

EDGE EFFECTS ON FRUGIVOROUS AND NECTARIVOROUS BAT COMMUNITIES
IN A NEOTROPICAL PRIMARY FOREST IN FRENCH GUIANAMarguerite DELAVAL¹ & Pierre CHARLES-DOMINIQUE²

SUMMARY. — The impact of a road crossing a continuous Guyana primary forest was studied through the analysis of qualitative and quantitative changes in a frugivorous and nectarivorous bat community at different distances from forest edge. Bats were captured along three 3-km forest transects perpendicular to the edge, and at the Nouragues Station located 150 km in the interior of the primary forest block, in an uninhabited area. Along the 3-km transects, we caught over seven times more individuals than in primary forest, this value decreasing according to the distance from the edge. Moreover, at the very edge, species richness was higher than along transects, probably due to exchanges between primary forest and the open habitats. On the contrary, diversity values at forest edges were lower than in primary forest, with a demographic explosion of a few opportunistic phyllostomid species such as *Carollia perspicillata* and *Artibeus jamaicensis*. Species restricted to degraded habitat like *Glossophaga soricina* and *Artibeus cinereus* were still present 3 km away from the edge, where the proportion of *C. perspicillata* was seven times higher than in primary forest at Nouragues. These changes in the community of bats have important consequences on seed and pollen dispersal. So edge effects may significantly affect both faunal and floral assemblage. We conclude that changes in bat community occur up to at least 3 km from forest edge, i. e. at a greater distance than that found for all other vertebrates previously studied. By their implications our results should be considered in habitat and species conservation management plans.

RÉSUMÉ. — *Effets de lisière sur les peuplements de chauves-souris frugivores et nectarivores de forêt primaire néotropicale en Guyane française.* — Afin d'étudier l'impact d'une route traversant une forêt primaire guyanaise continue, nous avons étudié les changements quantitatifs et qualitatifs du peuplement de chiroptères frugivores et nectarivores à différentes distances de la lisière. Les captures ont été effectuées le long de trois transects de 3 km chacun, partant de la lisière vers l'intérieur du bloc forestier ainsi qu'à la Station des Nouragues, située 150 km dans l'intérieur du bloc forestier, dans une zone intacte inhabitée. En lisière nous avons capturé sept fois plus d'individus qu'en forêt primaire, le nombre de captures diminuant au fur et à mesure que l'on s'éloigne de la lisière. De plus, les bordures révèlent une plus grande richesse spécifique que le long des transects, sans doute à cause de l'échange de chauves-souris entre forêt primaire et milieu ouvert. En revanche la diversité spécifique sur les 3 km de profondeur de lisière est plus faible qu'en forêt primaire témoin, avec une explosion démographique de quelques frugivores opportunistes comme *Carollia perspicillata* et *Artibeus jamaicensis*. A 3 km de la lisière, des espèces inféodées aux milieux ouverts comme *Glossophaga soricina* et *Artibeus cinereus* sont encore présentes, et la proportion de *C. perspicillata* y est sept fois plus grande qu'en forêt primaire des Nouragues. Ces changements dans la communauté de chiroptères ont des conséquences sur la pollinisation et sur la dispersion des graines. La lisière affecte donc les communautés animales et végétales. Nous concluons que les changements dans les communautés de chauves-souris ont lieu au moins jusqu'à 3 km des lisières, ce qui est plus important que ce qui avait été estimé jusqu'alors pour d'autres vertébrés. Ces résultats devraient être pris en compte par les gestionnaires de l'environnement et de la conservation des espèces.

Deforestation occurs at an alarming rate in the lowland tropics and constitutes a major threat to global biodiversity (Bierregaard & Laurance, 1997). Worldwide Biodiversity conser-

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vation in increasingly fragmented natural habitats requires an understanding of the effects of habitat edges on plant and animal communities. Edge effects result from interactions between two adjacent ecosystems that are separated by an abrupt transition (edge) (Murcia, 1995). The construction and maintenance of roads lead to habitat alteration with the consequent population size reduction of many species, and the creation of edges with alien fauna intruding into natural habitats (Goosem, 1997).

Murcia (1995) distinguished three types of edge effects: (1) abiotic effects involving changes in physical environmental conditions that result from proximity to a structurally dissimilar matrix such as increased amounts of sunlight, higher wind speeds, and larger fluctuations in temperature and humidity (Kapos *et al.*, 1997; Malcolm, 1994); (2) direct biological effects involving changes in the abundance and distribution of species caused directly by the physical conditions near the edge and determined by the physiological tolerances of species; (3) indirect biological effects, involving changes in species interactions, such as predation, competition and biotic pollination and seed dispersal. So, abiotic conditions affect plant community composition and structure (Malcolm, 1994; Didham & Lawton, 1999) and hence animal communities.

Several studies have shown that up to several hundred meters inwards, edge effects can have consequences on vegetation structure (Laurance *et al.*, 2003), on seed predation (Burkey, 1993), and can affect assemblages of underground birds (Restrepo & Gomez, 1998; Dale *et al.*, 2000), light-loving butterflies (Lovejoy *et al.*, 1986), rodents and small marsupials (Laurance, 1991b). Laurance (1991a) concluded that edge effects often penetrate 200 m into rainforest and may be detectable up to 500 m from the edge. However, edge is often considered as beneficial to wildlife because species diversity generally increases near habitat edges (Yahner, 1988).

Several studies have demonstrated that species composition and abundance of bat community are negatively affected by forest fragmentation and perturbation (Fenton *et al.*, 1992; Ochoa, 1992; Estrada *et al.*, 1993; Brosset *et al.*, 1996; Laurance & Bierregaard, 1997; Cosson *et al.*, 1999; Law *et al.*, 1999; Ochoa, 2000; Schulze *et al.*, 2000; Estrada & Coates-Estrada, 2002). But, studies of edge effects on bats in Neotropical rainforests are lacking.

Bats constitute a good mammalian model for studying habitat changes and have a great potential as indicators of levels of habitat disruption in many parts of the world (Fenton *et al.*, 1992; Medellín *et al.*, 2000). Because of their high mobility, bats are able to respond quickly to environmental modifications and are of valuable interest in the study of the deforestation impacts in both short and long term (Charles-Dominique, 1986; Fleming, 1986; Estrada *et al.*, 1993; Brosset *et al.*, 1996).

Bats are of paramount importance in neotropical rainforest ecosystems because of their abundance, diversity and ecological roles. They account for approximately 50% of the neotropical mammal species and constitute the most important order of mammals in neotropical rainforest (Emmons & Feer, 1990). Up to 76 bat species may coexist in a given forest site in French Guiana, corresponding to as many species as all other species of mammals (Simmons & Voss, 1998; Charles-Dominique *et al.*, 2001; Charles-Dominique, pers. obs.). Bats pollinate many plants and contribute to forest regeneration by dispersing seeds (Gardner, 1977; Heithaus, 1982; De Foresta *et al.*, 1984; Charles-Dominique, 1995) and are thought to disperse more seeds than birds (Medellin & Gaona, 1999). Zoochory is particularly widespread within pioneer plants and nearly half of the most abundant species are bat dispersed (Charles-Dominique, 1986).

We studied the effect of the edge created by a road in French Guiana, asking how distance from the edge affected the community of bats by analyzing changes in structure community, number of individuals, species richness and relative abundance of species. Moreover, we look whether edge effects have consequences up to 500 m from edge in reference to Laurance (1991a).

MATERIAL AND METHODS

STUDY SITE AND SAMPLING

Three independent transects, called here "road study sites", starting from the edge toward the forest interior were located along the roads RN1 and D21 in the North of French Guiana (5°09'N, 52°52'W; 5°18'N, 53°02'W; and 5°16'N, 52°55'W). RN1, the only road joining the country from East to West, is daily used by a great number of cars, whereas D21 is mainly used by trucks. Both roads are about 5-6 m wide with two 40-50 m wide road shoulders covered with second growth vegetation made of pioneer plant species such as *Solanum* spp., *Piper* spp., *Vismia* spp. and *Cecropia* spp. As this vegetation is regularly clear-cut, the secondary growth is maintained, making a real habitat disruption with the

native vegetation bordering the road (Goosem, 1997). The three 3 000 m long transects were established perpendicularly to the edge (only on one side of the road), distant of 15 kilometres from each other. We checked by direct observations and with a Landsat satellite image taken in 2001 that no other perturbations were present in these areas. In order to study the progressive decreasing of edge effects, captures were performed for each transect in nine sites located at the following distances: edge, 50 m, 200 m, 400 m, 600 m, 800 m, 1 000 m, 2 000 m, and 3 000 m.

The primary forest used for comparisons with the “road study sites” is “Les Nouragues” Biological Station (CNRS-UPS 656, $-4^{\circ}5'N$, $52^{\circ}42'W$). This uninhabited forest, 25 km from the first village or the first road, is situated 150 km away “road study sites”. However both sites belong to the same continuous primary rainforest block. Despite their relative remoteness, but considering the continuity and the uniformity of the forest, we can postulate that bat communities present high similarity between these two sites. Indeed, forest physiognomy and floristic are similar with the same dominant families of trees (Caesalpiniaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae) (Sabatier & Prévost, 1990; Sabatier, 1993; Poncy *et al.*, 2001). There are only some slight differences at the specific level (Brosset *et al.*, 1996; Simmons & Voss, 1998), and we can consider that general structures of bat communities were initially very close.

Bats were captured using mist nets (10 m \times 2 m or 12 m \times 2 m, mesh size 16 mm) set at ground level. Nets were continuously checked from dusk (18:30 hours) until after midnight or until dawn. In each location of each transect mist nets were set at two different places, during two successive nights. For each location, the number of mist nets, their length and the operating time of capture were noted in order to estimate an index of abundance (number of captures/hour/m of mist net). For each capture, the station, time, species, sex, reproductive status, weight and forearm length were noted. Each species was assigned to a guild according to our observations and additional information provided by literature (Bonaccorso, 1979; Brosset & Charles-Dominique, 1990; Kalko, 1995; Simmons & Voss, 1998): (1) canopy frugivores (forage mostly on fruits that grow in the trees of the canopy and subcanopy level), (2) understorey frugivores (forage mostly on fruits of shrubby and epiphytes understorey plants), (3) nectarivores and (4) insectivores-nectarivores (feeding mostly upon insects and pollens). Taxonomic nomenclature follows Charles-Dominique *et al.* (2001).

DATA ANALYSES

We used ANOVAs, after logarithmic transformation, for inter-transect and inter-net-site comparisons, Chi-square test of independence for guild proportion comparisons between netting stations. Linear regression was performed to evaluate the relationship between capture rate and distance from edge. Community diversities were estimated with the Shannon index ($H' = -\sum p_i \times \ln(p_i)$) where p_i is the relative proportion of species i .

Differences in the specific composition of bat guilds between pairs of habitats were evaluated using the similarity coefficient of Morisita-Horn ($C = 2\sum(a_{ni} \times b_{ni}) / [(da + db) \times aN \times bN]$), with $da = \sum a_n^2 / aN^2$, where aN is the total number of individuals in a site A, and a_n the number of individuals of species i in the site A (alike for bN and b_n in a site B) (Magurran, 1988). This index ranges from 0 (very dissimilar habitat) to 1 (very similar habitat).

We analyzed patterns of bat species accumulation against sampling effort. The number of individuals is the best measure of sampling effort when density varies among sites (Willott, 2001). Curves were smoothed by the mean of 100 randomisations (Estimates Software, Colwell, 1997) and fitted with a Clench model. This model assumes that the probability of adding species to the list decreases with the number of species already recorded, but increases over time: $S(t) = at / (1 + bt)$ where t is a measure of effort (in our case the number of individuals), $S(t)$ is the predicted number of species at t , a represents the rate of increase at the beginning of the sampling, and b is species accumulation. The predicted asymptote was calculated as a/b . In order to statistically discriminate between these predicted species richness, we performed the same calculation directly from raw capture data for each habitat, and reiterated this procedure after each of 15 random reorganization of the raw capture data set. This produced 15 estimations of species richness for each site that were compared using the nonparametric Mann-Whitney U test. Statistics analyses were performed with SYSTAT 9.0, and Chi-square test of independence with StatBoxPro 5.0.

RESULTS

During this study, 1430 frugivorous, 698 nectarivorous and 80 insectivorous-nectarivorous bats belonging to 20, 6 and 6 species respectively were recorded (Table I). These guilds represent 83% of the total bat captures and 52% of the total bat species recorded during this study. Because there was no difference between the three transects in the capture rate value ($F = 0.324$; $df = 2$; $P = 0.73$) or in the number of species ($F = 0.239$; $df = 2$; $P = 0.79$) we pooled data. No significant differences in capture rate and in number of species were recorded for net-sites between 50 m and 1 km ($F = 1.487$; $df = 5$; $P = 0.23$ and $F = 0.955$; $df = 5$; $P = 0.46$ respectively). Likewise, net-sites between 2 km and 3 km were not significantly different ($F = 0.006$; $df = 1$; $P = 0.94$ for capture rate and $F = 0.068$; $df = 1$; $P = 0.79$ for number of species). Consequently, we pooled transect data from 50 m to 1 km and from 2 km to 3 km for comparison tests.

BAT SPECIES RICHNESS IN PRIMARY FOREST AND EDGE

The rate of capture is 7 to 8 times higher on edge than in primary forest (Table I). The total capture rate decreases significantly with distance from edge ($r = 0.706$; $P = 0.01$).

TABLE I

Bats captured along forest transects (from edge to 3 km) and at Nouragues station (primary forest)

| | Guild ^a | Edge | 50m-200m | 400m-600m | 800m-1km | 2km | 3km | Nouragues | Total |
|--|--------------------|--------------------------|-----------------|-----------------|-------------------------|----------|----------|--------------------------------------|-------|
| Carollinae | | | | | | | | | |
| <i>Carollia brevicauda</i> | GF | | | | | | | 19 | 19 |
| <i>Carollia perspicillata</i> | GF | 224 | 91 | 27 | 53 | 46 | 42 | 97 | 580 |
| <i>Rhinophylla pumilio</i> | GF | 3 | 7 | 11 | 44 | 10 | 27 | 150 | 252 |
| Stenoderminae | | | | | | | | | |
| <i>Artibeus cinereus</i> | CF | 9 | 8 | 2 | 2 | 1 | 2 | | 24 |
| <i>Artibeus concolor</i> | CF | 5 | | | | | | 5 | 10 |
| <i>Artibeus gnomus</i> | CF | | 1 | 2 | | | | 20 | 23 |
| <i>Artibeus jamaicensis</i> | CF | 27 | 18 | 23 | 8 | 4 | 6 | 138 | 224 |
| <i>Artibeus lituratus</i> | CF | 2 | 2 | 3 | 1 | 1 | | 32 | 41 |
| <i>Artibeus obscurus</i> | CF | 5 | 6 | 6 | 14 | 5 | 6 | 118 | 160 |
| <i>Chiroderma trinitatum</i> | CF | 1 | | | | | | 3 | 4 |
| <i>Chiroderma villosum</i> | CF | | | | | | | 3 | 3 |
| <i>Ectophylla macconnelli</i> | CF | | 1 | 1 | 3 | 1 | 2 | 17 | 25 |
| <i>Platyrrhinus brachicephalus</i> | CF | 1 | | | | | | | 1 |
| <i>Platyrrhinus helleri</i> | CF | 1 | | | 1 | | | 15 | 17 |
| <i>Sturnira lilium</i> | GF | 4 | | | | | | | 4 |
| <i>Sturnira tildae</i> | GF | 2 | | 2 | | | | 18 | 22 |
| <i>Uroderma bilobatum</i> | CF | 1 | | 1 | 1 | | | 7 | 10 |
| <i>Vampyressa brocki</i> | CF | | 1 | | | | | 1 | 2 |
| <i>Vampyrodes caraccioli</i> | GF | | | | | | | 1 | 1 |
| Glossophaginae | | | | | | | | | |
| <i>Anoura caudifer</i> | N | 3 | | | | | 1 | | 4 |
| <i>Anoura geoffroyi</i> | N | | | | | | | 147 | 147 |
| <i>Glossophaga soricina</i> | N | 5 | 4 | | 4 | 5 | 2 | | 20 |
| <i>Lichonycteris obscura</i> | N | 1 | | | | | | | 1 |
| <i>Lionycteris spurrelli</i> | N | 1 | | 1 | | | | 321 | 322 |
| <i>Lonchophylla thomasi</i> | N | 1 | | 8 | 1 | 2 | 1 | 190 | 203 |
| Phyllostominae | | | | | | | | | |
| <i>Glyphoncycteris sylvestris</i> | I-N | | | | | | | 4 | 4 |
| <i>Phyllostomus discolor</i> | I-N | | | | 1 | | | | 1 |
| <i>Phyllostomus elongates</i> | I-N | 1 | 7 | 2 | 3 | 7 | 3 | 16 | 39 |
| <i>Phyllostomus hastatus</i> | I-N | | 1 | | | | | 7 | 8 |
| <i>Phyllostomus latifolius</i> | I-N | | | | | | | 13 | 13 |
| <i>Phylloderma stenops</i> | GF | | | | | | | 8 | 8 |
| <i>Trinycteris nicefori</i> | I-N | 1 | 2 | | 1 | 1 | | 10 | 15 |
| Number of captures | | 298 | 149 | 89 | 137 | 83 | 92 | 1 360 | 2 208 |
| Number of species | | 20 | 13 | 13 | 14 | 11 | 10 | 25 | 32 |
| Net-hour length (m) (m.h.10 ³) | | 4.6 | 5.5 | 5.1 | 11.9 | 9.1 | 10.6 | 170.5 | |
| Capture rate (10 ⁻²) | | 6.5 | 2.7 | 1.7 | 1.2 | 0.9 | 0.8 | 0.8 | |
| Diversity (Shannon index H') | | 1.13 | 1.47 | 1.93 | 1.67 | 1.57 | 1.53 | 2.34 | |
| Sampling periods ^b | | 2001 (d + w) 2002 (d) | 2001 (d + w) | 2001 (d + w) | 2001(d + w) 2002 (d) | 2002 (d) | 2002 (d) | 2000 (d) 2001 (d + w) 2002 (d) | |

^a Guilds are as follows: CF = canopy frugivore; GF = understorey frugivore; N = nectarivore; IN = insectivore-nectarivore;^b d = dry season; w = wet season.

Species richness, both observed and extrapolated by Clench model appears to be greater in Nouragues than in transects ($U = 55$; $P = 0.017$ for 50 m-1 km and $U = 1000$; $P = 0.000$ for 2 km-3 km), but, it is not significantly different from edge. Edge species richness is significantly higher than that observed at 50 m-1 km ($U = 42$; $P = 0.003$) and than that recorded at 2 km-3 km ($U = 0,000$; $P = 0.000$). Moreover, species richness at 50 m-1 km section is greater than that recorded for 2 km-3 km section ($U = 0.000$; $P = 0.000$) (Fig. 1).

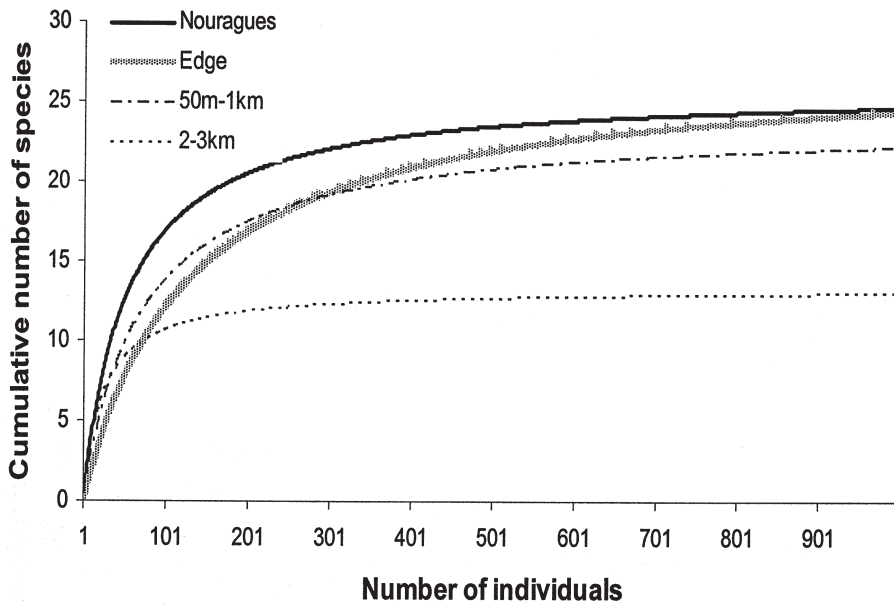


Figure 1. — Curves extrapolated by Clench model. Constants values (a and b) and value of bat species richness (predicted asymptote calculated by a/b) are: a = 0.22, b = 0.008, a/b = 28 species for edge; a = 0.332, b = 0.014, a/b = 24 species for 50 m-1 km; a = 0.544, b = 0.041, a/b = 13 species for 2 km-3 km and a = 0.399, b = 0.015, a/b = 27 species for Nouragues.

The guilds at edge and along transects displayed similar characteristics. Dominant species were identical when using the Morisita-Horn's similarity coefficient: $C = 0.82$ for both edge and 50 m-1 km section; $C = 0.81$ for edge and 2 km-3 km section; and $C = 0.97$ for 50 m-1 km and 2 km-3 km sections. In contrast, the specific composition of guild at the Nouragues primary forest control site was highly dissimilar to that, both in edge and transects: $C < 0.3$ for all edge and transect sites.

Along edge, understory frugivore guild represents more than 75% of the total bat captures against 21% at Nouragues. At 3 km from edge, understory frugivores still represent 54% of captures. There is no difference between Nouragues and transects for proportions of insectivore-nectarivore guild, but this proportion appears to be significantly reduced at the edge. Nectarivore and canopy-frugivore guilds are significantly more abundant at Nouragues

TABLE II

Proportion (%) of individuals per guild Chi-square tests of independence between guilds and habitats. Dependence between guilds and habitats is significant ($df = 9$; $\chi^2 = 735.5$; $p < 0.001$)

| | Nouragues | Edge | 50 m-1 km | 2 km-3 km |
|---------------------------|----------------|----------------|----------------|----------------|
| Canopy Frugivores | 26.4 (+) ** | 17.4 (-)*** | 28 (+) NS | 16 (-)*** |
| Understorey Frugivores | 21.5 (-)*** | 78.2 (+)*** | 62.7 (+)*** | 71.4 (+)*** |
| Nectarivores | 48.4 (+)*** | 3.7 (-)*** | 4.8 (-)*** | 6.3 (-)*** |
| Insectivores-Nectarivores | 3.7 (+) NS | 0.7 (-)*** | 4.5 (+) NS | 6.3 (+)* |

(+): observed proportion > predicted proportion.

(-): observed proportion < predicted proportion.

Test results are indicated by * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$).

Shannon-Wiener diversity is lowest at edges. It increases from edge up to 600 m and is stabilized up to 3 km. However, diversity values at 3 km still remain lower than those at Nouragues (Table I).

COMMUNITY STRUCTURE

Dominant species in edge is *Carollia perspicillata* with more than 75% of total captures. The number of *C. perspicillata* decreases significantly with distance from edge ($r = 0.695$; $P = 0.012$) but at 3 km from edge it still remains seven times that of Nouragues values. Curves of rank abundance are similar for both edge and transect, with few dominant species (*C. perspicillata* and *Artibeus jamaicensis* at edge and up to 600 m from edge; *C. perspicillata* and *Rhinophylla pumilio* from 600 m to 3 km from edge), the other species being uncommon. At Nouragues, the curve is very different and represents equilibrium communities, and the three more abundant species are nectarivores (Fig. 2).

Seven of 16 bat species found in Nouragues primary forest were not found in edge and transects (principal species are *Carollia brevicauda*, *Anoura geoffroyi*, *Phyllostomus latifolius* and *Phylloderma stenops*). These species had been apparently virtually eliminated from altered habitats. On the other hand, between edges and transects, 16 species (particularly *C. perspicillata*, *A. jamaicensis*, *Artibeus cinereus*, *Glossophaga soricina*) are present in both habitats. Five species (in particular *Sturnira lilium* and *Artibeus concolor*) are present on edge but not along transects, and six species are found along transects but not on edges (mainly *Artibeus gnomus* and *Ectophylla macconnelli*).

G. soricina and *A. cinereus*, which are absent from Nouragues, are still found at 3 km from the edge.

DISCUSSION

COMMUNITIES STRUCTURE

The first result of this study is the confirmation of the great abundance of *C. perspicillata* and *A. jamaicensis* in edge habitats, as pointed out by Cosson (1994) and Brosset *et al.* (1996) who described a proliferation of some opportunistic frugivorous phyllostomid species in deforested areas. Dominance of a few number of species and low diversity are the consequences of an alteration of the environment, whereas high diversity values and low relative abundance of the most common species are related to undisturbed habitats (Medellin *et al.*, 2000). Young regrowth are characterized by a small number of plant species which are present in high densities (Prévost, 1981) and produce fruit all along the year (De Foresta *et al.*, 1984). This permanent food concentration localized along the road favours both *C. perspicillata* which feeds

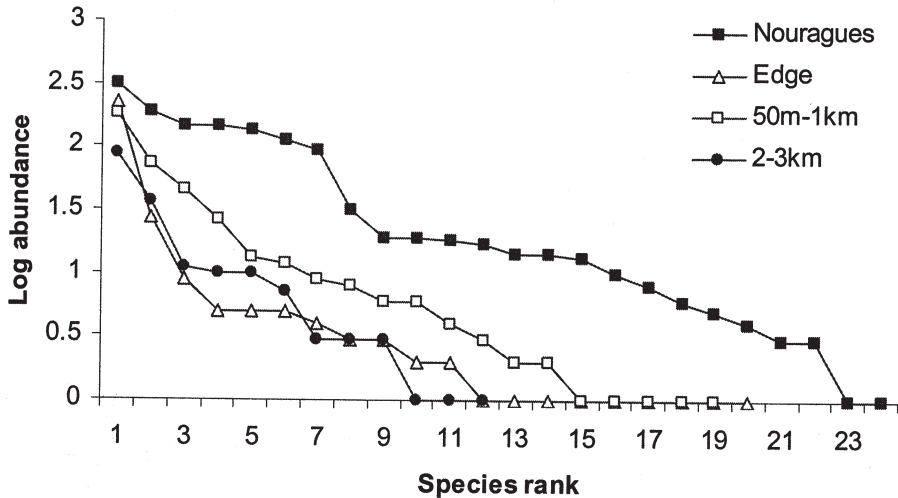


Figure 2. — Curve of rank abundance for each habitat.

mostly upon genera *Piper*, *Solanum* and *Vismia* (Fleming, 1988) and *A. jamaicensis* which is the main consumer of *Cecropia obtusa* and *C. palmata* (Charles-Dominique, 1986). This situation explains the high abundance of the understory frugivore *C. perspicillata* at the edge and its progressive decrease toward the forest interior (Restrepo *et al.*, 1999). However, at 3 km from the edge its relative abundance is still 7 times higher than in Nouragues, representing 46% of the total captures, against 7% in Nouragues. The daily movements of *C. perspicillata* were estimated by radio tracking to 1.5 km in primary forest (Charles-Dominique, 1991), but Fleming (1988) and Estrada & Coates-Estrada (2002) recorded movements of ca 3 km between forest fragments at Los Tuxtlas, Mexico.

The canopy frugivore *A. jamaicensis* is abundant at the edge and in the first 600 m of transects (6 to 8 times higher than in Nouragues) but at 3 km its relative abundance is close to those observed in Nouragues. This species is known to make long flights up to 10 km to feed in flocks on large concentrated fruit productions (Morrison, 1978a, b, 1980; Charles-Dominique, 1986). In the present situation, the edge favours a food concentration, different by its temporal permanence from large trees producing many fruit during a short period, such as *Ficus* spp., while *Cecropia obtusa* and *C. palmata* generate fruit during long periods (Charles-Dominique, 1986), but very localized. *A. jamaicensis* making their long range movements above the canopy, it seems normal that they are only abundant near the edge and not 2 or 3 km farther in the understory.

The insectivores-nectarivores of the subfamily Phyllostominae seem to be particularly sensitive to habitat disturbances, with the dominance of *Phyllostomus elongatus* and the very low representation of the other species of its category along transects. For Medellín *et al.* (2000) a high number of Phyllostominae bats in a community is a good indicator of a low level of disturbance.

One may rightfully ask whether differences between transects and Nouragues are due to edge or site effect. There is no difference in bat diversity between 500 m and 3 km from the forest edge. Nevertheless, bat diversity is clearly inferior to that observed at Nouragues. Curves of ranks of abundance show that the bat community structure at edges and along transects, with a few dominant species and a lot of uncommon species, is different from that at Nouragues community structures.

However, presence or absence of caves can be decisive for some species which are specialized to these shelters (Brosset *et al.*, 1996). This applies in our study to *Phyllostomus latifolius* (for the insectivorous-nectarivorous category), *Anoura geoffroyi* and *Lionycteris spurrelli* (for the nectarivorous category), which are present in Nouragues (caves) and absent from the area of the road (no caves). Nevertheless, many species present in Nouragues and absent from the road area roost in hollow trunks.

In French Guiana, some bat species, such as *Glossophaga soricina*, *Artibeus cinereus*, *Platyrrhinus brachycephalus* or *Sturnira lilium*, are principally found in relatively open habitats, such as coastal savannahs and secondary growth bordering these formations. They are never found in the inland primary forest, far from modified habitats, with the exception of *S. lilium* which was captured in very rare occasions in Nouragues, and *G. soricina* which can be encoun-

tered in some big rock savannahs of the interior, probably indicating a past distribution (Brosset *et al.*, 1996; Charles-Dominique *et al.*, 2001). These four species were regularly caught on the border of the road which acts as a corridor facilitating their penetration into the forest block. *Glossophaga soricina* was still present at 2 and 3 km from the border of the road, continuing to be numerically more abundant than other nectarivorous species. We observed the same trend with *Artibeus cinereus* which was present at 2 and 3 km from the edge, at higher abundance than its primary forest “counterpart species” *A. gnomus*.

The situation of *Carollia perspicillata* and its “sibling species” *C. brevicauda* is particularly interesting. In Nouragues, but also in different places of the inland primary forest (Charles-Dominique pers. obs.) both species cohabit, *C. perspicillata* being 4 to 5 times more abundant than *C. brevicauda*. The former species is a little bit bigger and heavier (mean body mass 16.6 g against 11.3 g), which could explain a behavioural dominance. In areas where *C. perspicillata* is abundant, as on the borders of the roads, even at several km from the edges, *C. brevicauda* is absent (present work and Cosson, 1994; Brosset *et al.*, 1996; Simmons & Voss, 1998). An exception is the Petit Saut dam, at St Eugène, where *C. brevicauda* numerically dominates *C. perspicillata* in the small islands resulting from the water flooding, but the St Eugène situation is not equivalent to those found near deforested areas (Cosson *et al.*, 1999).

Compared to transects, the border of the forest (edge) exhibits a higher specific richness (but lower than in Nouragues). This relative high edge richness could be explained by exchanges between the primary forest and the open habitats. However along transect as well as at edge, species diversities remain low. Many edge-sensitive species apparently disappear (see Lovejoy, 1986 for fragmented habitats). These results suggest that forest edges and forest blocks provide bats with different environmental conditions, and that the distribution of a species vary according to its ecological requirements. The ecological specialization is responsible for a relative inability of some species to adapt to the new environments created by man-made modifications. For instance, some species appear to be roost-limited (Humphrey, 1975), and some others foraging habitat-limited (Fenton *et al.*, 1992), whereas some others seem to be limited by these two factors. For example, the distribution of the understorey frugivore *R. pumilio*, specialized on Cyclanthaceae and Araceae fruit (Cockle, 1997) and roosting in leaves modified into tents (Charles-Dominique, 1993), is strongly restricted to primary rain forest and old secondary habitat. By contrast, the opportunist frugivorous species *C. perspicillata* is well adapted to open areas; it feeds upon a great variety of pioneer plants and can roost in water tunnels below the roads or in other human structures (Cosson, 1994). The concentration of these opportunistic species, as well as the arrival of alien species coming from open areas and invading the edges could exert a strong competitive pressure on the less ecological flexible species adapted to the primary forest conditions.

CONSEQUENCES ON FOREST ECOSYSTEM

Edge area species can penetrate relatively far into the forest where they disperse seeds and pollen of pioneer plants (Morrison, 1978a; Charles-Dominique, 1991; Handley *et al.*, 1991). Laurance (1991a) has shown that non-native plants of the genus *Solanum* penetrate the forest interior up to at least 500 m. Over the entire length of transects, up to 3 km from the forest edge, we collected faeces of *C. perspicillata* containing seeds of *Solanum* spp., *Piper* spp. and *Vismia* spp. which were probably coming from the edge. Bats affect not only the reproductive phenology and population structure of plants, but also the natural processes of forest regeneration (Heithaus *et al.*, 1975; Heithaus, 1982; Charles-Dominique, 1986; Fleming, 1988). In addition, increase in some generalist bat species may eliminate other more specialized species performing specific interactions with peculiar plant species. In consequence, the modifications observed in the bat community may have important consequences on seed and pollen dispersal with significant effects on ecosystem processes through ecological interactions (Fleming, 1988; Fleming *et al.*, 1993).

CONCLUSION

This study demonstrates that the presence of an artificial clearing such as a road can influence the bat community in the adjacent rainforest, at least 3 km away from the border. This influence is greater than that depicted in all previous studies on vertebrates (Laurance, 1991a; Laurance, 1991b; Restrepo & Gomez, 1998; Manson *et al.*, 1999; Dale *et al.*, 2000; Goosem, 2000). It would be necessary to perform captures at still greater distances to find out the real critical distance of edge effects.

ACKNOWLEDGEMENTS

We gratefully thank Gilles Peroz and Sylvie Jouard for their technical assistance. Many thanks to Doris Gomez, Konstantinos Theodorou, Martine Perret and Michael Henry for their helpful suggestions. We thank the administrative staff of CIRAD for their permission to live at Paracou. The Landsat satellite image was provided by the "Laboratoire de Télédétection" of IRD in Cayenne, French Guiana.

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