ZOOLOGÍA

SPECIES RICHNESS, DENSITIES AND BIOMASS OF NINE PRIMATE COMMUNITIES IN EASTERN COLOMBIA

Thomas R. Defler*

ABSTRACT

Defler T. R.: Species richness, densities and biomass of nine primate communities in eastern Colombia. Rev. Acad. Colomb. Cienc. **37** (143): 253-262, 2013. ISSN 0370-3908.

This is a preliminary comparison of nine primate communities from Colombian Llanos and Amazonia, including three communities in Llanos gallery forest and six communities from the Amazon basin. Total primate biomass in the extreme eastern Colombian Amazon is considerably lower than reported at other sites at longitudes of 5°-8° south of the Amazon-Solimões in Brazil and Peru. Primate richness at the Colombian sites (up to 10 sympatric species) was below that found at other sites in Brazil and Peru (up to 14 sympatric species), where the highest neotropical species richness seems to be situated. Although primate species richness was reduced in the Colombian gallery forest sites, biomass per community surpassed *terra firme* moist eastern forest sites, but was comparable to biomass of the only black-water igapó forest in this study.

Key words. primate communities, primate densities, primate biomass, primate species richness, Colombian Amazon.

RESUMEN

Este estudio presenta una comparación preliminar de nueve comunidades de primates en Colombia que incluye tres comunidades en bosque de galería en los Llanos Orientales y seis comunidades en la cuenca amazónica. La biomasa de primates en la Amazonia colombiana fue considerablemente más baja en comparación con las biomasas reportadas en otros estudios en longitudes entre 5°- 8° al sur del río Amazonas-Solimões en Brasil y Perú. La riqueza de primates en los sitios colombianos (hasta 10 especies simpátricas), también fue más baja en comparación con otros sitios localizados en Brasil y Perú (hasta 14 especies simpátricas), donde la riqueza más alta de primates neotropicales parece estar concentrada. Aunque la riqueza de especies de primates se redujo en los bosques de galería en Colombia, la biomasa por comunidad sobrepasó los sitios de bosques húmedos del oriente de *terra firme*, pero es comparable con la biomasa reportada en el único sitio localizado en bosque inundable por aguas negras (*igapó*) de este estudio.

Palabras clave. Comunidades de primates, densidades de primates, biomasa de primates, Amazonia colombiana.

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* Departamento de Biología, Universidad Nacional de Colombia, Bogotá, Colombia. E-mail: thomasdefler@gmail.com

Introduction

Data on the diversity and density of neotropical primates has multiplied in the past few years, providing a clearer idea of the great variability of primate communities in Amazonia and elsewhere. **Peres & Palacios** (2007) compare 101 neo-tropical sites having data for mid-sized to large vertebrate species, including primates. Moreover, **Peres** (2008) compares soil fertility, including 96 Amazonian forest sites. That analysis suggests that soil fertility had a significant positive effect on primate biomass, while hunting pressure has a ne-gative effect on the primate community. More recent reports show great variability from species poor and low-density si-tes to communities with 14 syntopic species and high densi-ties (**Endo et al.**, 2009).

Since primates are often considered flagship-species and are used to evaluate the health of forest ecosystems, as well as providing a high percentage (24%-40%) of frugivore bio-mass, their importance to tropical forests has often been underlined (**Dietz et al.,** 1994; **Defler**, 2010; **Palacios & Peres**, 2005; **Maldonado**, 2012). This makes them one of the most suitable candidates for regional-scale ecological comparisons, as they represent one of the most important biomass components of arboreal vertebrate assemblages (**Emmons**, 1984; **Peres**, 2008). Primates´ ecological roles in seed dispersal, as well as prey and as predators are in-creasingly appreciated for their impact on diversity (**Howe & Smallwood**, 1982; **Garber & Lambert**, 1998; **Stevenson et al.,** 2002; **Stevenson & Pilar Medina**, 2003; **Chapman & Russo,** 2007). Additionally, these charismatic animals are effectively used as flagship species for habitat conservation (**Dietz, et al**. 1994; **Maldonado**, 2012).

In this study I calculate and compare primate diversities in eastern Colombian Amazonian forest with that of some sites in the Colombian Llanos. I also compare eastern Colombian Amazonian sites (over 3200 mm precipitation) with some other selected Amazonian non-Colombian sites. Various studies show correlations of increases of primate species ri-chness and plant diversity up to about 2,500 mm of annual precipitation and a decrease in rates of primate and plant species richness inversely correlated with higher precipita-tion (**Peres & Janson**, 1999; **Gentry**, 1982, 1989; **Kay et al**. 1997). Eastern Colombian Amazonian forests typically show annual precipitation above about 3200 mm.

A priority of this study is to characterise primate communi-ties unaffected by human activities to provide baseline data for eastern Colombia. Information on intact primate commu-nities is especially important because the alterations caused by hunting and habitat disturbance make it difficult to draw meaningful ecological conclusions, since some comparisons

are distorted by human interference (**Voss & Emmons**, 1996; **Peres**, 1993, 2008). In this study I attempt to show why pri-mate biomass and species richness is so much lower through-out the Eastern Colombian Amazon where precipitation reaches levels considerably over 3,000 mm as compared to other high biomass and species rich sites that are especially found south of the Amazon river, although in Colombia more elevated primate biomass is reported elsewhere. Compari-sons in this study with the Colombian Llanos also underline fundamental differences from eastern Colombia, especially with species like *Alouatta seniculus* and *Cebus apella*.
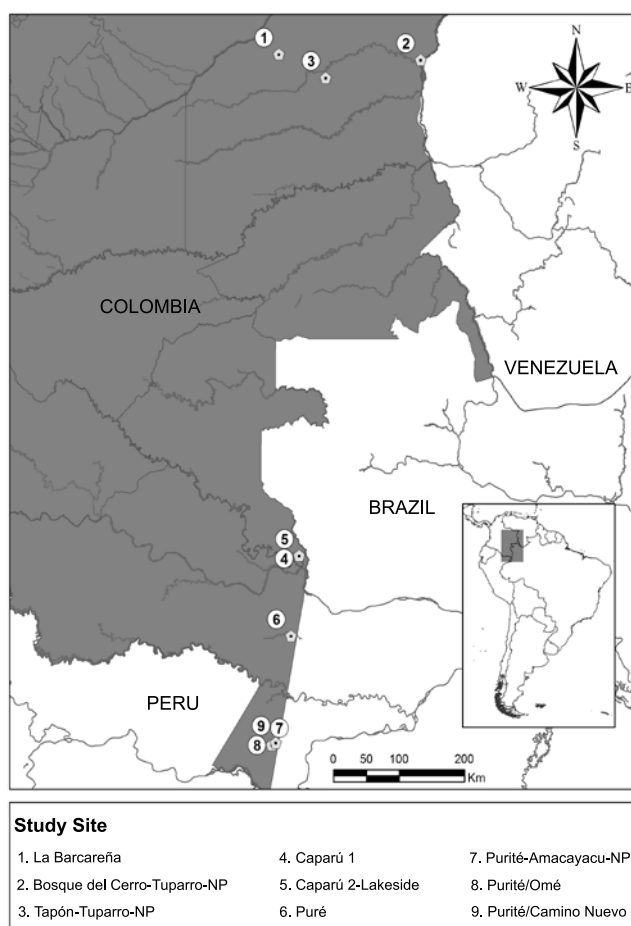
Methods

Study sites

I censused three sites from the eastern Colombian llanos and six Amazonian sites in southern Colombia (Fig. 1). Data across these locations were obtained between the years 1977 – 2008, with the object of making a comprehensive, com-parative study of primate density in eastern Colombia. Nine sites (1-9) were located in areas with minimal or no human intervention. "Igapó forest" is used as a term in the sense of Pires & Prance (1985) for blackwater and clearwater rivers, which is the case for the Apaporis river, which has origins of both blackwater and clearwater affluents (**Hoorn et al.,** 2010). Although the Apaporis river has been considered a blackwater river by many (**Goulding et al**. 2003; **Correa**, 2008; **Davis**, 1996; Umaña et al. 2011) it does not show all the characteristics of igapó from the central Amazon, espe-cially the highly sandy soils of the flooded forests, especially because of its mixed origins, underlined by **Junk & Furch** (1985). The Apaporis has its origins in a southern extension of the Llanos Orientales and in its lower parts, including the Lago Taraira, the waters are sometimes blackwater and so-metimes turbid and muddy.

In the Caparú surveys (sites 4-5), two different habitats: (upland forest and seasonally flooded igapó forest) were censused. Both forest types were used by the same primate population. In the Purité river surveys, sites 7 & 8 were se-parated by about 2 km, although they were on opposite sides of the river. Sites 8 & 9 were separated by about 8.3 km and were on the same side of the river. All the Amazonian sites were located in a zone of very high precipitation above 3,200 mm.

Following **Peres** (1997), these non-hunted sites (1-9) showed no evidence of hunting or rubber tree (*Hevea* spp.) exploita-tion. The extremely isolated Puré and Purité Rivers are both well over 100 km upriver from their respective river mouths. The only possibility of significant primate hunting would

Study Site

1. La Barcareña	4. Caparú 1	7. Purité-Amacayacu-NP
2. Bosque del Cerro-Tuparro-NP	5. Caparú 2-Lakeside	8. Purité/Omé
3. Tapón-Tuparro-NP	6. Puré	9. Purité/Camino Nuevo

Figure 1. Map of the 13 study sites located in the Colombian Llanos and Colombian Amazon

have been over 30 years ago, when primates were used as bait in commercial hunting of spotted cats (**Defler**, 1983). Earliest censuses followed **NRC** (1981) and were later conducted according to **Peres** (1993, 1999) and **Buckland** *et al*. (2001) using standardised line-transect census protocols for all census sites studied in recent years.

Census techniques

Gallery forests.

Densities at El Tuparro (2-3) were determined by direct count, since the main research included many hours habituating and observing the primates of those clearly-defined forests (**Defler & Pintor**, 1985). At La Barcareña I walked a previously cut 5 km transect and measured perpendicular distances by first measuring the distance to the first observed animal(s) and the angle between the observation distance

and the transect, in order to convert to perpendicular distance to the group. Perpendicular distance to first animal observed were measured by tape. Density was calculated using (D = ND/L 2(ESW)) where D= group density, ND = number of sightings per species, L = cumulative transect length walked at each site, ESW = effective strip width or largest perpendicular distance observed for each species excluding outliers. There is a controversy whether detection distance should be to the center of the group or to the first animal, but in practice one most easily focuses on the first animal detected, since the group center is not easily identified. For detection widths I drew a frequency distribution of the various distances where groups had been observed, then truncated it at the point where observations fell off; multiplying this by two yielded a detection width for calculating densities as follows :

Amazonian sites

For Caparú (4-5) I used a five km transect perpendicular to lake´s edge for the no. 4 site and a 10 km canoe transect (equals 5 km census for both sides of the lake route) for the *igapó* habitat. The line transect censuses were carried out over 2.5 years, twice a month, for a total distance census of 476 km including 212 km of censuses by canoe in *igapó* and 264 km of censuses in *terra firme* forests. Group size used for each detection event of *Lagothrix* was 24 individuals rather than a direct count, as 24 was the known count of the two groups most commonly detected along the transect route and no local group was less than 20. This was considered to provide a more accurate estimate as long as there was no danger of counting subgroups as separate groups. The census data were analysed using DISTANCE 4.0 software when an adequate sample was available. Low densities required the use of detection distances for the analysis (as described above), since there were not enough observations for the use of DISTANCE. Some species were never detected during censuses though their presence was confirmed. For example, during inland transect censuses at Caparú *Cacajao melanocephalus* was never detected, though densities have been reported for this site using other techniques (**Defler**, 2001). Caparu's data set for *Lagothrix* was analysed using both methods and compared to a previous direct count (**Defler**, 1983).

Robust estimates may not be feasible for species that are rarely observed. Nevertheless, estimates are presented here for most species where adequate data have been collected. In order to improve the reliability of the estimates by avoiding outliers, perpendicular distances were truncated at the point where detection events fell off and this distance was doubled for the analysis. To estimate biomass, I multiplied the mean body mass per km^2 for each species by 80% of average adult weights, following **Peres** (1997).

Soil characteristics were determined for sites no. 1 and 4 -9 via four widely separated collections per site and values were averaged. Physico-chemical characteristics were determined at the soil laboratory of the Instituto Augustín Codazzi in Bogotá for micronutrients. Methods used at the Laboratorio Nacional de Suelos (IGAC) can be reviewed at the following link (http://www.igac.gov.co/wps/wcm/connect/ dd516280464b0aab8a70cb525e257f7f/LISTADO+DE+ME TODOS+EMPLEADOS+EN+EL+LABORATORIO+NAC IONAL+DE+SUELOS.pdf?MOD=AJPERES).

Results and Discussion

Primate species richness in nine different communities (Table 3) varied from 2-10 species and estimated primate community biomass ranged from 87 along the Puré river to 387

Table 1. Characteristics of the nine sampling sites included in this study

Census Site	Forest Type[1]	Hunting pressure	No. of Species[2]	Census Period	Census Effort	Density[3] (ind/km²)	Biomasa[3] (kg/km²)
1. La Barcareña 5º24'46"N-69º47'44"W	GF	None	2	March-1995	50	114	387
2. Bosque del Cerro-Tuparro-NP[4] 5°20′20.9"N-67°50′43.5"W	GF	None	3	Jan-June-1977	67	66	190
3. Tapón-Tuparro-NP 5º06'33.8"N-69º08'58"W	GF	None	4	Aug-Dec-1977	56	77	370
4. Caparú 1 1º04'19.4"S-69º30'56.6"W	OTF	None	8	1984-1987	264	48.2	133
5. Caparú 2-Lakeside 1°05′02"S-69º30′53.24"W	*Igapó*	None	8	1984-1987	212	97.1	215
6. Puré 2º07'16.2"S-69º37'31.2"W	OTF	None	10	Nov – Dec-1999	50	47.9	87
7. Purité-Amacayacu-NP 3º32'0.2"S-69º54'16.3"W	OTF	None	9	2000-2001	321	61	114
8. Purité/Omé 3º32'09.8"S-69º53'27.2.6"W	OTF	None	9	2000-2002	370	66.1	161
9. Purité/Camino Nuevo 3º30'7.92"S-69º50'8.85"W	OTF	None	9	2002-2003	220	61.2	118

[1]   **Forest Type**: **GF**: Gallery Forest-Llanos; **OTF**: Oligotrophic *terra firme* forest adjacent to black or clear water sources; *Igapó*: seasonally flooded forest by black water.
[2]   Number of primate species including *Aotus* spp.
[3]   Density and biomass of diurnal primates only
[4]   **NP**: National Park;
[5]   **SANP**: Southern Amacayacu National Park

Table 2. Soil properties from seven census sites, compared to high primate biomass site along the Duda river, Meta

(mEq/100g)

	%Sand	%Silt	%Clay	PH	Al	Ca	Mg	K	Na	P (P₂O₅)	CEC
Barcareña	37	43	20.0	3.93	3.35	0.16	0.30	0.33	0.06	1.6	4.20
Caparú1	40	39.5	20.5	4.2	3.35	0.20	0.20	0.12	0.06	0.1	3.93
Caparú2	15	18	67.0	4.9	9.6	0.20	0.20	0.15	0.10	0.2	10.25
Puré	45	36	19.0	3.6	4.73	0.26	0.20	0.20	0.02	0.3	5.40
Purité-Amacayacu NP	75	17	7.5	3.45	2.45	0.13	0.11	0.10	0.02	0.3	2.80
Purité-Omé	51	23.3	26.0	3.53	5.15	0.22	0.25	0.19	0.02	0.5	5.83
Purité-Camino Nuevo	34	36.6	39.3	3.52	8.26	0.13	0.20	0.18	0.04	0.3	8.82
Duda river*	-	-	-	5.0	-	13.5	8.45	15.7	23.5	1.5	-

CEC = catión exchange capacity
P= parts per million
*Hirabuki & Izawa, 1990

Table 3. Primate community censuses in eastern Colombia expressed as number of groups observed / 10 km of census trail (SR); number of individuals/km² (D); kilograms of biomass/km² (B); figures in brackets correspond to direct count.

Primate species		1. La Bar-careña	2. Bosque deTomás	3. Tapón Tuparro NP	4. Caparú 1	5. Caparú2-Lakeside	6. Puré NP	7. Purité ANP	8. Purité-Omé	9. Purité-Camino Nuevo
Large body size (>4.0 kg)										
Lagothrix lagothricha	SR				0.53	0.57	0.2	0.32	0.54	0.35
	D	-	-	-	13.1	13.7	4.8	9.7	13.1	6.9
	B				91.1	95.3	33.4	67.5	91.2	48
Aloutta seniculus	SR	3.7		1.8		1.32			0.135	0.09
	D	42.5	[30]	[30]	+	15	+	+	1.4	9
	B	221	119.6	140		78			5.8	4.7
Medium body size (1.5 - 4.0 kg)										
C acajao melanocephalus	SR					0.84				
	D	-	-	-	[4.15]	12	-	-	-	-
	B				10.6	30.7				
Cebus apella	SR	4.5		5.1	0.53		0.6			
	D	71.5	-	[19]	8	+	9	-	-	-
	B	166		87.5	18.6		20.9			
Cebus albifrons	SR					0.1	0.2	0.32	0.51	0.48
	D	-	36	-	+	2.2	4.4	6.8	15.8	8.2
	B		79.2			4.8	9.7	15	34.8	18
Pithecia monachus	SR						0.4	0.96	0.65	1.22
	D	-	-	-	-	-	4	10	7.6	14.5
	B						7	17.6	13.4	25.5
Small body size (<1,5 kg)										
Saimiri sciureus	SR				0.3	0.24	0.6	0.39	0.24	0.26
	D	-	-	-	8.85	6	17.7	11.5	10.5	8.5
	B				6.64	5.8	13.2	8.6	8	6.4
Callicebus torquatus	SR			3.1	0.68			0.06	0.16	1.18
	D	-	-	28	6.08	+	+	9	2.7	12.7
	B			26.9	5.8			0.86	2.6	12.2
Aotus spp.		-	+	+	+	+	+	+	+	+
Saguinus fusci-collis	SR						0.8			
	D	-	-	-	-	+	8	-	-	-
	B						2.5			
Saguinus nigri-collis	SR							1.32	1.08	1.83
	D	-	-	-	-	-	-	14	15	9.5
	B							4.76	5.1	3.23
Cebuella pyg-maea	SR									
	D	-	-	-	-	-	+	+	+	+
	B									

Symbols: (-) The species does not occur; (+) The species is present but was not detected during census.

kg/km² in a pristine gallery forest (Table 1). Densities of total individuals of all species varied from 47.9 – 114 individuals/km². These are modest numbers when compared to sites having high densities and many individuals, such as seen in studies by **Janson & Emmons,** 1990; **Puertas & Bodmer,** 1993; **Stevenson,** 1996; **Peres,** 1997; **Haugaasen & Peres,** 2005; **Endo *et al*.,** 2008 and others. The Colombian llanos gallery forest sites 1-3 had the highest biomass estimates registered in this study, while they had the lowest species richness (2, 3, 4 species) mostly due to *Alouatta* and *Cebus* species (either *C. apella* or *C. albifrons*); but site 2, a gallery forest, also exhibited one of the two highest densities of *Ca-*

llicebus torquatus calculated. In Colombia the highest densities and biomass known is found on the Duda river (Meta) in piedmont forest where some soil characteristics are known (**Stevenson,** 1996; Table 2).

Eastern Colombian Amazon sites in this study had much less primate biomass than the Llanos sites or the Duda river, except for the seasonable floodable igapó forest site at Caparú (no. 5). In fact, many un-hunted Amazonian sites in eastern Colombia had extremely low primate biomass and density of individuals (sites 4,6,7,8,9). The data broadly agree with density and biomass data collected by Palacios and Peres for the same region (**Palacios & Peres,** 2005; Table 4).

Soil characteristics for inland Amazonian sites in eastern Colombia (Table 2) showed extremely low fertility, including very low values for calcium, phosphorus, nitrogen and potassium, elements necessary for plant growth and probably at least partially explains the low biomass (**Jordan,** 1985; **Hirabuki & Izawa** 1990; **Peres,** 2008). Low phosphorus levels especially contrasted highly and significantly with high phosphorus and high biomass levels measured at La Barcareña and at the Duda river piedmont forest site in the western Amazon (Table 2; **Hirabuki & Izawa,** 1990). Very high rainfall (from 3200 mm in the south to 3950 mm) in Caparú in this part of eastern Colombia has washed soils causing low nutrient availability at all sites in this part of the Colombian Amazon.

The exception is the seasonally flooded igapó forest at Caparú, which nevertheless supports high primate biomass, especially during highwater in April-July. Here one must assume that the yearly influx of nutrients supports a high seasonal density of frugivorous primate species due to very high seasonal fruit and leaf production at that time (Figure 2a,b).

Comments on selected species

In Caparú I obtained three different densities for *Lagothrix*: 5.5 individuals/km² from the direct count method (**Defler,** 1989); 11 individuals/km² using line transects, analysed using as described above [see **Defler,** 1989]; and 13.1 individuals/km² using the same data base analysed with DISTANCE (**Defler,** 2003). **Palacios & Peres** (2005) censused the same primate population obtaining 6.6 individuals/km² using DISTANCE; this was closest to my direct count of 5.5 individuals/km². These divergent densities present a difficult interpretive problem that could be related to different methods. I conducted line transect census year round with an equal monthly effort whereas the study carried out by **Palacios & Peres** (2005) was conducted in November-December, a period of low resource availability when primate and other animal species often are obliged to concentrate on just a few key

Table 4. Characteristics of the 26 Amazonian primate communities compared with the 9 sites presented in this study

Study site	No. of species	Density (ind/km²)	Biomass (kg/km²)
Terra firme forest			
La Barcareña	**2**	**114**	**387**
Cerro de El Tuparro	**3**	**66**	**190**
Tapón El Tuparro	**4**	**77**	**370**
Caparú1	**8**	**48.2**	**133**
Puré	**10**	**47.9**	**87**
Purité-Amacayacu	**9**	**61**	**114**
Purité-Omé	**9**	**66.1**	**161**
Purité-Camino Nuevo	**9**	**61.2**	**118**
Caparú[1]-Colombia	8	61.9	175.7
Ayo[1]- Colombia	10	86.9	169.5
Pintadillo[1]-Colombia	10	37.4	88.9
Duda river[2]-Colombia	7	130.7	497.3
Porongaba[3], Brazil	12	209	158
Sobra[3], Brazil	11	174	117
Kaxinawá Reserve[3], Brazil	12	145	173
Condor[3], Brazil	11	194	274
Penedo[3], Brazil	10	129	118
Altamira[3], Brazil	12	227	463
Barro VermelhoI[3], Brazil	13	165	261
Fortuna[3], Brazil	14	216	297
Riozinho[3], Brazil	14	157	225
Igarapé Jaraquí[3], Brazil	13	137	131
Vira Volta[3], Brazil	13	182	282
Vai Quem Quer[3], Brazil	11	124	176
Urucu River[4], Brazil	13	146	381
Yavarí River[5], Perú	14	-	420
Cocha Cashu, Manu, Peru[6]	14	287	655
Varzea forest			
Caparú2	**8**	**97.1**	**215**
Sacado[3], Brazil	4	126	245
Nova Empresa[3], Brazil	6	185	410
Boa Esperança[3], Brazil	5	355	953
Barro Vermelho II[3], Brazil	7	213	361
Lago da Fortuna[3], Brazil	7	358	627
Lago Mamiraua[3], Brazil	3	270	429
Lago Tejú[3], Brazil	4	175	352
Cajuana Island[3], Brazil	6	120	389

Data source: [1]Palacios and Peres [2005]; [2]Stevenson [1996]; [3]Peres [1997]; [4]Peres [1993]; [5]Puertas and Bodmer [1993].

plant species necessitating the exploitation of highly patchy resources in a very irregular fashion (**Terborgh,** 1983). This may have skewed the results obtained by **Palacios & Peres** (2005) in comparison with my more evenly distributed data collection, nevertheless their results of 6.6 individuals/km²
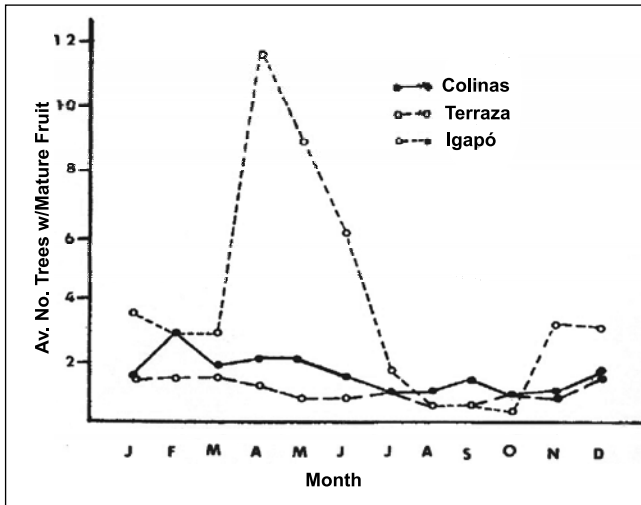
Fig. 2a. Seasonal variation in the availability of mature fruit crops in three habitats at the Estación Biológica Caparú (Defler & Defler, 1996).
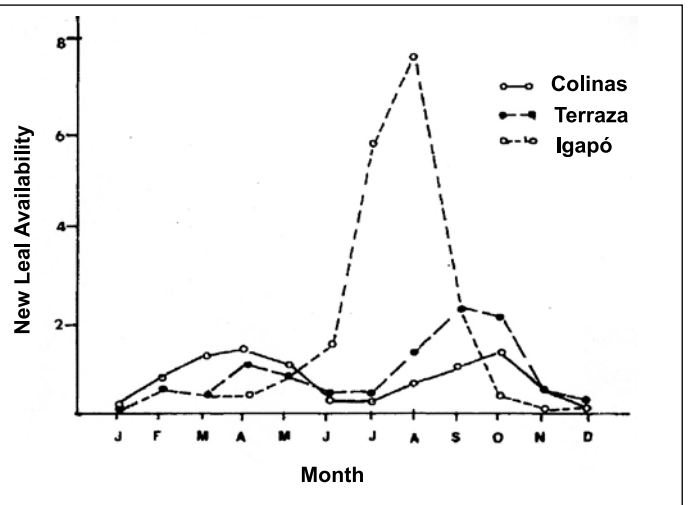
Fig. 2b. Seasonal variation in the availability of new leaves in three habitats at the Estación Biolóbica Caparú (Defler & Defler, 1996).

and my results of 5.5 individuals/km² calculated by direct count suggest that these low densities may be most accurate.

Because we knew the group size of the *Lagothrix* troops that were most commonly detected, we used 24 individuals to characterise each observation rather than the count of animals visible per detection. **Peres** (1999) argues that the use of average size for a species analysis may actually inflate the calculation, as subgroups may be counted as groups. In our case the data do not suggest that it was possible to have counted two subgroups, merely because observations were detected very far apart and any one observation represented the entire group. The difference between the putative direct count calculation of 5.5 individuals/km² and the DISTANCE calculation of 13.1 individuals/km² may illustrate the difficulty of making a direct count of animals based upon supposed recognition of groups in closed canopy rainforest or may illustrate inflated results for the DISTANCE calculation. In this paper we report calculations of *Lagothrix* at Caparú varying from 5.5 individuals/km² to 13.1 individuals/km².

Densities of *Alouatta* at almost all Amazonian sites are very low, at sites 4, 6-10 they were too low to calculate density using DISTANCE. At site 5 in an *igapó* forest, biomass and densities of *Alouatta* were the highest of all of the Amazonian sites, in agreement with other studies (**Haugaasen & Peres**, 2005; **Peres**, 1993, 1997). In contrast, in the llanos sites 1,2,3 *Alouatta* is a major component of primate biomass. Increase in *Alouatta* densities towards the north in Colombia and extremely high densities in Guarico state, Venezuela suggest that optimal habitat for *Alouatta* is the ecotone or edge

habitat surrounded by savanna and not in closed-canopy forest (**Crockett & Eisenberg**, 1987; Table 5). Habitat in flooded forest at Caparú produces extremely large pulses of new leaves and fruits, compared to other local *terra firme* habitats and as reported before in **Defler & Defler**, (1996); (Figure 2a & 2b). This preferred ecotone habitat explains the almost universal presence of *Alouatta* along river and lake edges and the very low densities or absence away from this habitat.

Table 5. Various densities of ***Alouatta seniculus***, increasing towards northwards (in Colombia) towards the center of the Venezuelan llanos, suggest elucidation of preferred habitat for this species.

Census Site (s)	Individuals/km²
Omé-río Purité (Defler, this study) terra firme	**1.8**
Sur del Vaupés (Palacios & Rodríquez, 2001) igapó	**4**
Río Juruá, Brazil (Peres, 1997) terra firme	**4.7** average of nine sites (range 1-8.4 ind/km²)
El Tuparro (Defler, 1981) gallery forest	**27-29**
Manu, Perú (Terborgh, 1983; Janson & Emmons, 1990) tropical moist forest	**30**
La Barcareña (Defler, this study) gallery forest	**42.5**
Río Juruá, Brazil (Peres, 1997) Várzea	**40.7** average of six sites (range 15.6-89.7 ind./km²)
Hato Masagural, Estado de Guarico, Venezuela (Crockett & Eisenberg, 1981) gallery forest	**83-118** data from four studies

The highest densities of *Cebus apella* were from La Barca-reña gallery forest site, the highest densities of which this author has knowledge. Other calculated densities of this species (Caparú and Purité River) were much lower. Considering the very wide distribution of this species throughout the Amazon basin, it is of great ecological interest that we have not registered *C. apella* in the majority of the Colombian trapezium (the local name for that portion of the Colombian Amazon between the Putumayo river and the Amazon river) at any of our study sites (7-13). Where *C. apella* is absent, densities of *C. albifrons* are much higher than the densities of this species where it is syntopic with *C. apella*, suggesting some sort of density compensation (**Peres & Dolman**, 2000). Like *C. apella*, the highest density of *C. albifrons* was also measured in the Colombian gallery forest (site 2). The pattern of dominance of *C. apella* when syntopic with *C. albifrons* also seems to be reflected in other Amazonian data sets (**Peres**, 1997; **Endo** *et al.*, 2009; **Palacios & Peres**, 2005; **Haugaasen & Peres**, 2005, among others). High densities of *Cebus* in gallery forest suggest a preference for edge habitat with high densities of *Cebus albifrons* in the llanos and may also suggest a preference for drier, more deciduous forests than in many parts of the Amazon.

Saimiri was present at most Amazonian sites at low densities of 6-18 individuals/km^2, reaching 24.6 individuals/km^2 at a site close to the Amazon River in the south (site 10). This species´ densities were also low in the *igapó* forest site 3 at Caparú.

Callicebus torquatus generally shows low densities for sites 4, 6, 7 and high densities in the gallery forest of El Tuparro. Why *C. torquatus* should show such high densities in a gallery forest in the Colombian Llanos is not clear, although fertility factors might have increased the preferred food available. *Callicebus* is notoriously patchy in distribution and censuses passing through habitat patches will register high densities (**Defler**, pers. obs.). These patches, separated by wide expanses of forest where *Callicebus* is absent, may be affected by fluvial and lacustrine forest, since all sites had populations of *Callicebus* close to the water in generally tall, well-stratified forest. In the gallery forest of Tapón of El Tuparro the habitat is probably more homogeneous, approximating a preferred habitat for the species throughout its length.

Pithecia monachus was present in four Amazonian sites south of the Caquetá River (sites 6-9) at moderate densities (4-14.5 individuals/km^2) and in clumped distributions. Like *Callicebus torquatus*, this species may be attracted to tall, well-stratified fluvial and lacustrine forest, since all sites had populations close to the water and they are frequently detected from boats. Their additional success in patches of vege-tation in fragmented regions suggests a certain tolerance for edge habiat [**Defler**, unpublished data].

Only The Puré (6) contained *Saguinus fuscicollis* at low densities (8 ind/km^2), but three sites had *Saguinus nigricollis* with moderate densities (14-15 ind/km^2) along the clear-water Purité River. Many *Saguinus* species seem to show higher densities around secondary vegetation (pers. obs. Defler, for *Saguinus fuscus* and *S. inustus* and *S. nigricollis*), perhaps because of fast-growing small, soft fruits and increased solar exposure, attracting many grazing insects (**Defler**, 2004, 2010), but this posited effect has not been reported or tested in the literature.

Community biomass comparisons with the Duda River community

Although the six sites in the eastern Colombian Amazon always had higher species richness than the western Amazonian Duda River community, total primate biomass on the Duda River, with an annual precipitation of 2600 mm, was far greater than any that I surveyed. **Stevenson** (1996) calculated a biomass of 497.3 kg/km^2 for the six species of diurnal primates at his site, which included *Lagothrix lugens*, *Ateles belzebuth* and *Alouatta seniculus* – a syntopic array of three large species of considerable biomass, which this author has never personally observed in eastern Colombia. I observed somewhat comparable high biomass communities (with lower species richness) only in the Llanos with 387 and 370 kg/km^2 (due to high densities of *Alouatta* and *Cebus* spp.). Amazonian primate communities in this study varied between 86 kg – 216.5 kg and averaged only 142.5 kg of primate biomass.

Edaphic factors, precipitation and biomass densities

The tropical moist forests in this comparative study experience precipitation between 3200-3950 mm per year. Consistently heavy rains leach soils of calcium, magnesium and potassium, causing a decrease in phosphorus availability and creating more acidic soil, all of which affect crop size and primary production (**Defler & Defler**, 1996; **Reed & Fleagle**, 1995). At higher primate biomass sites of La Barcareña and the Duda river, phosphorus levels are elevated, compared to measured sites in the eastern Colombian Amazon. I suggest this is the cause of reduced diversity and biomass in the eastern Colombian Amazon as discussed by **Peres** (2008).

General community characteristics

Based on information from a variety of field surveys cited above and sites in the eastern Colombian Amazon (as repor-

ted in this study) some general observations can be made. A typically species-rich Amazonian community usually possesses the large sympatric frugivores *Ateles* and *Lagothrix*, two species of *Saguinus* (not so in the Duda river), two species of *Callicebus* and two species of *Cebus* (not in the peripheral Duda river). When *C. albifrons* and *C. apella* are syntopic, the biomass of *C. apella* is usually much higher than that *of C. albifrons* (this study). In eastern Colombia, species richness is moderate and the densities of each species are notably lower than in many communities studied south of the Amazon River, while in eastern Amazonian Colombia there is only one large frugivore species, one *Saguinus* and sometimes only one *Cebus* species. It is noteworthy that not only were biomass values very low in eastern Colombia but species richness is moderate as compared to primate communities further south of the Amazon river at the same latitudes. It would seem that some of the factors that affect community biomass also affect species richness as well, especially phosphorus levels, and I suggest that high precipitations (well over 2500 mm) and soil impoverishment are the likely factors that suppress biomass and species richness.

Acknowledgments

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