazonian terra firme forests that are far removed from white-water rivers [Peres, 1997a]. The Pintadillo forest is not affected by seasonal floods from clear- or black-water rivers and is approximately 31 km from the nearest white-water river, the Río Caquetá. A low density of howlers was recorded even at the Ayo, located only 10 km from the Río Caquetá. This pattern is consistent with the hypothesis that both soil nutrient availability and the strength of rainfall seasonality affect foliage quality, which in turn constrains arboreal folivore densities in tropical forests. More seasonal, nutrient-rich forests often attain a higher howler monkey biomass [Peres, 1997a; Janson and Chapman, 1999]. The Colombian sites surveyed here are within one of the wettest regions of the entire lowland Amazon, and it rains for most of the year [IGAC, 1997, 1999]. More seasonal areas in Colombian Amazonia and neighbouring regions support far greater red howler monkey densities than those reported here (e.g. Tinigua National Park, 17–30 individuals km<sup>-2</sup> [Stevenson, 1996]).

Low densities of *Lagothrix* cannot be attributed to hunting pressure and are a distinctive feature of the primate communities at these sites. The higher density of woolly monkeys at the Ayo could be partly explained by the white-water river drainage and higher productivity of this site, although there was no difference in their densities between the Ayo and Caparú. While the floristic composition, and resulting spatial and temporal abundance of food resources, may have a large effect on the abundance and ranging ecology of primates at the three forests, higher densities of *Lagothrix* at the Ayo, which had been subjected to a history of very light hunting pressure, underlines the limited carrying capacity of forests on poor soils – particularly those associated with black-water rivers – to support a high biomass density of primates and other large vertebrates [Palacios, 2002]. The Colombian sites support woolly monkey densities 1.5–3.5 times lower than that at non-hunted terra firme sites of central-western Brazilian Amazonia [Peres, 1997a, b]. Density estimates for highly harvest-sensitive species such as woolly monkeys reported here are more comparable to lightly to moderately hunted forest sites in mesotrophic soils elsewhere in Amazonia [Peres, 1997a, b]. This provides an additional indication of the limited capacity of nutrient-poor forests in eastern Colombian Amazonia to sustain high densities of large-bodied primates.

On the basis of a census effort of 264 km carried out over 2 years, Defler [2003] estimated a density of 13.1 individuals km<sup>-2</sup> of *L. lagothricha* for Caparú, or almost twice that recorded in this study (table 1). The discrepancy between these density estimates could be simply attributed to the lack of a correction factor based on the mean group spread in Defler's estimate, as incorporated in this study, rather than an actual decline in the woolly monkey density. In fact, a density estimate for this species based on direct counts during many years and a detailed knowledge of his study group home range resulted in a density of 5.5 individuals km<sup>-2</sup> [Defler, 2003], which is more consistent with the density estimate presented here.

Population densities of small-bodied to mid-sized primates were similar to those of five other oligotrophic western Amazonian sites [Peres, 1990, 1997b]. In most cases, the mean densities we found for saddleback tamarin (*S. fuscicollis*), *S. sciureus*, the collared titi (*Callicebus torquatus*) and the monk saki (*Pithecia monachus*) fell within the range of values previously reported for other parts of the Amazon. Densities of brown capuchins (*C. apella*) at the three Colombian sites (20.4–30.9 individuals km<sup>-1</sup>) were higher than those of Brazilian Amazonia, whereas the opposite was true for white-faced capuchins, *Cebus albifrons* (southeastern Colombia: 1.8–3.6 individuals km<sup>-1</sup>; western Brazilian Amazonia: 2.1–20.2 individuals km<sup>-1</sup> [Peres, 1997b]). The explanation for this is not apparent, but Defler [2003] has suggested that some competitive displacement between *C. apella* and *C. albifrons* may account for the lower densities of the latter whenever they occur at a local scale.

## Conservation Implications

Our results agree with other studies presenting evidence that oligotrophic forests in lowland Amazonia typically sustain low biomass densities of primates and other mid-sized to large vertebrates [Freese et al., 1982; Emmons, 1984; Peres,



1997b, 1999a, b, 2000]. This finding is particularly important considering the disproportionately large representation of terra firme forest in the Amazon basin (approx. 95%) and the fact that many forest vertebrates are increasingly threatened by human activities in vast forest tracts of Colombian Amazonia. The density estimates presented here are unlikely to be representative of western Colombian Amazonia, where more nutrient-rich and recently eroded soils along the foothills of the Andes appear to support more productive forests [IGAC, 1999]. The low primate abundance in eastern Colombian Amazonia is almost certainly related to the highly weathered, nutrient-poor upland soils that predominate in this region [IGAC, 1999; Lips and Duivenvoorden, 1996]. Low population densities are often a consequence of greater spatial requirements, an important aspect when considering reserve design. Unfortunately, few studies have examined the relationship between forest productivity, primate abundance and a wide range of population responses to human habitat disturbance and hunting.

Non-indigenous rural folks and tribal and non-tribal indigenous peoples are allowed to harvest forest wildlife in Colombian protected areas for their subsistence [Rojas and Castaño, 1990, 1992]. However, little is known about the impact of hunting within or outside protected areas. For example, preliminary data indicate that hunting has drastically reduced the densities of large primates and other large vertebrates within indigenous reserves (or *resguardos*) of Colombian Amazonia [E. Palacios, unpubl. data], and similar results have been reported for Utría National Park of the Colombian Chocó [Ulloa et al., 1996; Rubio, 1996]. *Resguardos* of varying sizes and with varying levels of non-timber resource extraction account for over 52% of the 28,662,000 ha of the eastern Colombian Amazon area. It is likely that strictly protected areas will come under mounting extractive pressure as *resguardos* become systematically depleted of large game, such as the large ateline primates. This underlines the importance of obtaining baseline data on the abundance and distribution of the harvest-sensitive vertebrates. Ideally, a long-term survey programme should be implemented on selected sites, including areas given strict protection according to Colombian legislation (i.e. National Parks and Reserves) and the large *resguardos*, which also play an important role in regional forest conservation. This programme would eventually provide information upon which conservation actions could be defined and implemented. Much remains to be done to assure the persistence of this species-rich biological assemblage, and appropriate baseline information is vital for effective conservation planning and implementation by local, regional and national stakeholders.

## Acknowledgements

The Margot Marsh Biodiversity Foundation, the Centre for Applied Biodiversity Science at Conservation International and the British Council through a Chevening studentship at the University of East Anglia provided support for this study. Thanks go to Adriana Rodríguez for help during the Ayo survey, and continuous support, and to Dr. Anthony Rylands and an anonymous reviewer for providing useful comments on the manuscript. We also thank Elías, Juan and Julián Yucuna, José Acevedo, Hernán Tanimuca and Jaime Pinzón, for their invaluable assistance during fieldwork.

## References

- Aquino R (1988). Preliminary surveys on the population of *Cacajao calvus ucayalii*. *Primate Conservation* 9: 24–26.
- Bennett CL, Leonard S, Carter S (2001). Abundance, diversity, and patterns of distribution of primates on the Tapiche River in Amazonian Peru. *American Journal of Primatology* 54: 119–126.
- Buckland ST, Anderson DR, Burnham KP, Laake JL (1993). *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London. 446 pp.
- Burnham KP, Anderson DR, Laake JL (1980). Estimation of density from line-transect sampling of biological populations. *Wildlife Monographs* 79: 1–202.
- Chapman CA (1995). Primate seed dispersal: Coevolution and conservation implications. *Evolutionary Anthropology* 4: 74–82.
- Chapman CA, Chapman LJ (1995). Survival without dispersers: Seedling recruitment under parents. *Conservation Biology* 9: 675–678.
- Chapman CA, Peres CA (2001). Primate conservation in the new millennium: The role of scientists. *Evolutionary Anthropology* 10: 16–33.
- Clarke MR, Zucker EL (1994). Survey of the howling monkey population at La Pacifica: A seven year follow-up. *International Journal of Primatology* 15: 61–73.
- Defler TR (1996). Ranging and the use of space in a group of woolly monkeys (*Lagothrix lagothricha*) in the NW Amazon of Colombia. *International Journal of Primatology* 8: 289–302.
- Defler TR (2001). *Cacajao melanocephalus ouakary* densities on the lower Apaporis River, Colombian Amazon. *Primate Report* 61: 31–36.
- Defler TR (2003a). *Primates de Colombia*. Tropical Field Guides Series 24, Conservación Internacional Colombia.
- Defler TR (2003b). Densidad de especies y organización espacial de una comunidad de primates: Estación Biológica Caparú, Departamento del Vaupés, Colombia. In *Primatología del Nuevo mundo* (Pereira V, Nassar F, Savage A, eds.), pp 21–37. Bogotá, Fundación Araguatos.
- Defler TR, Defler S (1996). Diet of a group of *Lagothrix lagothricha* in southeastern Colombia. *International Journal of Primatology* 17: 161–189.
- Eisenberg JF, Thorington RW (1973). A preliminary analysis of a Neotropical mammal fauna. *Biotropica* 5: 150–161.
- Eisenberg JF, O'Connell MA, August PV (1979). Density, productivity, and distribution of mammals in two Venezuelan habitats. In *Vertebrate Ecology in the Northern Neotropics* (Eisenbergh JF, ed.), pp 187–207. Washington, Smithsonian Institution Press.
- Emmons LH (1984). Geographic variation of densities and diversities of non-flying mammals in Amazonia. *Biotropica* 163: 210–222.
- Estrada A (1982). Survey and census of howler monkeys (*Alouatta palliata*) in the rainforest of Los Tuxtlas, Veracruz, Mexico. *American Journal of Primatology* 2: 363–372.
- Freese CH, Helme PG, Castro N, Whitesides G (1982). Patterns and determinants of monkey densities in Perú and Bolivia, with notes on distributions. *International Journal of Primatology* 3: 53–90.
- IGAC (1997). *Zonificación Ambiental para el Plan Modelo Colombo-Brasilero (Eje Apaporis-Tabatinga: PAT)*. Bogotá, Instituto Geográfico Agustín Codazzi.
- IGAC (1999). *Paisajes fisiográficos de Orinoquia-Amazonia (ORAM) Colombia*. Análisis Geográficos 27–28. Bogotá, Instituto Geográfico Agustín Codazzi.
- Irion G (1978). Soil infertility in the Amazonian rainforest. *Naturwissenschaften* 65: 515–519.
- Janson CH, Chapman C (1999). Resources and primate community structure. In *Primate Communities* (Fleagle JG, Janson CH, Reed KE, eds.), pp. 237–267. Cambridge, Cambridge University Press.
- Kay RF, Madden RH, van Schaik CP, Higdon D (1997). Primate species richness is determined by plant productivity: Implications for conservation. *Proceedings of the National Academy of Sciences* 94: 13023–13027.
- Laake J, Buckland S, Anderson D, Burnham K (1993). *Distance sampling: Abundance Estimation of Biological Populations – Distance Users Guide version 2.0*. Fort Collins, CO, Colorado Co-Operative Fish and Wildlife Research Unit, Colorado State University.
- Lips JM, Duivenvoorden JF (1996). Regional patterns of well drained upland soil differentiation in the middle Caquetá basin of Colombian Amazonia. *Geoderma* 72: 219–257.
- Mendes-Pontes AR (1994). *Environmental Determinants of Primate Abundance in Maracá Island, Roraima, Brazilian Amazonia*. MPhil thesis, Cambridge University, Cambridge.
- Norconk MA, Grafton BW, Conklin-Brittain NL (1998). Seed dispersal by Neotropical seed predators. *American Journal of Primatology* 45: 103–126.
- Palacios E (1997). *Limitantes ecológicas de Alouatta seniculus en la Amazonía Colombiana*. Final report to Colciencias. Bogotá, 89 p.
- Palacios E (2000). Infanticide following immigration of a pregnant red howler, *Alouatta seniculus*. *Neotropical Primates* 8(3): 104–107.

- Palacios E (2002). *Large Vertebrate Densities in Undisturbed Amazonian Forests: Implications for Minimum Spatial Requirements of Viable Populations*. MSc dissertation, University of East Anglia, Norwich.
- Palacios E (2003). Uso del espacio por *Alouatta seniculus* en el bajo río Apaporis, Amazonía Colombiana. In *Primatología del Nuevo mundo* (Pereira V, Nassar F, Savage A, eds.), pp 85–95. Bogotá, Fundación Araguatos.
- Palacios E, Rodríguez A (2001). Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a southeastern Colombian rainforest. *American Journal of Primatology* 55: 233–251.
- Palacios E, Rodríguez A, Defler T (1997). Diet of a group of *Callicebus torquatus lugens* (Humboldt, 1811) during the annual resource bottleneck. *International Journal of Primatology* 18: 503–522.
- Peres CA (1990). Effects of hunting on western Amazonian primate communities. *Biological Conservation* 54: 47–59.
- Peres CA (1993). Structure and spatial organization of an Amazonian terra firme forest primate community. *Journal of Tropical Ecology* 9: 259–276.
- Peres CA (1997a). Effects of habitat quality and hunting pressure on arboreal folivore densities in Neotropical forests: A case study of howler monkeys (*Alouatta* spp.). *Folia Primatologica* 68: 199–222.
- Peres CA (1997b). Primate community structure at twenty western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 13: 381–405.
- Peres CA (1999a). Evaluating the sustainability of subsistence hunting at multiple Amazonian forest sites. In *Hunting for Sustainability in Tropical Forests* (Robinson JG, Bennett EL, eds.), pp 31–56. New York, Columbia University Press.
- Peres CA (1999b). Effects of subsistence hunting and forest types on the structure of Amazonian primate communities. In *Primate Communities* (Fleagle JG, Janson C, Reed KE, eds.), pp 268–283. Cambridge, Cambridge University Press.
- Peres CA (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14: 240–253.
- Peres CA, Janson CH (1999). Species coexistence, distribution, and environmental determinants of neotropical primate richness. A community level zoogeographic analysis. In *Primate Communities* (Fleagle JG, Janson CH, Reed KE, eds.), pp 55–74. Cambridge, Cambridge University Press.
- Peres CA, van Rossmalen GM (1996). Avian dispersal of mimetic seeds in *Ormosia lignivalvis* (Leguminosae: Papilionaceae): Deceit or mutualism? *Oikos* 75: 249–258.
- Rojas M, Castaño C (1990). *Áreas protegidas de la cuenca del Amazonas: diagnóstico preliminar de su estado actual y revisión de las políticas formuladas para su manejo*. Bogotá, Instituto Nacional de Recursos Naturales y Renovables.
- Rojas M, Castaño C (1992). Conservación y manejo de áreas protegidas en la Amazonía Colombiana. In *Amazonia Colombiana: diversidad y conflicto* (Andrade GI, Hurtado A, Torres R, eds.). Bogotá, Colciencias, Conia y Cega.
- Rubio H (1996). Diagnósticos de uso de fauna y de espacios de uso con las comunidades indígenas Embera y la Oweqa en la zona de influencia del Parque Nacional Natural Utría, Chocó. In *Investigación y manejo de fauna para la construcción de sistemas sostenibles* (De la Cruz H, ed.). Cali, Cipav.
- Rylands AB, Keuroghlian A (1988). Primate populations in continuous forest and forest fragments in Central Amazonia. *Acta Amazonica* 18: 291–307.
- Stevenson PR (1992). Diet of woolly monkeys (*Lagothrix lagothericha*) at La Macarena, Colombia. *Field studies of New World monkeys La Macarena Colombia* 6: 3–14.
- Stevenson PR (1996). Censos diurnos de mamíferos y algunas aves de gran tamaño en el Parque Nacional Tinigua, Colombia. *Universitas Scientiarum* 3: 67–81.
- Stevenson PR (1998). Proximal spacing between individuals in a group of woolly monkeys (*Lagothrix lagothericha*) in Tinigua National Park, Colombia. *International Journal of Primatology* 19: 299–311.
- Terborgh J (1983). *Five New World Primates: A Study of Comparative Ecology*. Princeton, Princeton University Press.
- Terborgh J (1990). Seed and fruit dispersal – Commentary. In *Reproductive Ecology of Tropical Forest Plants* (Bawa KS, Hadley M, eds.). Paris, Parthenon Group.
- Ulloa A, Rubio H, Campos C (1996). Conceptos y metodologías para la preselección y análisis de alternativas de manejo de fauna de caza con indígenas Embera en el Parque Nacional Natural Utría PNNU, Chocó, Colombia. In *Manejo de fauna en comunidades rurales* (Campos C, Ulloa A, Rubio H, eds.). Bogotá, Fundación Natura.