

EDGE HABITAT PREFERENCES IN THREE TITI MONKEY SPECIES IN COLOMBIA (*CHERACEBUS LUGENS*, *CHERACEBUS TORQUATUS LUCIFER* AND *PLECTUROCEBUS ORNATUS*)

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Abstract

The three titi monkeys *Cheracebus lugens*, *Cheracebus torquatus lucifer* and *Plecturocebus ornatus* prefer edge habitat when occurring in extensive forests. We present preliminary data showing that these three species exhibit their highest densities at the edges of forest types. In gallery forests of Vichada department, *Cheracebus lugens* has densities of 8 groups / km². We found that the same species had crude densities of 0.68 groups/km² in Vaupés department, while their densities increase in edge habitats to 17.5 groups/km². *Cheracebus torquatus lucifer* in Amazonas department exhibits 0.47 groups/ km² crude densities, while their highest densities are in edge habitats along the Cotuhé River at 17.5 groups/km². In a large 1,080 ha forest fragment in Meta department, *Plecturocebus ornatus* exhibit higher densities (around 15 - 17 individuals /km²) in edge habitats facing savanna, as opposed to their overall crude densities throughout this large forest fragment (1.07 ind/ km²). In the case of these *P. ornatus*, the edge habitat is floristically more diverse than the forest 600-700 m away from the forest edge. But, in Vaupés, the edge habitats used by *C. lugens* are less diverse than forest in hilly areas found towards the interior of the forest, where *Cheracebus* densities are lower. There are no comparative floristic diversity data for the forest inhabited by the *C. torquatus lucifer* in this study. Edge habitat preference is an ecological advantage for species like *P. ornatus* when its habitat experiences high rates of loss and fragmentation.

Keywords: Forest choice, primate microhabitats, titi monkeys.

Resumen

Cheracebus lugens, *Cheracebus torquatus lucifer* y *Plecturocebus ornatus* prefieren hábitat de borde de bosque cuando estos primates se encuentran en bosques extensos. Presentamos datos preliminares que muestran que estas tres especies presentan densidades más altas en los bordes de bosques de varios tipos. En bosques de galería del departamento del Vichada, Colombia, *Cheracebus lugens* presenta densidades de 8 grupos / km². La misma especie tiene densidades brutas de 6.1 grupos/km² en el departamento del Vaupés, mientras que sus densidades aumentan en hábitats de borde de bosque a 17.5 grupos/km². *Cheracebus torquatus lucifer* en el departamento de Amazonas tiene una densidad bruta de 8.1 grupos / km², mientras que sus densidades más altas se encuentran en hábitats de borde a lo largo del río Cotuhé (17.5 grupos / km²). En un gran fragmento de 1,080 ha en el departamento del Meta, observamos las densidades más altas de *Plecturocebus ornatus* (alrededor de 50-60 individuos / km²), en hábitats marginales frente a una sabana, en comparación con densidades brutas totales de 1.07 ind/ km² en este fragmento grande de bosque. En el caso de estos *P. ornatus*, el hábitat de borde de bosque es florísticamente más diverso que el bosque a 600-700 m del borde del bosque. Sin embargo, en Vaupés, los hábitats del borde utilizados por *C. lugens* son menos diversos que los bosques en las zonas de colinas encontradas hacia el interior del bosque, donde las densidades de titis son más bajas. No hay datos comparativos de diversidad florística para el bosque habitado por *C. torquatus lucifer* en este estudio. La preferencia del hábitat de bordes de bosque es una ventaja ecológica para especies como *P. ornatus* cuando el hábitat experimenta altas tasas de pérdida y fragmentación.

Palabras clave: Selección de bosque, microhábitats para primates, micos titi.

Introduction

Interesting and variable densities have been observed in various titi species, which often vary according to forest types. For example, several species of titi monkeys are known to have patchy distributions with low densities in extensive, closed-canopy forests and high densities in other types of forest habitat. *Plecturocebus moloch* of the Xingu-Tocantins interfluvium in the southern Brazilian Amazon shows sparse and interrupted distributions (Ferrari et al., 2007) suggesting habitat preferences. *Callicebus personatus*

have high densities in areas of secondary vegetation as opposed to lower densities in adjacent montane pluvial forest (Déda-Chagas and Ferrari, 2010; Pinto et al., 1993; Garcia-Chiarello, 1994). Wagner et al., (2009) found high densities of *Plecturocebus ornatus* in many fragments in the Llanos Orientales but there was no correlation of densities to fragment size and densities of this species are higher in fragments and secondary and disturbed forest, than in primary forests (Wagner et al., 2009; Mason, 1968; Polanco and Cadena, 1993; Hernández-Camacho and Cooper, 1976).

In Peru, van Kuijk (2013) found that *Plecturocebus oenanthe* preferred the boundary between primary and secondary forest over the primary and secondary forest interiors. In Ecuador *Plecturocebus discolor* was detected most often in liana forest (28%), in forest clearings (24%) and in high forest (24%) located in valleys (28%), slopes (24%), and terraces (24%) (Poza, 2004).

Several species of titi monkeys live in forest fragments and many are endangered. *Plecturocebus barbarabrownae* are found in very reduced populations distributed in dry forest fragments in Bahia, Brazil. The species is Critically Endangered and there is not enough of the original forest to be able to define the species' habitat preferences (Printes et al., 2011). *Plecturocebus modestus* (En – Endangered, Veiga et al. 2008a) and *P. olallae* (En – Endangered, Veiga et al. 2008b) (the two species in the Río Beni, Bolivia) exist in remnants of forest vegetation surrounded by grazed woodland on cattle ranches, just as *Plecturocebus ornatus* and *Plecturocebus caquetensis* (Defler, 2010; García and Defler 2013). The first two species are over-hunted and currently three are listed an endangered (EN) (Felton et al., 2006; Veiga et al., 2008a, 2008b) while *Plecturocebus caquetensis* is listed as Critically Endangered (CR) (Defler and García 2012).

Here we discuss the patterns of density in three titi taxa (*Cheracebus lugens*, *Cheracebus t. lucifer* and *Plecturocebus ornatus*; *Cheracebus torquatus lucifer* is a taxon with the same karyomorph as *Cheracebus torquatus* (Bueno and Defler 2010; Benirschke and Bogart 1976), so we consider that *Cheracebus lucifer* is not a good species but is rather a subspecies of *Cheracebus torquatus*). We consider some hypotheses that could explain these variable densities. We also recognize that habitat preferences of many titi species include a positive edge effect and this is positive for their survival in forest fragments. There is no confirmation that *Cheracebus lugens* in Colombia is actually that species rather than *C. t. lucifer*. Despite distinguishing characters defined by Hershkovitz (1990) between these two species, the phenotypes are not distinguishable and can only be distinguished by karyotype and molecular differences (Defler, unpublished data). Hernández-Camacho realized that phenotypically the two were not distinguishable so he named all black *Cheracebus* in Colombia *C. lugens* (Hernandez-Camacho and Cooper, 1976). Using karyotype, we have confirmed that southern populations of *Cheracebus* in Colombia are, indeed, *C. torquatus lucifer* (not *C. lucifer*) (Bueno and Defler, 2010). But whether the northernmost populations of *Cheracebus* are *C. lugens* must be confirmed, although that species has been identified on the right bank of the Río Negro and naturally could extend into Colombia (Casado et al. 2006).

Methods

Density estimations

Densities of *Cheracebus lugens* in Vichada, Colombia, gallery forests, were calculated using a series of experimental

transect censuses during 1979 in El Tuparro National Park, Colombia. The censuses began near the western gateway to the Park, Tapón (5°06'46"N, 69°08'55"W). Because the primate densities were already known from direct counts and knowledge of the groups present, the idea was to evaluate the efficacy of transect censuses on the three diurnal primates that were present. Since the program DISTANCE was unknown at the time, averages were calculated from repeat censuses and a detection width was used to calculate actual densities (Defler and Pinto 1985) (Fig. 1).

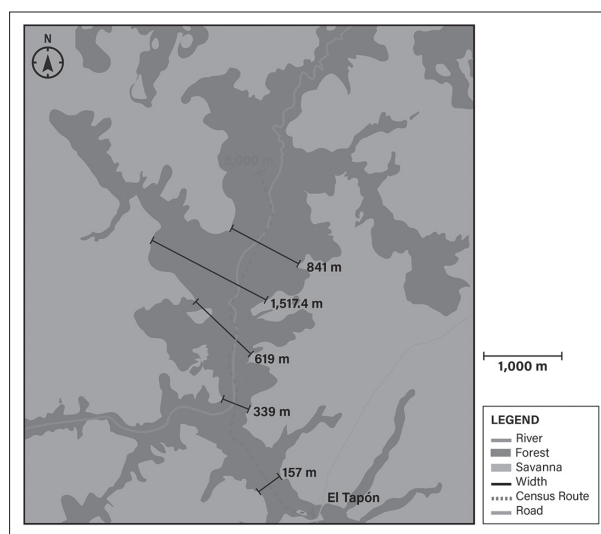


Figure 1. A censused gallery forest at Tapón (El Tuparro National Park) in Vichada, Colombia, showing the 5km census route and some measurements of the width of the forest.

2. During the years 1982-1984 six primates of a pristine closed-canopy forest in southern Vaupés (Estación Biológica Caparú, since changed to Estación Biológica Mosiro Itajura – Caparú - 1°04'58"S, 69°30'49"W) were censused monthly using a line transect, beginning from the edge of a lake towards the interior of the forest to 5 km (accumulated repeat censuses equaled 264 km). The transect towards the forest interior included 900 m of Plio-Pleistocene terrace forest and 4 km of hill forest. Also, the edge of the Igapó forest (blackwater flooded forest) was censused by canoe for 10 km (five on each side of the lake). The repeat censuses on the lake totaled 212 km. DISTANCE 4.0 was used to calculate the six primate species' densities. There was an adjacent band of *C. lugens* groups parallel to the Igapó edge (although they only very rarely entered the Igapó), following the edge of the Pleistocene river terrace above the lake. The band parallel to the lake edge was calculated theoretically based on an adjacent string of four known groups at the edge of the Pleistocene river terrace, that in all cases descended to the edge of the local Igapó using a transition type forest between the Igapó and the Pleistocene terrace forest. A similar band of *C. lugens* groups was found along a creek one kilometer from lakeside. The animals entered and used two different forest types on the opposite sides of the creek (Fig. 2). Habitat types were previously identified by Carvajal et al. (1976).

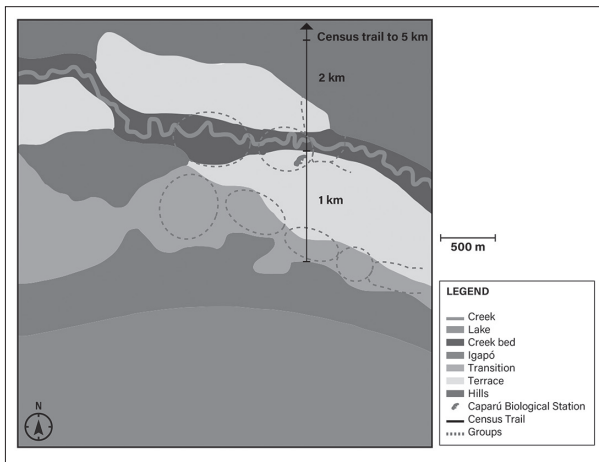


Figure 2. Census area at Estación Biológica Mosiro Itajura - Caparú from lake-side through forest types of Transition (between the Igapó and Pleistocene terrace forest), Pleistocene terrace forest, Creek bottom forest and, Hill forest (see Defler and Defler, 1996 for more discussion of forest types).

3. At the study site of another pristine forest site ($3^{\circ}32'09.8''S$, $69^{\circ}53'27.2.6''W$) in southern Colombia, department of Amazonas, and parallel to the Amacayacu National Park, a census series of a five kilometer transect into the interior of the forest was carried out during the years 2000-2001 for a total of 264 km of repeat censuses, and was analyzed via the DISTANCE 4.0 program. Again, a population of *Cheracebus t. lucifer* along the edge of the river Purité, of five known groups, was used to calculate a theoretical density along the river that was much higher than that on the interior of the forest (Defler, 2013) (Fig. 3).

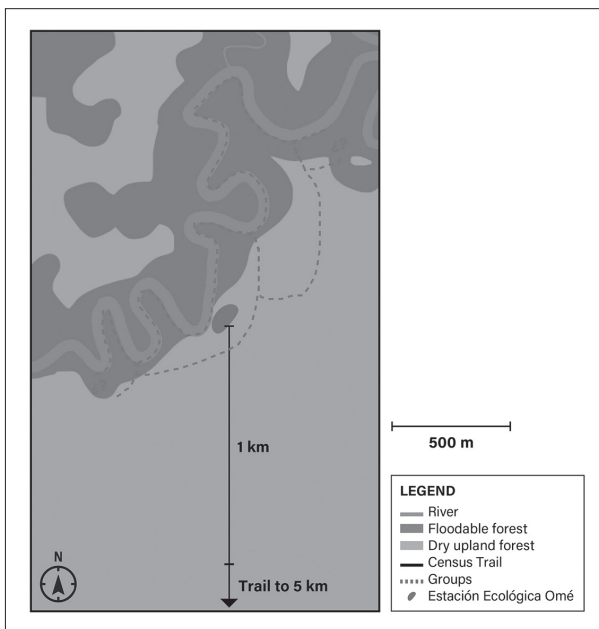


Figure 3. Census site on Purité River, Amazonas department (Omé Ecological Station) showing differing topography from floodable forest to dry upland forest.

4. During the years 2004-2009 eight forest fragments north of the town of San Martín, Meta department ($3^{\circ}41'54''N$,

$73^{\circ}41'56''W$) were censused for local primates, and densities calculated based on direct counts of individuals or troops at each fragment. A large fragment totaling 1,050 ha was censused and data was processed using DISTANCE 6.0 (Fig. 4).

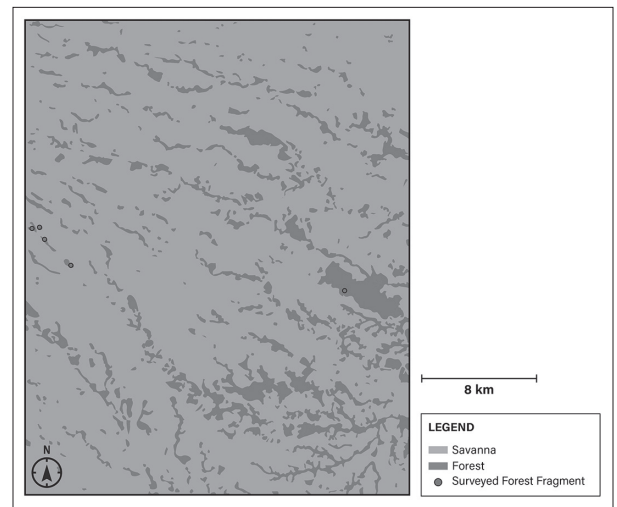


Figure 4. Census sites in Meta department, near San Martín, during 2004-2009. The largest fragment with the red dot is shown with more detail in figure 5. It is part of the Las Unamas Reserve, a private natural reserve belonging to RESNATUR (Association of the Colombian System of Natural Reserves of the Civil Society).

5. During 2010-2012 the same large fragment that had been censused by Carretero-Pinzón (2013ab) (Fig. 5; $3^{\circ}34'27.1''N$, $73^{\circ}27'09.9''W$) was analyzed for the edge population of *P. ornatus* closest to the savanna (Defler, unpublished data). We calculated an ecological density using a determined home range of one group (about 5 ha), built up using about 250 hours of observations and extending these data through the observed band of interlocking groups (Fig. 5).

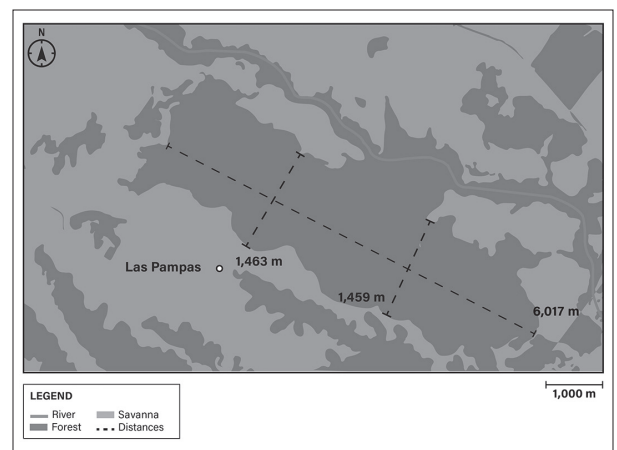


Figure 5. Large 1,000 ha forest (the Unamas Natural Reserve, $3^{\circ}34'27.1''N$, $73^{\circ}27'09.9''W$) in Meta department, Colombia, with some measurements indicated. The white circle marks the owner's house.

Results

The calculated densities are listed in Table 1.

Table 1. Titi densities in different types of habitat in eastern Colombia.

Species	Type of Habitat	Densities	Citation
<i>C. lugens</i>	Gallery forest	8 groups/ km ²	Defler and Pintor, 1985
<i>C. lugens</i>	Interior of Amazonian forest, Estación Biológica Mosiro Itajura - Caparú, Vaupés, Colombia	0.68 groups/ km ²	Defler, 2003, 2013
<i>C. lugens</i>	Parallel to igapó in Amazonian forest, Estación Biológica Mosiro Itajura -Caparú, Vaupés, Colombia	17.5 groups/ km ²	Defler, 2013
<i>C. lugens</i>	Creek bottom in Amazonian forest, Estación Biológica Mosiro Itajura -Caparú, Vaupés, Colombia	17.5 groups/ km ²	Defler, 2013
<i>C.t. lucifer</i>	Interior of Amazonian forest, Estación Ecológica Omé, Amazonas, Colombia	0.16 groups/ km ²	Defler, 2013
<i>C. t. lucifer</i>	River edge in Amazonian forest, Estación Ecológica Omé, Amazonas, Colombia	18.1 groups / km ²	Defler, 2013
<i>P. ornatus</i>	Forest fragments, Meta, Colombia	7.61 – 52.98 groups km ²	Carretero-Pinzón, 2013a,b
<i>P. ornatus</i>	1,000 ha forest “Las Unamas”, Meta, Colombia (crude density)	1.07 groups/km ²	Carretero-Pinzón, 2013a,b
<i>P. ornatus</i>	Population bordering savanna (ecological density) or large 1,000 ha forest “Las Unamas”, Meta, Colombia	15-17 groups / km ²	Defler, unpublished data

In the Vichada gallery forest (Fig. 1) the titi monkeys have a border (or edge) on two sides of their territory. This should hypothetically promote a strong “edge effect” and perhaps be reflected in the fairly high densities of 8 groups/km² that we calculated, based only on 56 accumulated kilometers of census effort. However, the well-defined borders of the habitat and visual recognition of each group resulted in high confidence in the calculation.

Figure 2 depicts the more complex topography and forest types in Estación Biológica Mosiro Itajura - Caparú and outlines known groups of *Cheracebus lugens*. The highest densities at Mosiro Itajura-Caparú are found in the band of transitional vegetation that extends from the edge of the Igapó up to the Pleistocene terrace forest, which is 10-11 m above the highwater of the Igapó. These high densities are repeated along the “bajo” or flood plain of the inland creek that passes near the installation of the research station (1 km via the principle trail from the edge of the Igapó), and ecological densities here attained about the same densities as the lakeside *Cheracebus*. The Plio-Pleistocene hill forest, considered the most diverse forest type botanically according to Defler and Defler (1996), was later contradicted by Clavijo et al. (2009) who concluded that the Pleistocene terrace forest is the most diverse forest type. The Pleistocene terrace forest is not used by the titis except from the creek flood plain and from the transition forest. The hill forest is very sparsely inhabited by titis.

Figure 3 illustrates the use of forest along the Purité River, including high densities of titis along the Purité River (a partial limit of the Amacayacu National Park). The

majority of the forest use of the titis takes place over seasonally inundated forest, but the use extends partially into forest on hilly topography that does not flood. After leaving the influence of the utilized edge vegetation after about 800 m, there was only one group of titis along the rest of the 5km trail.

Figure 4 illustrates the highly fragmented habitat in western Meta Department, where censuses has taken place. The largest censused fragment is a 1,000ha forest that is part of the Natural Reserve Las Unamas and represents perhaps, the last of the remaining forest of western Meta, except for a large, closed-canopy forest along the Guayabero River to the south. The interior of these large forest appears to have very low densities of titis.

Figure 5 shows a closer view of the large, 1,000 ha forest in Las Unamas Natural Reserve. Extensive censuses here show very low densities except for the edges, where high densities are present.

Discussion

Although the majority of edge effects on different biota are negative, some species have been affected in positive ways. Some species might show positive, negative and neutral responses according to the edge type (Ries and Sisk, 2004; Murcia, 1995). There are three categories of effects on any habitat type, abiotic effects (changes in the environmental conditions), direct biological effects (changes in abundances and distribution of the species caused by the physical conditions) and indirect biological effects (species interactions,

pollination and seed dispersal) (Murcia, 1995). An abrupt end to a forest that might be facing a savanna or a body of water is an extreme edge that might generate extremely different conditions, such as xeric or hydric conditions and a complete absence of the forest type (abiotic effects). But other edges can be the interface of two types of forest (such as at the Estación Biológica Mosiro Itajura - Caparú) that also generate an edge effect because of very different flora that do not sustain the same fauna or, does so very poorly (direct and indirect effects).

Faunas can be abruptly different across different floras that are in contact (direct biological effect), for example, Klein (1989) and Spector and Ayzama (2004) have illustrated the abrupt changes in dung and other beetles across changes in vegetation, both within a forest and the forest/savanna ecotone. Many edge effects of birds have been illustrated (Broadbent et al., 2008; Burkey, 1993) and mammals (Harding and Gomez, 2006; Offerman et al., 1995). Several species of primates have also been identified that are sensitive to edge effects both positively and negatively, such as positive effects for lemur density (Lehman et al., 2006), positive effects for *Alouatta macconnelli* and *Saguinus midas*, and negative effects for *Ateles paniscus*, and neutral effects for *Chiropotes chiropotes*, (Lenz et al., 2014).

Titi distributions often show strikingly dissimilar abundances within their distributional areas. Since the previous genus *Callicebus* has recently been split into three genera (Byrne et al., 2016) (*Callicebus*, *Cheracebus* and *Plecturocebus*), it seems a bit more complicated to treat the group as one, although the group as a whole has many similarities such as general morphology, monogamy (rare in primates), territorial defense (but with some home range overlap), paternal care of infants, frequent use of lower forest strata (8-15 m), and, frequent terrestrial behaviors including travel between forest fragments (Bicca-Marques and Heymann, 2013). Some differences have been noted, such as supernumerary adults observed in some species but not in others (*Cheracebus lugens*, *C. t. lucifer*, *Plecturocebus cupreus*, *P. modetius* and *P. personatus*; Bicca-Marques and Heymann, 2013; Defler, 1983).

Only a few titi species have been identified that seem to have greater abundances along water courses, on edges of forest types or other special but often undefined vegetation types, but often the same species abundances fall (sometimes drastically) in parts of the same forest but away from the high-density areas. Ferrari et al. (2007) found no *P. moloch* whatsoever while censusing 812 km of forest within the known distribution of the species. Kulp and Heymann (2015) found no effects of forest edges and secondary forest on red titi (*P. cupreus*) abundances. Heiduck (2002) found that *P. melanochir* preferred primary forest and avoided disturbed forest.

An important difference of our studies from some of these other studies is that the edges of the forests that we studied

along savannas were undisturbed, natural edges that had not been disturbed by recent fragmentation. Our data showed that *Cheracebus lugens* and *C. t. lucifer* and *P. ornatus* enjoyed high densities in certain types of forest such as northern gallery forests of Vichada, and vegetation bands associated with wetlands in Vaupés and in southern Amazonas, Colombia. They were very sparsely distributed in upland, inland forest. We found high densities of *P. ornatus* in forest fragments and along the edge of a large, 1,000 ha forest, bordered by savanna.

Cheracebus lugens in the Estación Biológica Mosiro Itajura – Caparú, generally show widely separated groups in the interior of the forest. For example, a five-kilometer census at this site only detected one group in the last four kilometers of the trail, despite 250 km of repeat surveys over that trail. This pattern of very low densities in the interior of the forest is repeated by *Cheracebus t. lucifer* on the Purité River, southern Colombian Amazon (Defler, 2013) and by *Plecturocebus ornatus* in closed-canopy Colombian forest near the Duda River, Meta department (Carretero-Pinzón, 2013a,b; Polanco and Cadena 1993; Stevenson pers. com.). The more homogeneous densities of *C. lugens* in the Vichada gallery forests may be due to the fact that the habitat was all edge habitat. This may explain the often, high densities of *P. ornatus* found in fragments in the llanos of western Meta as well (Carretero and Defler, 2013; Wagner et al., 2009; Carretero-Pinzón, 2013a,b) in contrast to the very low crude species densities in a large 1,000 ha fragment in Meta, Colombia.

Despite low overall crude densities of *C. lugens* in a pristine rainforest habitat in Vaupés, edge habitats defined by different forest types support an ecological density that was much higher than the crude density throughout the forest. Although these high density ecological belts were not at the edge of a forest bordering savanna, they were centered over special types of forest (Transition forest and Creek bottom forest) while extending in part into Pleistocene river terrace forest. The transition forest was sandwiched between Igapó forest (where the animals were never observed) and the river Terrace forest which were found to be of high diversity (Defler and Defler, 1996; Clavijo et al., 2009). The Creek bottom forest was sandwiched between high diversity hilly Pliocene forest and the high diversity river terrace forest. In the Colombian Llanos, where *Cheracebus lugens* exists in some pristine gallery forests of Vichada, the density of this primate was elevated and evenly spread throughout the study forest (Defler and Pintor, 1985).

In southern Colombia, a population of *Cheracebus t. lucifer* repeated the pattern of *Cheracebus lugens* at Caparú with a low, overall crude density throughout the interior of the forest, but with a very high ecological density along the Purité River. These data show that *Plecturocebus ornatus*, *Cheracebus. lugens* and *C. t. lucifer* generally have higher densities in edge habitats, whether the edge of a forest or a habitat defined by specific types of vegetation (*C. lugens*) such as at Mosiro Itajura - Caparú).

What it is that attracts several species of *Callicebus* to edge habitat is not so clear. One assumes that these habitats have a higher concentration of foods for these monkeys. In the large 1,000 ha forest at Las Unamas the edge habitat is botanically more diverse than interior parts of the forest (Carretero and Defler 2016). This could be part of the explanation, but in the Estación Biológica Mosiro Itajura - Caparú, the high-density strip around the lake is found in low-diversity vegetation, while the highest diversity vegetation in hilly forest (beginning about 1 km from the lake and its Igapó) has very low densities of *Cheracebus lugens* (Defler and Defler, 1996; Cano and Stevenson, 2009). Plant diversity at the Omé Ecological Station is unknown, although the high density *Cheracebus* habitat tends to be in low-lying parts of forest that floods when the nearby river floods. The inland, sparsely populated forest is hilly and well-above floods.

Alouatta seniculus is known to have similar edge habitat preferences in Colombia, although this species is more apt to concentrate in edge habitat over seasonally flooded vegetation when leaf flush is high. This large primate has been found in higher densities along the edge of the Amazonian lake where the species has been studied (Palacios and Rodríguez, 2001). From extensive censuses in that locality we know that *A. seniculus* densities in the interior of the forest are so extremely low, that we could not even detect the species during the 2 ½ years of censuses. But the species was easily detectable from the edge of the forest and especially when there was leaf flush. During early high water in the llanos of Vichada the high densities of *A. seniculus* are obvious due to their vocalizations, just as they are in the Amazonian lake where the Estación Biológica Mosiro Itajura - Caparú is located. We have posited that the high *A. seniculus* densities are due to the early high-water leaf flush which is extensive (Carretero and Defler, 2017), and typical of early high water tropical environments. But this does not seem to be an adequate explanation for high edge densities of the various species of titis discussed in this article.

Edge effects might have ecotone effects that allow the titis to exploit more than one habitat type, since the ecotone presents a variation in plant species available. From this perspective, an edge to a forest might allow an elevated insect and spider population and some preferred trees that are attractive to many titis. Ecotones in a closed-canopy forest might also support a special mix of vegetation that is especially attractive to titis and that allows the maintenance of the local titi population. In future research a careful analysis of specific requirements for the titi population living in one of these higher density population should eventually identify special characteristics of this type of habitat that support such a population.

References

- Benirschke, K. and Bogart, M. H. 1976. Chromosomes of the tan-handed titi (*Callicebus torquatus*), Hoffmannsegg, 1807). *Folia Primatol.* 25:25-34.
- Bicca-Marques, J. C. and Heymann, E. W. 2013. Ecology and behavior of titi monkeys (genus *Callicebus*). In: *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*, Veiga, L. M., Barnett, A. A., Ferrari, S. F. and Norconk, M. A. (eds.), pp. 196-207. Cambridge University Press, Cambridge
- Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C. and Silva, J. N. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* 141:1745-1757.
- Burkey, T. V. 1993. Edge effects in seed and egg predation at two Neotropical rainforest sites. *Biol. Conserv.* 66:139-143.
- Bueno, M. and Defler, T. R. 2010. Aportes citogenéticos en el esclarecimiento de la taxonomía del género *Callicebus* - Citogenetical approach to clarify the taxonomy of the genus *Callicebus*. *Orinoquia* 14 (sup1):139-152.
- Byrne, H., Rylands, A. B., Carneiro, J. C., Lynch Alfaro, J. W., Bertuol, F., da Silva, M. N. F., Messias, M., Groves, C. P., Mittermeier, R. A., Farias, I., Hrbek, T., Schneider, H., Sampaio, I. and Boubli, J. P. 2016. Phylogenetic relationships of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy based on molecular evidence. *Front. Zool.* 13:10
- Cano, A. and Stevenson P. R. 2009. Diversidad y composición florística de tres tipos de bosque en la Estación Biológica Caparú, Vaupés. Colomb. For. 12:63-80.
- Carretero-Pinzón, X. 2013a. An eight-year life history of a primate community in the Colombian Llanos. In: *Primates in Fragments: Complexity and Resilience*, Marsh L. K., Chapman C. A. (eds.), pp. 159-179. Springer, New York.
- Carretero-Pinzón, X. 2013b. Population density and habitat availability of *Callicebus ornatus*, a Colombian endemic titi monkey. In: *Los Primates Colombianos en Peligro de Extinción*, Defler, T. R., Stevenson, P., Bueno, M. L. and Guzman, D. (eds.), pp. 164-173. Asociación Primatológica Colombiana, Bogotá
- Carretero-Pinzón, X. and Defler, T. R. 2016. *Callicebus ornatus*, an endemic Colombian species: Demography, behavior and conservation. In: *Phylogeny, Molecular Population Genetics, Evolutionary Biology and Conservation of the Neotropical Primates*. Ruíz-García and M., Shostell, J. M. (eds.). Nova Science Publisher Inc., New York,
- Carretero-Pinzón, X. and Defler, T. R. 2017. Primates and flooded forest in the Colombian Llanos. In: *Primates in Flooded Habitats*. Barnett, A.A., Matsuda, I., Nowak, K., (eds.), Cambridge University Press, Cambridge.
- Carvajal, L. F. J., Posada, A. F. N., Molina, M. L. C., Delgado, F. A., Acero, D. L. E., Araujo, M. O. and Rodríguez, M. F. 1976. Bosques. In: *La Amazonia Colombiana*

- y sus Recursos. pp. 217-322. Proyecto Radargramétrico del Amazonas, Bogotá.
- Casado, F., Bonvicino, C. R. and Seuánez, H. N. 2006. Phylogeographic analyses of *Callicebus lugens* (Platyrrhini, Primates). *Journal of Heredity*, Volume 98(1):88–92.
- Clavijo, L., Betancur, J. and Cárdenas, D. 2009. Las plantas con flores de la Estación Biológica Mosiro-Itajura-Caparú, Vaupés, Amazonia colombiana. In: Alarcón-Nieto, G. and Palacios, E. (eds.) *Estación Biológica Mosiro Itajura-Caparu*. Conservación Internacional Colombia, Bogotá, pp. 55-98.
- Déda Chagas, R. R. and Ferrari, S. F. 2010. Habitat use by *Callicebus coimbrai* (Primates: Pitheciidae) and sympatric species in the fragmented landscape of the Atlantic Forest of southern Sergipe, Brazil. *Zoologia* 27(6):853-860.
- Defler, T. R. 1983. Observaciones sobre los primates del bajo Mirití-Paraná, Amazonas, Colombia. *Lozania* 46:1-13.
- Defler, T. R. 1996. Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagothricha*). *Am. J. Primatol.* 38:289-302.
- Defler, T. R. 2003. Densidad de especies y organización espacial de una comunidad de primates: Estación Biológica Caparú, Departamento del Vaupés, Colombia. In: *Primatología del Nuevo Mundo*. Pereira-Bengoa, V., Nassar-Montoya, F., Savage, A. et al. (eds.), pp. 23-39. Centro de Primatología Araguatos Ltda., Bogotá.
- Defler, T. R. 2010. *Historia Natural de los Primates Colombianos*. Universidad Nacional de Colombia, Bogotá.
- Defler, T. R. 2013. Species richness, densities and biomass of nine primate communities in eastern Colombia. *Rev. Acad. Colomb. Cienc. Exactas Fis. Nat.* 37:143:253-262.
- Defler, T. R. and Pintor, D. 1985. Censusing primates by transect in a forest of known primate density. *Int. J. Primatol.* 6(3):243-260.
- Defler, T. R. and Defler, S. B. 1996. Diet of a group of *Lagothrix lagothricha lagothricha* in southeastern Colombia. *Int. j. Primatol.* 17(2):161-190.
- Defler, T.R. and García, J. 2012. *Callicebus caquetensis*. The IUCN Red List of Threatened Species 2012: e.T14699281A14699284. <http://dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T14699281A14699284.en>. Downloaded on 15 July 2016.
- Felton, A., Felton, A. M., Wallace, R. B. and Gómez, H. 2006. Identification, behavioral observations, and notes on the distribution of the titi monkeys *Callicebus modestus* Lönnberg, 1939 and *Callicebus olallae*, Lönnberg 1939. *Primate Conserv.* 20: 41-46.
- Ferrari, S. F., Bobadilla, U. L. and Emidio-Silva, C. 2007. Where have all the titis gone? The heterogenous distribution of *Callicebus moloch* in eastern Amazonia and its implications for the conservation of Amazonian primates. *Primate Conserv.* 22:49-54.
- Flaspohler D. J., Temple S. A. and Rosenfield R. N. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecol. Appl.* 11(1):32-46.
- García-Chiarello, A. 1994. Density and habitat use of primates at an Atlantic forest reserve of southeastern Brazil. *Rev. Bras. Biol.* 35(1):105-110.
- García, J. and Defler, T. R. 2013. Análisis preliminar de la pérdida y fragmentación del hábitat de *Callicebus caquetensis*. In: *Primates Colombianos en Peligro de Extinción*, Defler, T. R., Stevenson, P. R., Bueno, M. L. and Guzmán Cano, D. C. (eds.), pp. 259-276. Asociación Primatología de Colombia, Bogotá.
- Harding E. K. and Gomez S. 2006. Positive edge effects for arboreal marsupials: an assessment of potential mechanisms. *Wildlife Res.* 33(2):121-129.
- Hernández-Camacho, J. and Cooper, R. W. 1976. The non-human primates of Colombia. In: *Neotropical Primates: Field Studies and Conservation. Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates*. Thorington, R. W. and Heltne, P. G. Jr., pp. 35-69. National Academy of Sciences, Washington, D. C.
- Hershkovitz, P. 1990. Titis, new world monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): a preliminary taxonomic review. *Fieldiana Zool. New Series*, Field Museum of Natural History, Chicago.
- Heiduck, S. 2002. The use of disturbed and undisturbed forest by masked titi monkeys *Callicebus personatus melanochir* is proportional to food availability. *Oryx* 36:13-139.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70(6):1715-1725.
- Kulp, J. and Heymann E. W. 2015. Ranging, activity budget, and diet composition of red titi monkeys (*Callicebus cupreus*) in primary forest and forest edge. *Primates* 56:273-278.
- Lehman, S. M., Rajaonson, A. and Day, S. 2006. Edge effects and their influence on lemur density and distribution in southeast Madagascar. *Am. J. Phys. Anthropol.* 129:232-241.
- Lenz, B. B., Jack, K. M. and Spironello W. R. 2014. Edge effects in the primate community of the biological dynamics of forest fragments project, Amazonas, Brazil. *Am. J. Phys. Anthropol.* 155:436-446.
- Mason, W. 1968. Use of space by *Callicebus* groups. In: *Primates: Studies in adaptation and variability*. Jay, P. (ed.), pp. 200-216. Holt, Rinehart and Winston, New York.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10(2):58-62.
- Offerman H. L., Dale V. H., Pearson S. M., Bierregaard R. O. and O'Neill R. V. 1995. Effects of forest fragmentation on neotropical fauna: current research and data availability. *Environ. Res.* 3:191-211.
- Palacios, E. and Rodríguez, A. 2001. Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a southeastern Colombian rainforest. *Am. J. Primatol.* 55: 233-51.
- Pinto, L. P. A., Costa, C. M. R., Strier, K. B. and da Fonseca, G. A. B. 1993. Habitat, density and group size of primates in a Brazilian tropical forest. *Folia Primatol.* 61:135-143.

- Polanco–Ochoa R. and Cadena A. 1993. Use of space by *Callicebus cupreus ornatus* (Primates: Cebidae) in La Macarena, Colombia. *Field Studies of New World monkeys, La Macarena, Colombia* 8:19-32.
- Pozo-R., W. E. 2004. Preferencia de hábitat de seis primates simpátricos del Yasuní, Ecuador. *Ecol. Appl.* 3(1,2):128-133.
- Printes, R. C., Rylands, A. B. and Bicca-Marques, J. C. 2011. Distribution and status of the Critically Endangered blond titi monkey *Callicebus barbarabrownae* of north-east Brazil. *Oryx* 45(3):439-443.
- Ries, L. and Sisk, T. D. 2004. A predictive model of edge effects. *Ecology* 85(11): 2917-2926.
- Spector, S. and Ayzama, S. 2003. Rapid Turnover and Edge Effects in Dung Beetle Assemblages (Scarabaeidae) at a Bolivian Neotropical Forest–Savanna Ecotone. *Biotropica* 35(3):394-404.
- Van Kuijk S. 2013. Living on the edge: Critically endangered San Martin titi monkeys (*Callicebus oenanthe*) show a preference for forest boundaries in C.C. Ojos de Agua, Peru. *Canopy* 14(1):18-20.
- Veiga, L. M., Wallace, R. B. and Martinez, J. 2008a. *Callicebus modestus*. The IUCN Red List of Threatened Species 2008: e.T41550A10498144. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41550A10498144.en>. Downloaded on 11 January 2016.
- Veiga, L. M., Wallace, R. B. and Martinez, J. 2008b. *Callicebus olallae*. The IUCN Red List of Threatened Species 2008: e.T3554A9939925. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T3554A9939925.en>. Downloaded on 11 January 2016.
- Wagner, M., Castro, F. and Stevenson, P. R. 2009. Habitat characterization and population status of the dusky titi (*Callicebus ornatus*) in fragmented forests, Meta, Colombia. *Neotrop. Primates* 16(1):18-24.
- Wallace, R. B., Gómez, H., Felton, A. and Felton, A. M. 2006. On a new species of titi monkey, genus *Callicebus* Thomas (Primates, Pitheciidae), from western Bolivia with preliminary notes on distribution and abundance. *Primate Conserv.* 20: 29-39.