

STUDYING PRIMATES IN EASTERN COLOMBIA: THIRTY FIVE YEARS OF A PRIMATOLOGICAL LIFE

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ABSTRACT

Defler T. R.: Studying primates in eastern Colombia: Thirty five years of a primatological life. Rev. Acad. Colomb. Cienc. **36** (140): 421-434, 2012. ISSN 0370-3908.

A history of some details the author's research in eastern Colombia is presented for the last 27 years since 1977 in Vichada, Vaupés, Amazonas and most recently in Meta up to the present. Some comments are made about each research project in the context of primatology and some hypotheses and ideas of the author are presented about species, populations and other groups of mammals in the country. Especially discussed are aspects of *Cebus albifrons* and its relation to *Sapajus* (= *Cebus*) *apella* (a new taxonomic change) and the primates *Callicebus lugens*, *Alouatta seniculus*, *Lagothrix lagothricha*, *Cacajao melanocephalus*, *Callicebus caquetensis* and *Callicebus ornatus*.

Key words: primatology, Colombia, Thomas Defler

RESUMEN

Se relata algunos detalles de la historia de las investigaciones del autor en el oriente de Colombia durante 27 años de trabajo en Vichada, Vaupés, Amazonas y más recientemente en el Meta, desde 1977 hasta el presente. Se hace comentarios sobre cada investigación, ubicándola en el contexto de la primatología y se destacan algunas hipótesis e ideas del autor en cuanto a la naturaleza de las especies, poblaciones de primates y otros grupos de mamíferos en el país. Especialmente se discute aspectos de los primates *Cebus albifrons* y su relación con *Sapajus* (= *Cebus*) *apella* (nuevo cambio taxonómico), y los primates *Callicebus lugens*, *Alouatta seniculus*, *Lagothrix lagothricha*, *Cacajao melanocephalus*, *Callicebus caquetensis* y *Callicebus ornatus*.

Palabras claves: primatología, Colombia, Thomas Defler

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Introduction

It seemed the culmination of my life to come to Colombia 36 years ago in order to work as a Peace Corps volunteer primatologist with the former INDERENA. The choice of Vichada as my first objective was a long process of consultation with professor Jorge Ignacio Hernández-Camacho, my mentor and my last professor; we talked about many aspects of Colombia, including field work in primatology, possible species present, research tactics, local relations and personal security, even before we decided upon the Faunistic Territory of El Tuparro in eastern Vichada (declared a National Park in 1982). In December, 1976 I made a preliminary trip to El Tuparro and the area seemed to be a magnificent point to begin my Colombian career, even though my original plan had been to work in the Colombian Amazon. But this would come later.

El Tuparro, the Llanos Orientales and Vichada

At the time there was not much information about primates in El Tuparro. Profesor Hernández-Camacho suggested a long list of possible primates, but nobody had reconnoitered that very large territory for primates; there were many regions that had not been visited by park officials. Only some primate collections by INDERENA employees had identified four species in the western border, defined by Hormiga Creek. These were *Sapajus apella* (earlier known as *Cebus apella*, but separated from *Cebus* by Lynch-Afaro *et al.* 2012; Solari *et al.*, en press), *Callicebus torquatus lugens*, *Alouatta seniculus*; and *Cebus albifrons* had been identified in the eastern regions of the reserve.

Two aspects had called themselves to my attention when I first arrived in El Tuparro: *Cebus albifrons* was a very poorly-known species at the time and *Sapajus apella* (known to be often sympatrically distributed with *Cebus albifrons* in the Amazonian forest to the south) was in fact parapatrically distributed with relation to *Cebus albifrons*---that is one species seemed to strictly replace the other species in El Tuparro. Because of these facts I decided to study the ecology and behavior of *Cebus albifrons* and to learn more details about the distributions of these two species that had been considered before to be congeneric (Defler, 1979a, 1979b, 1980, 1982, 1985a, 1985b). The group that I studied lived in a forest that clothed a prominent inselberg (*monadnock, bornhardt, pan de azucar*) close to the administrative center, overlooking the Orinoco River. In this region, inselbergs were a common feature of the landscape, great gneiss granitic islands of rock surrounded by savanna. The runoff from rain usually maintained a substantial forest around its base, where three species of monkey roamed.

To me at that time, the most important ecological questions were densities and species richness in the east of the country, as well as actual distributions, since there existed and still exist so many unknown facts about El Tuparro. Most of these problems I discussed with professor Hernández-Camacho in our nocturnal Bogotá chats over cuba libres. Many unknowns had already been posed by him in his very important publication with the North-American veterinarian Robert W. Cooper, on the non-human primates of Colombia (Hernández-Cooper & Cooper, 1976), the primate article most often cited in the field of primatology at that time. I came to believe that the ecological relations between *Cebus (Sapajus) apella* and *Cebus albifrons* in the eastern parts of the country needed to be elucidated, especially since these relationships changed to the south in the closed-canopy forest.

Making life more interesting, a healthy population of the giant otter *Pteronura brasiliensis* existed within the Territorio. This was a mammal species that had always interested me. So I resolved to include a census of its presence in the region during the various years that I traveled the rivers of El Tuparro studying the distributions of *Sapajus apella* y *Cebus albifrons* and other primates in heretofore unknown corners of El Tuparro. (Defler, 1985a,b).

Callicebus torquatus, Alouatta seniculus, Aotus sp.

In 1978 I moved to the western side of the Territory in order to study primates in a type of forest that I hadn't known before, the typical gallery forest of the llanos, growing along Hormiga Creek. This forest contained populations of *Callicebus lugens* (known as *C. torquatus* at that time) as well as populations of *Alouatta seniculus*, *Aotus sp.* and *Cebus (Sapajus) apella*.

I was able to gather basic ecological data on *Callicebus torquatus*, including densities, home range sizes, group sizes and other details of these interesting monkeys. Parallel to this effort I added to my knowledge of *Alouatta seniculus*, a very widely distributed Colombian primate but of variable home range and group size. These data became valuable when I was able to compare the home ranges and group sizes of the species across several forest types, thus suggesting a preferred habitat for this species (more on this below). I collected the same type of information on the *Cebus (Sapajus) apella* of the forest.

In Tapón I experimented with techniques of censusing primates and I clarified some details that should be used when censusing. This seems valuable when we consider the great effort that has been made in censusing primates throughout South America (Defler, 1983, Defler & Pintor, 1985). In 1982, while I was working on the western part of El Tuparro,

the Territorio Faunístico El Tuparro was declared a Parque Nacional Natural.

Having calculated densities for various primate species throughout El Tuparro, I decided to pursue as a long-time project the calculation of primate densities in a transect from northern Vichada to southern Amazonia. This project was pursued intermittently during the next twenty years and the results of which I now publish in this journal (Defler, en prensa). Census sites included the source of the Bitá river in Vichada, the two extremes of El Tuparro, Lake Taraira in Vaupés, the Puré River (located inside PNN Río Puré, Amazonas) and the Purité River beside the Amacayacu National Park, Amazonas (Fig. 1).



Figura 1. Census sites.

The basis of these transect censuses from the Llanos Orientales to the Amazon allow three hypotheses to be tested.

1. According to censuses of other organisms, including primates in other places outside of Colombia, primate richness should increase inversely with a decrease in latitude (Terborgh, 1992; Huston, 1994; Rosenzweig, 1997; Peres & Janson, 1999).
2. Some of the highest species richness known should be found in the exuberant forest of the Colombian Amazon

since Colombia is the country with the highest species richness of birds (Hilty & Brown, 1986; Renjifo et al., 2002; Stevenson, 2001)

3. According to variable density results from low to high densities, the data on densities should provide indications on preferred habitats for a species, accepting that high density habitats are preferred habitats (Johnson, 2007).

Methods

Vichada

Using *al azar* observational methods (Altmann, 1974) I collected data on all aspects of *Cebus albifrons* in a forest surrounded the Cerro Rocoso in El Tuparro as described in Defler (1979a,b).

Using observations of *Alouatta seniculus* I calculated densities and group make-up of groups of *Alouatta* (Defler, 1981). In Tapón gallery forest I collected demographic data on *Callicebus torquatus* as described in Defler (1983). I collected *al azar* data on *Sapajus apella* during several years (Defler, 1982) and experimented with census techniques, as described in Defler and Pintor (1985). I developed a five kilometer trail and did strip census of primates in a forest along an upper tributary of the Bitá River in 1985 (Defler, in press). I collected population data on the *Pteronura brasiliensis* of El Tuparro, using a small unmotorized canoe traveling downriver (Defler, 1982, 1984, 1986).

Methods used for studying *Cebus albifrons* can be found in Defler (1979a, 1979b), for the distribution and state of the population of *Pteronura brasiliensis* in Defler (1982), for the distribution of *Cebus (Sapajus) apella* and *C. albifrons* in the región of El Tuparro in Defler (1985), for densities of *Alouatta seniculus* en El Tuparro en Defler (1981) and for methods of censusing primates en El Tuparro in Defler & Pintor (1985).

Densities in El Tuparro were determined via direct counts since the study forests were clearly delineated from the savanna, allowing specific areas to be covered [Defler & Pintor, 1985]. In the Hato La Barcareña in northern Vichada calculations were made by repeated censuses along a 5 km trail, calculation of perpendicular distances to the groups observed and calculation of a detection distance for each species (Robinette et al., 1974; Defler & Pintor, 1985; Peres, 1999).

Methods used at the Estación Biológica Caparú in Vaupés for studying the general ecology of *Lagothrix lagothricha* can be found in Defler (1987, 1989), for the time budget of

Lagothrix lagothricha **Defler** (1995), for the diet of *Lagothrix lagothricha* in **Defler y Defler** (1986), and for the use of space and for locomotion in **Defler** (1996) and in **Defler** (1999). Additionally, study methods for the *Cacajao melanocephalus* research can be found in **Defler** (1999, 2001).

Research methods on density of primates have been described in various places; my method involved repeated censusing of 4-5 km transects from the edge of the lake into the forest, where 264 km were accumulated and where the group's numbers of individuals and distance perpendicular to the trail were registered. Various methods of calculating density were applied; in the case of *Sapajus apella* there were sufficient observations to be able to use the program DISTANCE (**Peres**, 1999a; **Defler**, en prensa).

Vaupés

After five years of work in Vichada, I developed a research plan to study the ecology of *Lagothrix lagothricha* and *Cacajao melanocephalus* in the Colombian Amazon. I established myself in a station that I developed a kilometer north of the shore of the unpopulated Lake Taraira in southern Vaupés, this the most extensive river-lake found in the Colombian Amazon (**Defler**, 2009). During the 16 years spent at this station my wife and I received many primate orphans that were sent to us by INDERENA and by private citizens who charged us with an attempt to reintroduce the primates to the forest. Also, during this time a series of primate censuses were accomplished during 2 ½ años.

The development of the Estación Biológica Caparú (1°04'25.65"S, 69°31'15.71"W) for Amazonian biological research was a personal plan dating back to 1982, impelled by my curiosity about the primate species *Lagothrix lagothricha* and *Cacajao melanocephalus*, two species that at the time were very poorly known. With the help of two Yucuna Indigenous men whom I had known from a previous trip that I made to the Mirití-Paraná to reconnoiter the Amazon in 1981, I identified a region in southern Vaupés department with these two species and six other species or primates (*Aotus vociferans*, *Saimiri sciureus*, *Cebus albifrons*, *Sapajus apella*, *Callicebus lugens*, *Saguinus leucopus*). The area included the river-lake Lake Taraira (1°08'35.55"S, 69°29'21.63"W, 56 msnm), a 24 km long ancient cut-off meander of the lower Apaporis river. The area's topography was made up of a complex of igapó (seasonably flooded forest with black water), Pleistocene river terrace and Plio-Pleistocene hills (**Carvajal-L. et al.**, 1976; **Palacios et al.**, 2009).

The Apaporis River shows evidence of tremendous floods at the end of the Pleistocene when the glaciers melted and

sent extreme volumes of water down the river courses of eastern Colombia. These floods formed extensive river terraces about 11-15 m above the average high water marks of today (**Van der Hammen et al.** 1992a, 1992b, **Carvajal-L. et al.**, 1976; **Ibarra et al.**, 1976). Currently these ancient river terraces are covered by high and distinctive forests, particularly of *Oenocarpus bataua*, *Euterpe* sp. y *Mauritica flexuosa* and trees important to *Cacajao* and *Lagothrix* such as the *carquero* (*Eschweilera* sp.) and the very tall *yetcha* (*Micrandra spruceana*) (**Carvajal-L. et al.**, 1976; **Ibarra et al.**, 1976; **Defler & Defler**, 1996; **Rangel-Ch. et al.**, 2008).

I studied a group of *Lagothrix lagothricha* from 1984-1989), especially for spatial use, time budget and diet as described in **Defler** (1987, 1989a, 1989b, 1990a, 1995, 1996a, 1996c, 1999b) and **Defler & Defler** (1996). During 1994-1998 I studied the ecology of *Cacajao melanocephalus* around Lake Taraira (**Defler**, 1991, 1999, 2001; **Barnett et al.**, in press). I also carried out a series of primate censuses during the first 2 ½ years of residence.

Amazonas

After leaving Vaupés in 1998 because of pressure from the guerrillas, I searched for a place in the upper Purité River beside Amacayacu National Park in order to continue primate research.

Along the Purité River on a hill site above the flooding river and outside the park I developed a new research site, the Estación Ecológica Omé. Posterior archaeological research by professor Marcote of the Instituto de Ciencias Naturales determined this was an ancient inhabited site of indigenous people dated from 670-1350 BP (+/- 50 years) (3°32'07.92"S, 69°53'26.75"W - 104 msnm) (**Morcote-Ríos**, 2008). I selected the area because of its isolation from negative influences in the region, but it proved to be so isolated that it has been difficult to access because of the necessity of traveling various days on the Amazon and Ica-Putumayo rivers, then traveling upriver on the Purité river to enter Colombian again. This station was developed during brief two month visits that have allowed a large series of primate censuses and some research on the use of space of the primate *Callicebus torquatus lucifer* (= *C. lucifer* according to other authors) (**Defler**, in press).

Generally when moving from place to place all observations of primates were registered using the most exact coordinates possible, given the maps available. It was not until 1995 that it was possible to begin registering observations using the new GPS system.

Results and discussion

Since *Cebus albifrons* had been observed in the field only very briefly before beginning my study, any new natural history observation was valuable (Defler, 1979 a,b). I first realized that the groups were very large in comparison with the numbers reported in the literature. My study group was made up of 35 animals and the neighboring groups were similar, illustrating perhaps a type of ecological release (Tabla 1) (where in the absence of some competitors the densities rise (according to Peres & Dolman, 2000) or “ecological release”, (defined by Terborgh & Faaborg, 1973, as “an expansión or increase in density, distribution or commonly observed behavior when a species is observed under different intensities of competition”). The putative effects of competition with *S. apella* have been implicated in limiting *Cebus albifrons* group sizes.

Table 1. Groups sizes reported for *Cebus albifrons*

Group Sizes	Source
7 & 8	Matthews, 2009
8-15 (máx. 20)	Terborgh, 1983
9, 10	Defler, obs. pers. in Amazonian forest
10-20	Hernández & Cooper, 1976
10, 12	Terborgh, 1983; van Schaik & van Noordwijk, 1989
35 (Llanos Orientales)	Defler, 1979a,b

Studying this species in a forest limited by savanna was a great help, since the limits of the home range for any group are much clearer in comparison with studies in continuous forest without border limits. The home range in El Tuparro was about 120 ha for the defended territory of the group, the first territory that had been calculated for this species. Ecological densities were the highest reported in the literature with much lower densities in closed canopy forest.

Cebus albifrons and *Sapajus apella*

I wanted to know more about the ecological interaction that *Cebus albifrons* has with *S. apella*, which is evidently the strongest competitor of *C. albifrons*. A question that I posed was “What type of interaction do these two species have in their contact zone in El Tuparro?” where they are essentially parapatric in distribution, where one species replaces the other. So I decided to study the distribution of the two species in the región and undertook a series of voyages by canoe, motor bike and on foot to see if the distribuciones were truly parapatric. The result of this was more than 2000 km of travels (1500 km by canoe), where I found a strict separation of the two species in the north along the Tomo River, but in the south of the park, especially along the Tuparro River, the separation was not so clear, especially on the left bank of the

Tuparro where I found groups of *Cebus albifrons* integrated into a population of *Sapajus apella* (sympatry) and ultimately lower down on the Tuparro river I found a forest with the two species sympatrically distributed just before the beginning of a pure *Cebus albifrons* population to the east. Along the same river *C. albifrons* used flooded forests and *Sapajus apella* (observed closest to the river on the south bank), did not use flooded forests (Defler, 1985a). Fig. 2.

The population of *Cebus albifrons* studied in El Tuparro is isolated from the principal population that extends southward from the south bank of the Vichada River. With field work in that region, It was possible to prove that *Sapajus apella* and *Cebus albifrons* are sympatric south of the Vichada River and that *Cebus albifrons* exists in very low densities and in groups much smaller than those in El Tuparro (Bennett et al. 2001; Terborgh, 1983; Haugaasen & Peres 2005, 2009; Defler, 2010; Lynch-Alfaro et al., 2012).

Lynch-Alfaro et al. (2011, 2012) suggest the “gracile” *Cebus* (i.e. *Cebus albifrons*, *C. capucinus* and *C. olivaceus*) originated in the Amazon while the “robust” *Cebus* (that is the *Sapajus*) originated in the Atlantic forest (Mata Atlántica) and invaded Amazonia about 400.000 years ago. The last common ancestor of *Cebus* and *Sapajus* has been calculated at about 6 MA. Considering the ecological dominance of *Sapajus* in many parts of Amazonia (measured by the densities shown by Peres, 1993, 1997a, b; Haugaasen & Peres, 2005, 2009) and the much higher densities in parts of the Colombian and Venezuelan llanos and the success of *C. capucinus* in the Chocó and Central America, this author suggests some other origin for *Cebus*, perhaps on the periphery of Amazonia in forests less humid and associated with sabanas and dry forests. I suggest that if the gracile *Cebus*

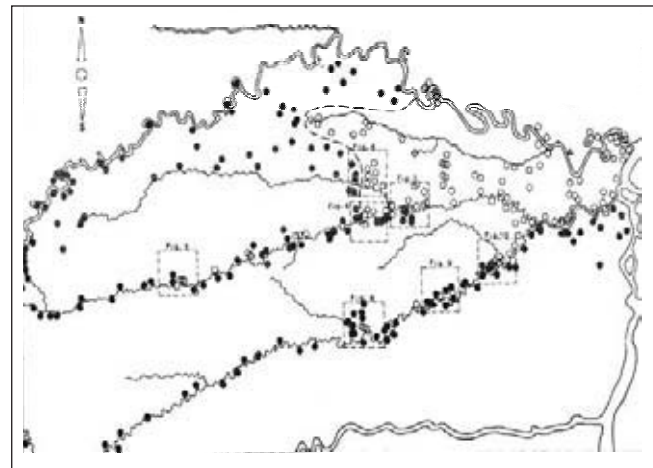


Figura 2. Distribution of Cebus/Sapajus in El Tuparro National Park.

originated in the Amazon they would be ecologically dominant to *Sapajus*, which is clearly not the case. The isolated population of *Cebus albifrons* in NE Vichada with parapatric *Sapajus apella* to the west and to the south suggests to me that *Sapajus apella* arrived after *Cebus albifrons* and that the more recent species was able to out-compete *Cebus albifrons*. This accords well with the ecological dominance of *S. apella* in Amazonia where the two species are sympatric.

Cebus albifrons and *Cebus olivaceus* in Venezuela are genetically related species and have many similarities, suggesting that they have common ancestors. Perhaps *C. olivaceus* comes from *C. albifrons* and they are sister groups with *C. capucinus* (Lynch-Alfaro *et al.*, 2012; Ruiz-Garcia *et al.* 2010). It is possible that the llanos could be a principal factor in permitting the persistence of these two species and that their presence in the forests to the south might be the result of an invasion from the savannas during a glacial maximum when there were many more savannas and an Amazonia much more fragmented. This hypothesis is supported by molecular studies showing that various subpopulations of *Cebus albifrons* exist in the Amazon within what we generally see as *Cebus albifrons* (Ruiz-Garcia *et al.*, 2010; Lynch-Alfaro *et al.*, 2012).

During my stay in El Tuparro professor Hernández-Camacho asked me to collect several examples of *Cebus albifrons*, an unwelcome task for me, since I wasn't accustomed to collecting. But this was part of my education as a biologist, since my education outside of Colombia had not included the importance of study collections. Another project accomplished with professor Hernández-Camacho was the establishment from this collected material of a neotype for *Cebus albifrons*, since there were various problems with the original description of von Humboldt which was not supported with a holotype and which impeded comparison with other taxa that would allow the construction of an adequate taxonomy for the species (Humboldt & Bonpland, 1812; Defler & Hernández-Camacho, 2002). The problem of an adequate taxonomy for *Cebus albifrons*, however, was not solved by the establishment of a neotype, since we are now flooded by new molecular data that shows how complex the evolution of *Cebus albifrons* has been (Boubli *et al.*, 2012; Ruiz-Garcia *et al.*, 2010; Lynch *et al.*, 2012).

Attempts to study *Sapajus apella* in Tapón were not as successful as the study of *Cebus albifrons*. This was due, I think, to previous collections of primates in this forest by INDERENA employees that rendered the primates (especially the *Sapajus*) very timid. I was never able to habituate groups of *Sapajus*, whereas it was very easy to habituate the *C. albifrons* from eastern El Tuparro. Nevertheless, it was possible to distinguish several species differences between the two

that have been helpful in understand their competition (Defler, 1982).

Callicebus

In western El Tuparro a study of some population characteristics of the then denominated *Callicebus torquatus lugens* (now recognized as *Callicebus lugens*) elucidated group sizes (3.5), territory sizes (14.2 ha) and other details. This taxon is now recognized as *Callicebus lugens* because of the discovery in Brazil of the karyotype for this taxon, the lowest karyotype known among the primates ($2n=16$) (Bonvicino *et al.*, 2002). However, we now have a dilemma in Colombia. In order to confirm that what was denominated before as *Callicebus torquatus lugens* (sensu Hershkovitz, 1990) corresponds to the taxon *Callicebus lugens* with a karyotype $2n=16$, we have to determine the karyotypes of Colombian animals, work that is difficult because of Colombian legislation, resulting in many difficulties applying for official permission.

Thomas (1914) defined *lucifer* as animals with the ventral part of the tail and the body a reddish color, while von Humboldt & Bonpland (1812) defined *lugens* as a completely black animal (“d'un beu noir et un peu relevé: ce pelage est d'une teinte uniforme sur le corps entier, à l'exception de la face, du col et des mains de devant.”) with the exception of the face, neck and hands. Hernández-Camacho y Cooper (1976) distinguished only *Callicebus torquatus lugens* and *C. t. medemi* and Hershkovitz (1963) maintained that it was not possible to distinguish *lugens* from *lucifer* with the diagnostic characters that had been published. Nevertheless, Hershkovitz (1990) later distinguished between *lucifer* and *lugens*, placing the two in Colombia, separated by the Caquetá river and distinguishing them using the bands of color on the hairs of the neck and sides of the body, *lugens* with dark brown or blackish color with hairs of uniform color or weak bands of pheomelanin and *lucifer* with hairs of the neck and sides of the body colored brown or reddish brown with hairs strongly banded (with pheomelanin) (Hershkovitz, 1990).

After examining more than 100 skins of this complex from the two putative taxons, this author finds a range of color characteristics from both sides of the Caquetá river, at times the same, at times different, that makes it impossible to assign many specimens to the taxons as defined Hershkovitz (1990). For example, figure 3 and figure 4 show specimens that supposedly are assigned to one of the two taxons, but which on examining them, results impossible to place in any one taxon. Recently my colleague, the geneticist Marta Bueno of the Universidad Nacional de Colombia has determined the karyotype of a specimen from the north bank of the Ama-



Figure 3. Three *Callicebus torquatus lucifer* (*sensu* Hershkovitz, 1990) with widely varying phenotype.



Figure 4. Three *Callicebus torquatus lugens* (*sensu* Hershkovitz, 1990) with widely varying phenotypes.

zon River above Leticia. This karyotype ($2n=20$) does not seem to differ from karyotypic characteristics determined for other *Callicebus torquatus* (Egozcue *et al.*, 1969; Benirschke & Bogart, 1976). The specimen is definitely not *C. lugens* and must be placed in the *C. torquatus* complex. As we do not detect a genetic difference from other *C. torquatus*, we assign this Colombian *Callicebus* to a subspecies *C. torquatus lucifer*. Basically I suggest that *C. torquatus lucifer* and *C. t. medemi* are found in southern Colombian and that their karyotype is $2n=20$. The possibility that specimens north of the Caquetá River are *Callicebus lugens* must

await karyotypic designation, although at the moment we treat these animals north of the Caquetá River as *Callicebus lugens*.

Identical data was collected in the Hormiga Creek forest on *Alouatta seniculus* to that of Cerro Rocosó, and they were similar densities but with different group sizes (5.75 individuals Tapón, 6.8 individuals in Cerro Rocosó) and different home range size (13.3 ha in Tapón, 23.75 in Cerro Rocosó) and densities (23 individuals/km² for Tapón; 27 individuals/km² for Cerro Rocosó) (Defler, 1981).

An experiment examining how to best census primates clarified various important points. Especially it pointed out the difficulties of censusing a far-ranging species such as *Sapajus* in narrow forests that skewed the range of the animals from an idealized circle or oblong so that they were no longer detected *al azar*; thus inflating the densities of the animals (Defler & Pintor, 1985).

Vaupés, *Lagothrix lagothricha lagothricha*, *Cacajao melanocephalus*

My research in Vaupés (1983-1995) generated some of the first data on *Lagothrix lagothricha* and taught me about the effects of the poverty of eastern Colombia. Our data on precipitation at the research station in southern Vaupés includes more than 14 years and shows an average of 3950 mm per year, well above the precipitation for the majority of known Colombian Amazonian sites (Palacios *et al.* 2009). Various correlations with species richness in both plants and animals show an increase in species richness up to about 2.500 mm of annual precipitation, after which species richness levels off or declines (Gentry, 1988; for plant diversity; Kay *et al.*, 1997, for primary production; Peres & Janson, 1999; for neotropical primates). The number of primate species in southern Vaupés is 8 or 9 at only two degrees south of the equator; this is a moderate species richness compared to primate communities south of the Amazon river (with annual precipitations below 2.000 mm [Leticia has a multi-annual average of 3194 mm, according to SIATAC (2012) and precipitations shows a tendency to rise towards the north, towards the research station Estación Biológica Mosiro Itajura-Caparú at the coordinates 1°04'27.41" S, 69°31'01.73" W (92 m altitude) . Species richness south of the Amazon river reach 10-14 species, the highest of the neotropics. Calculations of densities of primates at Mosiro Itajura-Caparú are very low in comparison to data from Brazil, Ecuador and Peru and it is worthwhile making some comments here.

Hypotheses regarding an increase in species richness up to the equator are not valid for Colombian primates. Eastern Colombia is low in primate species richness, but it is also

low in densities or biomass of primates compared with the large data base published by **Peres**, (2005, 2007); **Peres & Janson**, (1999); **Defler**, en prensa; **Palacios & Peres**, (2005) as well as data in Colombia from the Duda River (**Stevenson**, 1996). Low biomass true for all of the eastern Colombian Amazon into the Colombian trapezium and the conservation of communities having such low densities comes with special problems, especially when certain species are heavily hunted preferentially (e.g. tapir, *Tapirus terrestres*, woolly monkey *Lagothrix lagothricha*, tayasuids *Tayassu peccari* y *T. tajacu*, deer *Mazama* spp.) (**Peres & Palacios**, 2007). Communities in Eastern Colombia are sensitive and can be easily perturbed by excessive hunting. Table 2 compares eastern Colombia primate species richness and densities with other selected sites in South America.

There are many species that cannot maintain themselves with sustained hunting (e.g. the cracids, the atelids, tapir) and automatically when there are low densities these species are unable to replace themselves compared to a forest with high species densities (which ultimately also may not be able to sustain populations with concentrated hunting). The moving of indigenous settlements from one place to another is often because the prey species have become very rare or extinct and the community requires a prey base that provides more protein. With a large enough forest and a small enough human population these moves allow the previous prey bases to recover. But with less forest and more people (for example in the Chocó), prey bases do not recover. (**Robinson & Redford**, 1991; **Robinson & Bennett**, 2000a, 2000b) and certain animals become more scarce and endangered (for example, *Ateles geoffroyi*).

Low densities of primates (and other animals) in Eastern Colombia can be explained by soil leaching due to high precipitation and to low productivity of plants due to absent nutrients (**Kay et al.**, 1997; **Peres**, 2008). High precipitation leaches soils, continuing to impoverish them and northward from Leticia (at 20000 mm) the precipitation continues increasing, reaching 4000 mm in southern Vaupés (**Palacios et al.**, 2009). Numbers in many fruit crops at the Estación Biológica Mosiro Itajura-Caparú are very low, even though the plant diversity is high (although how plant diversity at this research station compares to plant diversities in other parts of the Amazon has not been measured) (**Defler**, unpublished data). Fruit set is limited by deficiencies in nitrogen, phosphorus, potassium, calcium and an abundance of aluminum (**Jordan**, 1985). **Defler** (in press) show soil data for eastern Colombia for primate census sites (except for PNN El Tuparro) and extremely low values are evident in these Eastern Colombian forests. In contrast, the llaneron forests with much higher primate biomass also show much higher levels

Table 2. Characteristics of 26 primate communities in the Colombian Amazon compared with nine sites reported by **Defler** (en prensa). *Aotus* is excluded in this analysis.

Census Site	No. of Species	Density (ind./km ²)	Biomass (kg/km ²)
Terra firme forest	(con <i>Aotus</i>)		
La Barcarena (Llanos Orientales) ^{ES}	2	114	387
Bosque de Tomás, PNN Tuparro este ^{ES}	3	36	156
Tapón, PNN Tuparro oeste ^{ES}	4	77	254.4
Caparú Amazonia, NPP Yaigojé inland ^{ES}	8	40.18	132.75
Río Puré, NPP Puré – Amazonia ^{ES}	10	47.9	86.7
Río Purité, NPP Amacayacu – Amazonia ^{ES}	9	61	114.32
Río Purité, EEOmé – Amazonia ^{ES}	9	66.1	160.9
Río Purité, Camino Nuevo – Amazonia ^{ES}	9	69.3	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 Vermelho ³ , Brazil	13	165	261
Fortuna ³ , Brazil	14	216	297
Riozinho ³ , Brazil	14	157	225
Igarapé Jaraquá 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
Varzea forest			
Caparú Amazonia, NPP Yaigojé lakeside ^{ES}	8	48.9	214.6
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 Mamirau ³ , Brazil	3	270	429
Lago Tejú ³ , Brazil	4	175	352
Cajuana Island ³ , Brazil	6	120	389

Source: **Defler** (this article); ¹**Palacios & Peres** (2005); ²**Stevenson** (1996); ³**Peres** (1997); ⁴**Peres** (1993); ⁵**Puertas & Bodmer** (1993).

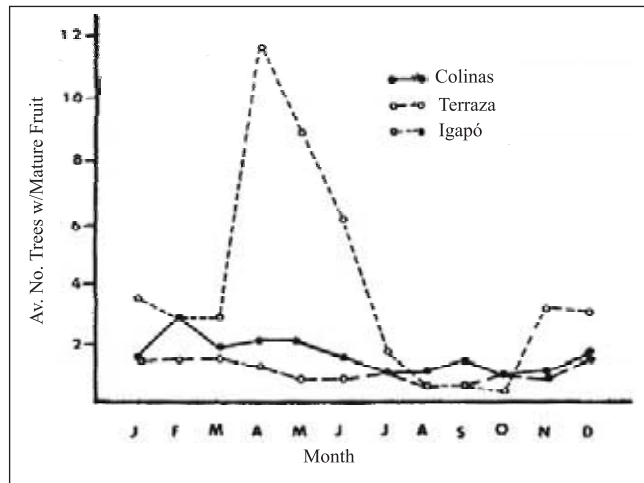


Figura 5. Seasonal variation in the availability of mature fruit crops in three forest types at the Estación Biológica Caparú (Vaupés) (with permission of Wiley-Blackwell).

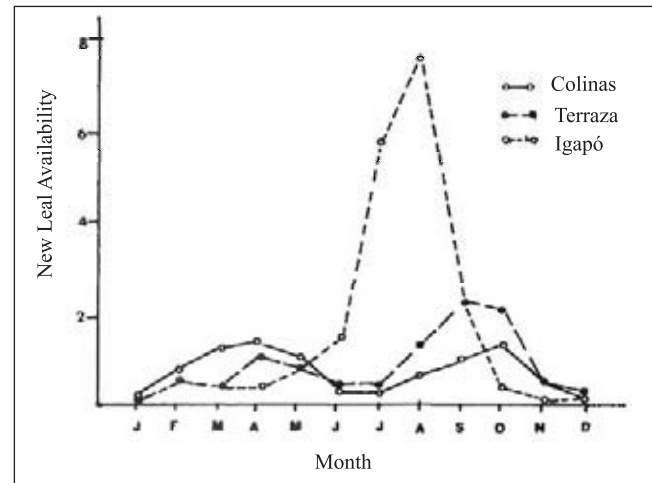


Figure 6. New leaf availability from three forest types at the Estación Biológica Caparú (Vaupés) (with permission from Wiley-Blackwell).

of soil nutrients and lower levels of aluminum. The only site that does not show tendencies for low primate biomass is the igapó of the Estación Biológica Mosiro Itajura-Caparú with the highest seasonal biomass found in any Colombian Amazonian site (214.6 kg/km²), even though the site has extremely high levels of aluminum and the same general low levels of other nutrients equal to terrestrial sites. Though research must be done, the hypothesis is that the high biomass of the igapó is due to a seasonal pulse in production of fruit biomass, itself due to a seasonal influx in the flooding water of enough nutrients to sustain a one-time fruit pulse that attracts the primates (*Lagothrix*, *Saimiri*) (Figure 5). Added to the fruit pulse in igapó is a young leaf pulse (*Alouatta*, *Lagothrix*) and a concentration in the production of the favorite *Cacajao* fruit *Eschweilera* spp. (Figure 6).

Some species show very interesting tendencies of densities. Besides *Cebus albifrons*, briefly discussed above, densities of *Alouatta seniculus* are some of the lowest densities in southern Vaupés, with ecological densities of around 3.85 individuos/km², based on research of **Palacios & Rodríguez** (2001). If the same site were calculated for crude density (i.e. an area of forest including both ecological density and forest without individuals) densities for *A. seniculus* in this regions would be much lower. High densities reported for central Venezuela of 83-118 individuals/km² in Guárico State at Hato Masaguaral are the highest known so far (**Crockett & Eisenberg**, 1987). Two places separated by 150 km in the Parque Nacional Natural El Tuparro have 30 individuals/km² at each site, and are similar to densities calculated in various other studies in the country. This author suggests that *A. seniculus* is found in an environmental cline where

the environmental conditions for *A. seniculus* improve from the south to the north from Amazonia towards the center of the Venezuelan llanos. Other censuses taken in the north of Vichada resulted in the highest densities for this species so far known in Colombia of 42.5 individuals/km² (**Defler**, in press). **Peres** (1997b) suggests that the species is sensible to changes in the quality of leaves in the closed canopy forests where he censused. More fertile forests must provide better hábitat for *A. seniculus*, which is more commonly found in the interior of forests to south of the Amazon river, but these conditions are not commonly found in Eastern Colombia.

Table 3. Increasing densities of *Alouatta* northward may define preferred habitat (see Fig. 1 for placement of Colombian sites)

Census Site	Density
south Vaupés (Caparú) (Palacios & Rodríguez, 2001)	4 ind/km ²
El Tuparro (Defler, 1981)	27-29 ind/km ²
La Barcareña (Defler, in press)	42.5 ind/km ²
Estado de Guárico, Venezuela (Crockett & Eisenberg, 1987)	83-118 ind/km ²

Looking at these densities for *A. seniculus*, perhaps we can identify the preferred hábitat for the species as well as for *Cebus albifrons*, concluding that the sites with the highest densities define preferred habitat (Table 3). There might be some problems with this interpretation, given that reproduction, survival and abundance may not all be positively correlated so that demographic data is needed to assure that there is high survival rate within the high density population (**Johnson**, 2007); some populations of birds and rodents at lower

densities have been shown to have higher survival rates than high density populations **Van Horne**, (1983). However, the majority of studies define preferred habitat using positive correlations with population densities, although demographic information should be included to measure survivability. Following this argument, can we not conclude something about the origin of such species if we know something about their preferences? For a first attempt on the problem of preferred habitat, areas of high density suggest a lot.

Although my research on *Cacajao melanocephalus* leaves much to be accomplished, despite the time I dedicated to it, I have recuperated from the destruction of my notes and library by the guerilla in 1998 that led to my leaving the Estación Biológica Mosiro Itajura-Caparú, and I have been able to publish some results. I managed to publish details such as densities of *Cacajao*, that like *A. seniculus* are ecological densities around the Taraira Lake of southern Vaupés (**Defler**, 2001). This is very definitely a special type of habitat of 48-50 km of lakefront igapó that provide habitat especially for these two species. Recently I have participated in writing another pair of articles about *Cacajao* to be included in a book on the Pitheciidae (**Barnett et al.** in press-a, in press-b).

I invested several years in the research on *Lagothrix lagothricha*, partly because of the huge home range that they utilized in southern Vaupés and their low density, due to habitat poverty. My study group of 24 animals utilized 760 h, which is one of the largest calculated. In contrast, groups on the Duda River used around 169 ha with densities of about 28 animals/km². These data show the extremes between two habitats, one very productive on the Duda river, another quite poor on the Apaporis river (**Defler**, 1987, 1989, 1995, 1996, 1999; **Defler & Defler**, 1996). Even smaller home ranges have been found by Pablo Stevenson's group from the University of Los Andes for *Lagothrix lagothricha* that have not been published.

Although I left the Estación Biológica Mosiro Itajura-Caparú in 1998 because of the guerilla, I am happy to know that the station has continued to function under the administration of Conservation International Colombia and that many young Colombians have been able to finish their thesis projects on primates and other fauna and flora (e.g., **Alarcón-Nieto & Palacios**, 2009). With a little luck and the support of others we hope that these activities continue into the future.

Amazonas

After leaving the Estación Biológica Mosiro Itajura-Caparú in 1998 I decided to search for another more isolated site to continue research in the field. During the search for a secure area, isolated from security concerns I arrived at the the Pu-

rité River, a border river of southern Amacayacu National Park. This place is extremely isolated, requiring six days of travel from Leticia (partly through Brazil) to arrive. Here I was able to construct three small buildings and to accomplish primate censuses at four sites along the Purité river, obtaining results that fully agree with other eastern Colombian censuses of very low population densities of primates (**Defler**, in press). Also, I was able to begin research on the use of space by the primate *Callicebus lucifer* (= *Callicebus torquatus lucifer*). However, the use of this new station (Estación Ecológica Omé) is logistically very complicated, and I have searched for yet another site, closer to Bogotá for my research.

Meta and private reserves

Due to the difficulties of managing the Estación Ecológica Omé and the total cost of a trip there I discovered a solution that allows more continued primate research in the field. I discovered the existence of a private reserve Las Unamas in Meta, made up of gallery forest and a very large 1.300 ha fragment that earlier was a part of a very wide gallery forest connected to the Camoa River, to the east of San Martín, Meta. This reserve forms part of one of the original homesteads (Haciendas) of this part of the llanos. The forest has been protected for many years (although there is some poaching). The primate fauna is made up of five species: *Sapajus apella*, *Alouatta seniculus*, *Saimiri sciureus*, *Callicebus ornatus* and *Aotus brumbacki*. Of these *Callicebus ornatus* requires the most attention due to being classified by the IUCN and Colombia as Vulnerable (VU). I choose to study population densities and preferences of habitat. There are indications that *Callicebus ornatus* can utilize degraded forests and it is common to find groups close to human populations as long as they are not disturbed. Because some studies have calculated extremely high populations in small fragments, it may be that many individuals have escaped forest being cut and have become refugees in nearby fragments (**Mason**, 1966; **Wagner et al.**, 2010). I hope to identify some habitat preferences of these primates and to indicate what natural population densities are. In this case, I hypothesize that the highest populations known do not correlate with the most preferred habitat, since these high populations are clearly related to habitat disturbance.

Callicebus ornatus belongs to a complex of small primates of *Callicebus* that are highly interesting, especially because they are monogamous, a reproductive system not common among the primates (**Defler**, 2010). These small monkeys defend small territories and they are basically frugivores, supplementing with a quantity of small invertebrates such as spiders and orthopterans.

Callicebus has become a strong interest of mine. I have described a new species from southern Caquetá with two colleagues of mine, *C. caquetensis* (Defler *et al.*, 2010). All indications suggest that this species is highly endangered due to destruction of its habitat (García *et al.*, 2010). We have fortunately been able to receive financial support from two Canadian oil companies that will permit two years of research for various persons in our group. The research will include aspects of the species' ecology and its molecular phylogeny.

Colombia continues to offer me many opportunities for primate research and I continue with this effort until I am no longer physically able to do so. This brief resume cannot include many details of my research that actually demand a book, a Project that is also in course.

Acknowledgements

I particularly thank the many Colombians who have given me support in my research during so many years of effort. I include especially professor **Jorge Hernández-Camacho**, Colombia's deceased source of knowledge of so much Colombian biota and my mentor during our time of association. I became a better Colombian biologist, having been associated with him. I also thank **José Vicente Rodríguez Mahecha** of Conservación Internacional Colombia and before that of INDERENA, who gave me physical and psychological support for many difficult efforts in the east of the country and also to my dear friends, the professors **Carlos Moreno Benavides y Amanda de Moreno** who offered me the stability and intellectuality of their home and the security of open arms. I thank my compadre Sr. **Hector Castillo**, a good friend, who has always supported my life and activities in Leticia, helping me to resolve difficult logistics problems. As well, I thank Sr. and Sra. **Pedro y Consuelo Pinzón** who provided a home in La Pedrera and helped resolve so many logistical problems there for my trips to Caparú. I thank professor **Moises Wasserman** of the Universidad Nacional de Colombia who as Decano of the Facultad de Ciencias listened to me and understood my *crie de coeur* and did what was necessary to continue my association with the UNC. I thank the Universidad Nacional de Colombia both in Leticia and in Bogotá for providing an academic home and support for my research endeavors. I thank **Russell Mittermeier**, President of Conservation International for various grants to myself and to so many other field researchers and to **Anthony Rylands**. Who always shared his knowledge when I needed it. I thank **Sara Bennett** for company and her dedication to the many orphan primates what arrived at Caparú, and that continue to appear in Amarayacu doe to human cruelty.

I particularly thank INDERENA, the wildlife Conservation Society, Conservation International, Margot Marsh Foundation for Biodiversity, National Geographic, The Woolly Monkey Foundation, International Primate Protection League, Conservación Internacional Colombia, Fundación Natura, Ohio Biodiversity Alliance, Louiseville Zoological Garden, Primate Action Fund (Conservation International), World Wildlife Fund USA, for the various financial grants given to me throughout the years.

I am especially thankful to Conservación Internacional Colombia for adopting and continuing maintenance of La Estación Biológica Mosiro Itajura – Caparú in Vaupés for the future generations of Colombians who will be able to accomplish research in the Colombian Amazon using this infrastructure.

I give particular thanks to the Universidad Nacional de Colombia (in Bogotá and in Leticia), the Department of Biology and the Facultad de Ciencias for having supported me in my research and for having provided a congenial intellectual home and appreciated colleagues who have provided me with an academic circle of dedicated biologists that has helped me to obtain my academic objectives in research and teaching. I also thank the active people of the Asociación Primatológica Colombiana, who have provided the primatologist-colleagues to make this life's voyage interesting.

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Recibido: 3 de julio de 2012

Aceptado para publicación: 5 de septiembre de 2012.