USE OF FOREST FRAGMENTS BY ANIMALIVOROUS BATS IN FRENCH GUIANA

Jean-Marc PONS[1] & Jean-François COSSON[2]

RÉSUMÉ

Les effets de la fragmentation de l'habitat sur la communauté des chauves-souris animalivores ont été étudiés dans les îlots forestiers formés en 1994 lors de la mise en eau du barrage de Petit Saut (Guyane française). Un protocole d'échantillonnage standardisé, incluant une zone de référence restée intacte tout au long de l'étude entre 1993 et 1997, a permis de suivre les modifications affectant la communauté des chauves-souris animalivores dans une île de 28 ha (île 2) bien isolée et dans 15 îlots d'une superficie inférieure à 6 ha plus ou moins isolés selon les cas. Les résultats obtenus ont été comparés avec ceux obtenus dans les mêmes conditions lors d'une précédente étude pour les chauves-souris frugivores et nectarivores.

148 chauves-souris animalivores glaneuses, 41 insectivores aériennes, 28 omnivores ou hématophages ont été capturées au cours de l'étude. L'analyse de ces captures montre que la richesse spécifique et l'abondance des individus ont chuté fortement en 1995 et 1996 dans l'île 2 et dans les îlots mais pas en 1997. Aucune différence de richesse ou d'abondance entre l'île 2 et les îlots de degré d'isolement comparable n'a été détectée. En revanche, les indices de richesse et d'abondance obtenus pour les îlots éloignés de plus de 150 m du bloc forestier sont significativement plus faibles que ceux obtenus pour les îlots situés à proximité immédiate de la forêt intacte. Il est suggéré que le survol d'une étendue d'eau libre pourrait constituer une barrière au déplacement notamment pour les espèces animalivores glaneuses de sous-bois.

Entre 1994 et 1997, la proportion relative de chauves-souris aériennes insectivores et glaneuses animalivores dans les îlots forestiers et dans le bloc forestier n'était pas différente, les glaneuses animalivores représentant 73 % des captures dans les deux milieux. De même, il n'y a pas de différence dans la contribution respective des guildes animalivores et frugivores aux peuplements insulaire et du bloc forestier. Les chauves-souris frugivores représentent autour de 80 % des captures dans les deux habitats. A l'intérieur de la guilde des glaneuses animalivores, il existe une forte corrélation entre l'abondance d'une espèce en forêt non perturbée et son abondance dans l'île 2 et dans les îlots. Une corrélation positive entre la taille corporelle et l'abondance a également été trouvée tous milieux confondus.

La portée des résultats obtenus ici est limitée du fait de la rareté et de la faible piégeabilité d'un nombre élevé d'espèces qui composent le peuplement des chauves-souris animalivores en forêt néotropicale. D'autres techniques de collecte et d'analyse des données, qui tiennent compte de ces particularités, devront être mises en œuvre pour pleinement évaluer l'impact de la fragmentation de l'habitat sur les communautés de chauves-souris animalivores à Saint-Eugène.

---

[1] Laboratoire de Zoologie (Mammifères et Oiseaux), MNHN, 55 rue Buffon, 75005 Paris. Email: pons@mnhn.fr

[2] Centre de Biologie et Gestion des Pullulations, Institut National de la Recherche Agronomique et Laboratoire Génome, Populations, Interactions, Université Montpellier II, CNRS UPR 9060, Place Eugène Bataillon C.C. 63, F-34095 Montpellier Cedex, France.

Rev. Écol. (Terre Vie), vol. 57, 2002.

SUMMARY

The effects of habitat fragmentation on animalivorous bats were studied on recent forest islands created in 1994, at the time of the filling of Petit Saut dam in French Guiana. A sampling strategy, including control sites located in a nearby forested area not fragmented during the whole study period (1993-1997) was designed. Modifications affecting animalivorous bat communities in a remote 28 ha island (island 2) and in 15 islets smaller than 6 ha more or less isolated from the nearby continuous forest were analysed. Results were compared to those obtained with the same methods for frugivorous and nectarivorous bats.

One hundred and forty eight gleaning animalivores, 41 aerial insectivores and 28 bats belonging to other guilds (omnivore, sanguivore) were trapped during the whole study. Capture analyses showed that species richness and abundance sharply declined in islets and in the island 2 in 1995 and 1996. However no significant difference was found between islands and continuous forest in 1997. There was no difference either in species richness or in abundance between the island 2 and several islets of comparable isolation. On the contrary, indices were significantly lower in far islets situated at more than 150 m from the continuous forest than in near ones. One possible explanation is the reluctance of understorey species to cross open water to reach far islands.

Between 1994 and 1997, we failed to detect any difference in the relative proportion of aerial insectivores and gleaning animalivores between islands and the continuous forest. Among non-frugivorous species, gleaning animalivores represented 73 % of the total number of captures made in the two habitats. Similarly no habitat differences were found in the respective contributions of frugivores and animalivores to bat communities. Frugivores made up roughly 80 % of the total number of bats captured during the study. Within the gleaning animalivores guild, there was a positive relationship between abundance of a species in islands and its abundance in the control area. Moreover, a positive correlation was equally found between body size and abundance in all habitats.

The contribution of our results to the understanding of the impact of habitat fragmentation on animalivorous bats is limited due to rarity and low detectability of a high number of species making up animalivorous bat communities in Neotropical forests. Therefore, additional methods to collect and analyse data that take into account these features should be implemented to evaluate more accurately the impact of habitat fragmentation on bat communities at Saint-Eugène.

INTRODUCTION

In ecosystems subject to anthropic or natural disturbances, changes in the species composition of bat communities constitutes, with bird community changes, one of the first indications of the ecological modifications in progress (Brosset *et al.*, 1996). Previous studies in tropical and inter-tropical countries (Estrada *et al.*, 1993; Fenton *et al.*, 1992), as well as in temperate ones (Jong, 1993), have demonstrated that, in spite of high dispersal abilities of most species, bat species and communities are indeed affected by forest fragmentation.

In French Guiana, bats represent more than 50 % of mammal species, and play an important role in the functioning of forest ecosystems through seed dispersal, flower pollination and insect predation (Charles-Dominique, 1995; Simmons & Voss, 1998). In this context, the study of the impact of forest fragmentation on bat communities, and the underlying ecological processes, while poorly studied by comparison with other animal and vegetal communities (cf. Laurance & Bierregaard, 1997; but see Estrada *et al.*, 1993 and Cosson *et al.*, 1999a), are of great interest for scientists involved in the management of biodiversity.

The filling of the Petit Saut electric dam in French Guiana created a large number of islands, islets and peninsulas of various sizes, shapes and degrees of isolation, providing an opportunity to study the impact of forest fragmentation. Using standard sampling procedures, we characterized the bat communities prior and after the fragmentation from 1993 to 1997, and compared community changes in the fragmented area to that of a contiguous area of similar size which was not directly affected by fragmentation. In a previous paper (Cosson *et al.*, 1999a), we demonstrated a sharp decrease in diversity and abundance of nectarivorous and frugivorous bats in islands after the flooding. Body sizes, home ranges and feeding strategies were all implicated, separately or in conjunction, in the observed changes. Understorey species appeared to be more sensitive than canopy ones, and large species were less affected than smaller ones.

In this article, we present short-term effects of forest fragmentation on the animalivorous bat communities and examine the following questions. (1) Did fragmentation cause any change in diversity and abundance of animalivorous bats at Saint-Eugène? (2) Were some species more sensitive to fragmentation than others? (3) How can similarities and differences with what had been observed for frugivorous bats be interpreted?

MATERIAL AND METHODS

THE STUDY SITE

The study was conducted at the Saint-Eugène station (4° 51' N, 53° 04' W). A detailed description of the study site can be found in Claessens *et al.* (2002). Two contiguous areas of similar size were sampled during the same season (October-November) over 5 years (1993-1997) including the year before flooding. This allowed a comparison of the initial state on both areas. During the flooding, which started in January 1994, one of these areas was fragmented into a large island (no. 2), initially estimated to 40 ha in Cosson *et al.* (1999) and more precisely recalculated to 28 ha in Claessens *et al.* (2002), surrounded by numerous islets of *c.* 5 ha. The second pre-flooding area was not fragmented and was chosen as the mainland control site. The location of the mainland sites and islands sampled for bats from 1993 to 1996 may be found in Cosson *et al.* (1999a). For the sake of clarity, we reported thereafter the numbers of islands sampled each year with the standard numbering of Claessens *et al.* (2002): 1994 (nos. 2, 21 and two islets flooded in 1995), 1995 (nos. 2, 5, 6, 9, 19 and 21), 1996 (nos. 2, 5, 6, 8, 9, 12, 16, 17, 19, 20, 21, 22, 24, 34 and 53) and 1997 (nos. 5, 6, 8, 17, 20, 22, 24 and 53). In 1996 and 1997, we distinguished two groups of islands according to their isolation to the mainland: the far islands (i.e. > 150 m to the mainland, nos. 2, 5, 6, 9, 19, 20, 21 and 22) and the near ones (i.e. < 150 m to the mainland, nos. 8, 12, 16, 17, 24, 34 and 53). The large island (no. 2) was not sampled in 1997.

TROPHIC GUILDS

In South and Central America, animalivorous species can be subdivided into five to ten guilds according respectively to Simmons & Voss (1998, p. 192) who made intensive studies at Paracou, a study site located at *c.* 25 km. from Saint-Eugène station and Kalko (1998) who worked at Barro Colorado Island in Panama. In the present study, analyses were focused on three guilds for which the sample sizes were large enough: (1) aerial insectivores (all nonphyllostomids except *Noctilio leporinus*). (2) Gleaning animalivores (all Phyllostomids except carolliines, stenodermatines, glossophagines, *Phylloderma stenops,* and *P. hastatus*), (3) omnivores (*Phylloderma stenops,* and *P. hastatus*). Besides bats belonging to these 3 guilds, several *Desmodus rotundus* (gleaning sanguivore) and *Noctilio leporinus* (gleaning piscivore) were trapped at Saint-Eugène during the study.

SAMPLING STRATEGY

Netting and sampling strategies have been described in detail in Cosson *et al.* (1999), and so only the main information is given herein. From three to four capture stations, each one corresponding to a line of two to four (usually three) mist nets (9-m × 2-m or 12-m × 2-m, mesh size 38 mm) placed at ground level were used to sample each site one time a year. Each bat was ringed or marked with a little fur mark. Between sites recapture rates were extremely low. On the other hand, within site recaptures during the same capture session were observed in several occasions and were counted as only one capture.

The sampling strategy was designed in order to obtain similar patterns of spatial arrangement of capture stations before and after flooding in the continuous area as well as in the fragmented one. Within each area, a number of replicate sites were equipped with four to eight capture stations randomly distributed but set apart by more than 100 m. Replicates corresponded to spatially separated sampling places in the continuous area and in the 28-ha island, and to the different islets sampled in the fragmented area. When possible, the same capture stations were sampled from year to year within each replicate. However, because of natural forest perturbation (e.g. tree fall) and the flooding, some of them had to be abandoned or displaced leading to an irregular number of capture stations from year to year. Capture rates were calculated using the length of net-night which corresponded to the total length of nets set in a given capture station during a whole night. Numbers of capture-stations and sites are given in table I. Nets were continuously checked from dusk to dawn. We avoided netting during bad weather conditions and nights with bright moon, which are known to influence bat capture rates.

DATA ANALYSIS

In a first step, data analysis was designed (1) to test for the similarity of bat communities in the two areas of natural forest before flooding, (2) to test for the effect of fragmentation by water, by comparing bat communities in the fragmented vs. continuous forest areas after flooding, (3) to test for the effect of island size by comparing bat communities in small vs. a large island of similar isolation (i.e. > 150 m from the mainland) after the flooding, and (4) to test for the effect of island isolation by comparing bat communities in near vs. far islets of similar size (i.e. < 5 ha). Capture rates (number of captures/length of net-night) and richness index (number of species caught/length of net-night) were used as standard indices of abundance and diversity respectively. We used ANOVA for inter-habitat comparisons within each year. Capture rates and richness indices were square root (n+1) transformed to reduce the correlation between variance and mean within samples. The residuals were approximately normally distributed.

TABLE I

Characteristics of the bat-trapping, number of captures and number of species caught at the control site, and in the nearby fragmented area.

	Isolation	Date			Net-night	Gleaners(1)		Aerial		Others	
		(Nov.)	sites	stations	length (m)	captures	species	captures	species	captures	species
Control site	-	1993	3	25	489	5	4	2	1	4	1
	-	1994	3	15	351	11	3	0	0	1	1
	-	1995	3	15	468	16	8	6	3	4	2
	-	1996	3	23	670	23	6	8	2	6	1
	-	1997	3	15	432	6	4	3	3	3	1
Fragmented area											
before fragmentation	-	1993	3	24	648	8	2	2	2	3	2
28-ha island	> 150 m	1994	3	21	531	6	3	2	2	2	1
28-ha island	> 150 m	1995	3	16	564	8	4	2	2	0	0
28-ha island	> 150 m	1996	3	12	439	5	5	3	3	0	0
5-ha islets	> 150 m	1994	3	10	237	3	3	0	0	1	1
5-ha islets	> 150 m	1995	6	23	732	7	4	1	1	0	0
5-ha islets	> 150 m	1996	7	25	732	9	4	3	3	2	2
5-ha islets	> 150 m	1997	4	13	384	5	4	3	2	0	0
5-ha islets	< 150 m	1996	7	22	654	27	6	3	3	2	2
5-ha islets	< 150 m	1997	4	13	312	9	2	3	2	0	0

(1) gleaners = gleaning animalivores, Aerial = aerial insectivores, Others = gleaning sanguivores and gleaning omnivores.

In a second step, data analysis was designed to test whether sensitivity of bat species to fragmentation could be related (1) to their abundance in the control site, and (2) to their trophic guild. To evaluate the different species' response to fragmentation, an index of sensitivity varying from -1 to +1 was attributed to each bat species trapped more than 14 times as (capture rate at the control site - capture rate in islets) / (capture rate at the control site + capture rate in islets). ANOVA and other statistics were performed with StatView 4.1.

RESULTS

One hundred and forty eight gleaning animalivores, 41 aerial insectivores and 28 bats from the other guilds were captured during the study (Table I). These 217 bats belonged to 26 different species and represented 28 % of total individuals and 65 % of total bat species captured during the study, the rest belonging to the nectarivorous and frugivorous trophic guilds.

ABUNDANCE AND SPECIES RICHNESS CHANGES

In 1993, before the disturbance, abundance and species richness did not differ significantly in both areas (Figs 1 & 2, abundance index: $F = 0.24$, $P = 0.63$, species richness $F = 1.01$, $P = 0.32$). During the flooding, in 1994, capture rates on the large and small islands were lower than those on the control sites, but differences were not significant ($F = 0.22$, $P = 0.81$). Differences in abundance and species richness became highly significant in 1995 (abundance: $F = 8.66$, $P < 0.01$, species richness: $F = 9.20$, $P < 0.01$) and 1996 (abundance: $F = 3.86$, $P < 0.01$, species richness: $F = 4.12$, $P < 0.01$). During these two years, capture rates in the control site were three times larger than those on far islands. In 1997, abundance and species richness were still lower on far islands but not significantly (abundance: $F = 0.22$, $P = 0.80$, species richness: $F = 0.46$, $P = 0.64$). During the whole study, there were no differences in abundance and species richness between the large island (no. 2) and the smaller ones of similar isolation (1994: abundance: $F = 0.12$, $P = 0.73$, species richness: $F = 0.04$, $P = 0.83$; 1995: abundance: $F = 0.10$, $P = 0.75$, species richness: $F = 0.01$, $P = 0.90$; 1996: abundance: $F = 0.61$, $P = 0.44$, species richness: $F = 0.34$, $P = 0.56$). By contrast, indices were lower in far islets than in near ones. Isolation effect was significant in 1996 (abundance: $F = 4.88$, $P = 0.03$, species richness: $F = 4.38$, $P = 0.04$) but not in 1997 (abundance: $F = 0.05$, $P = 0.83$, species richness: $F = 0.01$, $P = 0.94$). Finally, abundance and species richness varied significantly from year to year in the control site (abundance: $F = 7.01$, $P = 0.01$, species richness: $F = 6.50$, $P = 0.01$). In particular, we observed a sharp increase during the year after the flooding followed by a smooth decrease in 1997. These temporal changes were not so clear on islands (abundance: $F = 0.59$, $P = 0.67$, species richness: $F = 0.55$, $P = 0.70$).

SPECIES COMPOSITION CHANGES

We investigated whether there was a change in the contribution of the different guilds to the bat community after the stabilisation of the islands'

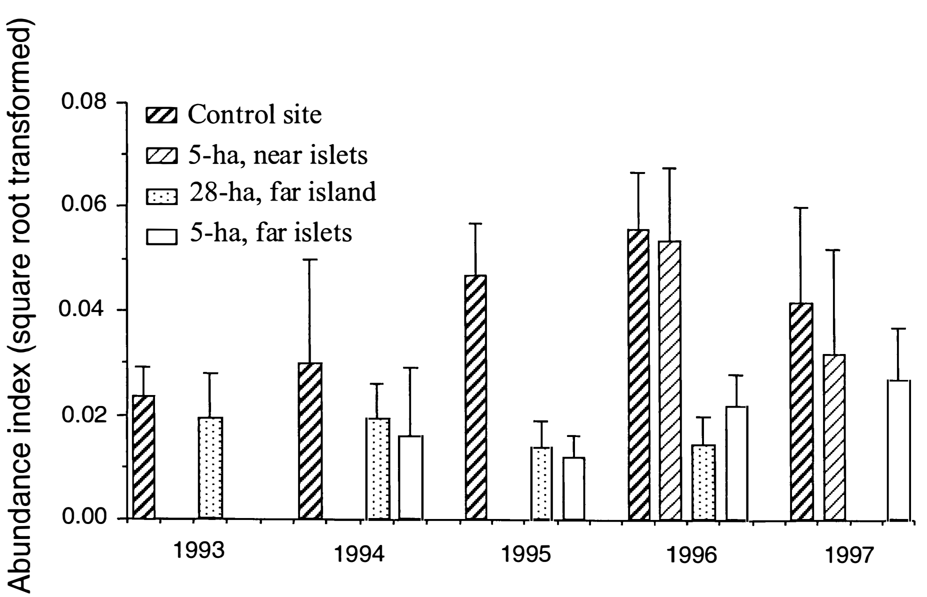

Figure 1. — Variation in abundance of animalivorous bats at the control site and in the nearby area fragmented in 1994 into a 28-ha island and several *c.* 5-ha islets at the Saint-Eugène field station, French Guiana. Two groups of islets were distinguished according to their isolation to the mainland: nearby islets (i.e. < 150 m to the mainland) and farther islets (i.e. > 150 m to the mainland). The 28-ha island is at more than 150 m from the mainland. Abundance was assessed with the number of individuals trapped divided by the length of net-night (see methods for definitions).

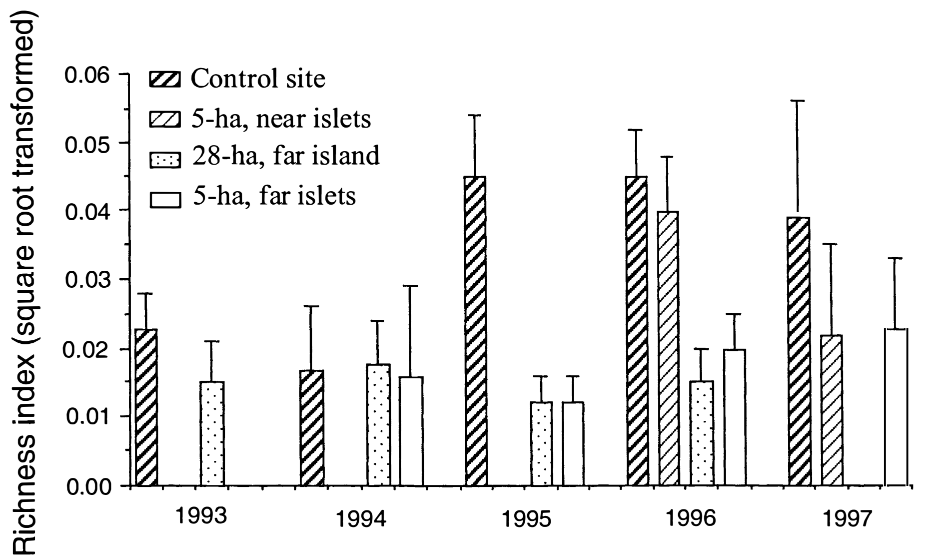

Figure 2. — Variation of richness index of animalivorous bats at the control site and in the nearby fragmented area (see legend Fig. 1).

shorelines (1995 to 1997). We failed to detect any significant difference in the relative abundance of individuals belonging to aerial insectivores or to gleaning animalivores guilds in islands and at the control site ($N = 189$, $\chi^2 = 0.02$, $df = 1$, $P = 0.90$). Gleaning animalivores accounted for 78 % of the number of captures made for these two guilds. In the same way, there was no significant difference in the relative abundance of animalivorous and frugivorous bats captured in islands and at the control site ($N = 712$, $\chi^2 = 1.30$, $df = 1$, $P = 0.25$). Frugivorous bats roughly accounted for 80 % of total captures in continuous forest as well as in fragmented habitat.

Most of the species were represented by a small number of individuals in our data set. Only 7 species over 26 were represented by more than 10 captures after the flooding (Table II). This seriously limits our analysis of species' specific changes induced by fragmentation. We thus restricted the following data analysis to the gleaning animalivores guild, which comprised the greatest part of the captures. Within this guild, we found a positive relationship between abundance at the control site and abundance in islands ($N = 13$, $r = 0.66$, $F\ (1,11) = 8.59$, $P = 0.014$). This indicates that the more a species is abundant at the control site the more it is in islands. There was also a strong positive correlation between abundance and body size ($N = 12$, $r = 0.75$, $F\ (1,10) = 12.47$, $P = 0.005$). Whatever the habitat considered, 55 % of the variation in species abundance was explained by interspecific variations in body size, so we failed to detect any clear influence of body size on the species' specific response to fragmentation.

Sensitivity indices suggested that some species are more sensitive to fragmentation than others. For instance, *Tonatia saurophila*, which displays a value of –0.19, may have even been favoured by the habitat fragmentation. However, most of species were less abundant in islands than in the control site. This seems especially true for the vampire *Desmodus rotundus*, the animalivore *Trachops cirrhosus* and the large understorey insectivore *Pteronotus parnellii* (Table II).

DISCUSSION

DID FRAGMENTATION CAUSE ANY CHANGE IN DIVERSITY AND ABUNDANCE?

Our results strongly suggested that flooding caused important changes in the abundance and diversity of animalivorous bats. This verifies previous studies conducted in other Neotropical localities, which showed that animalivorous bats, especially phyllostomines, are sensitive to habitat disturbance (La Val & Fitch, 1977; Fenton *et al.*, 1992; Wilson *et al.*, 1996). However, in our study, it is not clear whether observed changes could be related to factors directly linked to forest fragmentation *per se* like for instance isolation and edge effect, or to other factors mostly linked to the particular properties of the water matrix. Indeed, water is an important habitat for the larval development of most insects and the presence of large extents of open water could have greatly influenced the abundance and diversity of insectivores in the whole study area. Temporal variation in insect availability throughout the study could be one of the factors driving the sharp increase of the animalivorous bats abundance in the control area consecutive to flooding. Moving from flooded areas could also be invoked, as it was already

TABLE II

Abundance and sensitivity of bats species to fragmentation at the Saint-Eugène field station. The sensitivity index (see methods for definition) is only given for species trapped more than 14 times.

Species	Guild	Forearm (mm)(1)	Abundance			Sensitivity index
			Control	40ha island	Islets	
Phyllostomus elongatus	Gleaner(2)	66.6	4.59	4.98	5.31	–0.07
Mimon crenulatum	Gleaner	49.4	7.00	1.00	3.90	0.28
Tonatia saurophila	Gleaner	57.3	4.59	1.00	6.73	–0.19
Desmodus rotundus	Gleaner(3)	58.2	7.00	0.00	0.71	0.82
Pteronotus parnellii	Aerial(4)	63.6	7.00	1.99	0.35	0.90
Trachops cirrhosus	Gleaner	63.4	5.10	1.00	0.35	0.87
Tonatia sylvicola	Gleaner	59	3.82	1.99	0.71	0.67
Micronycteris megalotis	Gleaner	22.7	1.27	1.00	0.71	-
Saccopteryx bilineata.	Aerial	48.2	1.91	0.00	0.35	-
Saccopteryx leptura	Aerial	39.2	0.64	1.00	1.06	-
Phylloderma stenops	Gleaner (5)	69.4	1.27	0.00	0.35	-
Chrotopterus auritus	Gleaner	78.8	1.27	0.00	0.71	-
Thyroptera tricolor	Aerial	36.3	0.64	1.00	0.35	-
Myotis nigicans	Aerial	33.3	0.00	0.00	1.77	-
Micronycteris minuta	Gleaner	34.7	0.64	0.00	0.35	-
Trinycteris nicefori	Gleaner	38.4	0.64	0.00	0.00	-
Glyphonycteris sylvestris	Gleaner	38.7	0.00	0.00	0.35	-
Micronycteris hirsuta	Gleaner	43.2	0.00	0.00	1.06	-
Peropteryx macrotis	Aerial	42.9	0.64	1.00	0.00	-
Thyroptera discifera	Aerial	33(6)	0.00	1.00	0.00	-
Rhynchonycteris naso	Aerial	37.4	0.00	0.00	0.35	-
Furipterus horrens	Aerial	36.7	0.00	0.00	0.35	-
Peropteryx leucoptera	Aerial	43.1	0.00	1.00	0.00	-
Tonatia schulzi	Gleaner	43.7	0.64	0.00	0.00	-
Phyllostomus hastatus	Gleaner	84.1	0.00	0.00	0.35	-
Tonatia brasiliense	Gleaner	35.7	0.00	1.00	0.00	-

(1) data from Simmons & Voss (1998), (6) data from Eisenberg (1989). (2) = gleaning animalivore, (3) = gleaning sanguivore, (4) = aerial insectivore, (5) = gleaning omnivore. Abundance is the number of captures/1000 m of net-nights at the control site and in islands after flooding. Sensitivity index is defined in the text.

suggested for other highly mobile species like large mammals (Granjon *et al.*, 1996) and frugivourous bats (Cosson *et al.*, 1999) at Saint-Eugène. The lack of data on temporal variation in insect abundance unfortunately precludes disentangling the trophic and the moving hypotheses.

Whatever the ecological factors that drove temporal changes in animalivorous bat abundance in the control area, it is of great interest that "far" islands did not exhibit parallel patterns. Unlike what was observed in the control area, we did not detect any interannual change in bat abundance and diversity in "far" islands. As suggested for frugivorous bats (Cosson *et al.,* 1999), one can state that certain of animalivorous bats do not exploit forest patches, either (1) because the ecological quality of these patches is lower than that of same-size patches in the control sites, or (2) because they cannot cross the new habitats between these patches for behavioural and/or ecological reasons.

Islands could be less attractive to animalivorous bats than same-size patches in the control sites because of a lower availability of resources. Indeed, insects seem to be highly sensitive to forest fragmentation (Didham *et al.*, 1996), especially large beetles that constitute an important part of phyllostomines diet (Klein, 1989). On the other hand, we know little about the foraging behaviour of most phyllostomine species and it also seems plausible that, as suggested in other studies (Fenton *et al.*, 1992) and already reported for other understorey flying vertebrates and invertebrates in neotropical rainforests (Stouffer & Bierregaard, 1995; Didham *et al.*, 1996; Brown & Hutchings, 1997), the forest-dwelling phyllostomines are reluctant to cross open areas.

At Saint-Eugène, sensitivity indices of two gleaning animalivores, namely *Tonatia silvicola* and *Trachops cirrhosus*, suggested that these species negatively reacted to habitat fragmentation. These observations are in accordance with predictions made by Kalko *et al.* (1999) in a study dealing with the foraging and roosting behaviour of these two species. Using radio tracking, they found that these gleaning bats exhibited small foraging areas (3-12 ha) and short commuting distances (< 2 km). They concluded that, together with reluctance to cross open spaces, these features make *T. silvicola*, and to a lesser extent *T. cirrhosus*, vulnerable to habitat fragmentation.

ARE SOME SPECIES MORE SENSITIVE?

The response to isolation seems to be variable among species: some species are more sensitive than others. Overall, the species that were the most abundant in the islands were also among the most abundant at the control site. The higher vulnerability of rare species is a common feature in fragmentation studies (Terborgh, 1974; Sieving & Karr, 1977; Cosson *et al.*, 1999b). At Saint-Eugène, additional data would be necessary to investigate whether a similar pattern prevails or not.

We did not find any evidence of difference in the reaction to fragmentation of the different guilds. The relative proportion of aerial insectivores *vs.* gleaning animalivores was not different at the control sites and in the islands despite the fact that members from both guilds exploit very different food resources. We expected an increase in the relative abundance of aerial insectivores *vs.* gleaning animalivores in islands surrounded by the water matrix that constitutes *a priori* a very suitable habitat for aerial insects, riparian and aquatic habitats being known to represent important foraging areas for aerial insectivores (e.g. Grindal *et al.*, 1999). This was not confirmed by our data, suggesting that other autoecological factors such as predation escape and/or foraging behaviour might be implicated. Notice however that our sampling procedure was not well adapted for nonphyllostomids, which are poorly captured with mistnets (Kalko, 1998). It is possible that this sampling bias made it difficult to detect abundance changes within nonphyllostomids. It would be necessary to develop other sampling methods such as ultrasonic monitoring to clearly address the question of the use of islands by nonphyllostomids in Saint-Eugène. Such methods have already been successfully used to sample bat communities in association with mist netting (Kuenzi & Morrison, 1996; Kunz *et al.*, 1996).

SIMILARITIES AND DIFFERENCES BETWEEN ANIMALIVOROUS AND FRUGIVOROUS GUILDS

In Paracou, Simmons & Voss (1998) found that the decrease in animalivorous bats abundance in modified habitats was much higher than that observed for frugivorous bats. Such a pattern was not detected at Saint-Eugène where the relative abundance of gleaning animalivores and frugivores did not change in forested fragments. This difference between the two sites might be explained by the fact that, contrary to Saint-Eugène, secondary vegetation which constitutes a very attractive habitat for frugivores (Charles-Dominique, 1995) is well represented in Paracou.

At Saint-Eugène, large frugivorous species continued to exploit forested fragments whereas small species tended to disappear from there. Such a positive relationship between body size and persistence in fragments had already been observed in other zoological groups including lizards, primates and small terrestrial mammals (Ringuet *et al.*, 1999; Dalecky *et al.*, 2002). In the case of animalivorous and insectivorous bats, small species (forearm less than 45 cm) were so rarely captured in all habitats that it was not possible to test this relationship.

After the filling of the Petit Saut dam, forest fragmentation led to a simplification of the insular community of frugivorous bats. Abundance, species richness and diversity sharply decreased in islands (Cosson *et al.*, 1999a). For animalivorous bats, a decline in abundance and species richness was observed in far islands especially in 1995 and 1996. Sensitivity to fragmentation strongly varied from one species to another. Most species (*Desmodus rotundus, Tonatia silvicola, Trachops cirrhosus, Pteronotus parnellii*) seemed to react negatively to fragmentation, whereas in the same time *Tonatia saurophila* might have been advantaged.

Small sample sizes available in the present study for many species precluded us from performing a detailed analysis of the effects of habitat fragmentation on composition and structure of animalivorous guilds. This was partly due to the rarity and/or low detectability of many species. Moreover, mistnets set only at the ground level are not fit to detect possible modifications in vertical stratification, an important component of bats community structure in Neotropical forests (Bernard, 2001).

Clearly, additional studies including other sampling techniques like acoustic monitoring for aerial insectivores species are necessary (Kalko, 1998). Although not without controversy (see Barclays, 1999), acoustic methods give new valuable information about aerial insectivorous bats never trapped with mistnets (O'Farell & Miller, 1999). Moreover new data analyses methods taking into consideration heterogeneity in the probability of detecting species to evaluate species richness (Conroy & Nichols, 1996) are needed to precisely evaluate the impact of habitat fragmentation on animalivorous bats and possible implications for the functioning of this tropical rain forest.

APPENDIX

Over the whole study, 43 species were captured, all guilds comprised. This number is rather low in comparison with the 86 species expected for a primary forest station in French Guiana (cf. Simmons & Voss, 1998, p. 184). This can easily be explained by the absence of canopy netting and systematic censuses of potential roosts. The main purpose of our study was not to give an exhaustive list of bat species in the station, but to describe the effect of fragmentation on bat communities. We thus preferred netting in standard procedures to the setting of numerous opportunistic methods that certainly would have increased the total number of censused species. As a result, one can note in our list the absence of high-flying aerial insectivores like molossids, and other species mainly captured in canopy or in their roosts (e.g. *Cormura brevirostris*, *Ametrida centurio*) by Simmons & Voss (1998).

Note the capture of the very rare *Thyroptera discifera* that was previously cited only by Thomas (1928) in French Guiana, and of *Myotis albescens*, expected but not yet mentioned from French Guiana. A small colony of this last species (5 individuals) was found in the crevice of a flooded tree branch lying at some centimetres above the water surface, confirming the predilection of this species for open water.

Species list of bats taken in ground-level mistnets in primary forest at Saint-Eugène between 1993 and 1997.

(A) **Frugivores, Nectarivores** (*Phyllostomatidae*)	N captures	**(B)** **Insectivores, Carnivores, Sanguivores**	N captures
Rhinophylla pumilio (F)	187	*Phyllostomus elongatus (G) (P)*	35
Artibeus obscurus (F)	182	*Tonatia saurophila (G) (P)*	28
Artibeus jamaicensis (F)	160	*Mimon crenulatum (G) (P)*	27
Artibeus lituratus (F)	51	*Tonatia silvicola (G) (P)*	23
Lonchophylla thomasi (N/F)	39	*Desmodus rotundus (S) (P)*	22
Carollia perspicillata (F)	35	*Pteronotus parnellii (A) (M)*	18
Carollia brevicauda (F)	38	*Trachops cirrhosus (G) (P)*	15
Sturnira tildae (F)	18	*Micronycteris megalotis (G) (P)*	6
Artibeus gnomus (F)	13	*Saccopteryx bilineata (A) (E)*	5
Ectophylla macconnelli (F)	12	*Saccopteryx leptura (A) (E)*	5
Vampyrodes caraccioli (F)	13	*Phylloderma stenops (O) (P)*	5
Choeroniscus minor (N)	12	*Myotis nigricans* (A) (V)*	5
Platyrrhinus helleri (F)	5	*Chrotopterus auritus (O) (P)*	4
Chiroderma villosum (F)	2	*Thyroptera tricolor (A) (T)*	3
Anoura caudifera (N)	3	*Micronycteris hirsuta (G) (P)*	3
Chiroderma trinitatum (F)	1	*Micronycteris minuta (G) (P)*	2
Uroderma bilobatum (F)	1	*Peropteryx macrotis (A) (E)*	2
		Trinycteris nicefori (G) (P)	1
		Glyphonycteris sylvestris (G) (P)	1
		Thyroptera discolor (A) (T)	1
		Rhynchonycteris naso (A) (E)	1
		Furipterus horrens (A) (F)	1
		Peropteryx leucoptera (A) (E)	1
		Tonatia schulzi (G) (P)	1
		Phyllostomus hastatus (O) (P)	1
		Tonatia brasiliense (G) (P)	1

(A): Frugivores (F) et nectarivores (N).
(B): Omnivores (O), Aerial insectivores (I), Sanguivores (S), Gleaning animalivores (G), Phyllostomatidae (P), Mormoopidae (M), Thyropteridae (T), Furipteridae (F), Vespertilionidae (V), Emballonuridae (E)* may include *Myotis riparius* specimens.
Species seen or trapped outside capture stations: *Noctilio leporinus* (Piscivore), *Myotis albescens* (I).

ACKNOWLEDGEMENTS

We thank all those who helped in the field and especially Didier Masson who helped to trap bats in 1993 and 1994. Pierre-Michel Forget, Elizabeth Kalko made useful remarks on a previous draft. Many thanks to Agnès Dettaï for comments on the English text. Christian Erard and Gérard Dubost initiated this project, which was funded by "Electricité de France" (Convention MNHN/EDF GP 7531).

REFERENCES

BARCLAY, R.M.R. (1999). — Bats are not birds. A cautionary note on using echolocation calls to identify bats: a comment. *J. Mammal.*, 80: 290-296.

BERNARD, E. (2001). — Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. *J. Trop. Ecol.*, 17: 115-126.

BROSSET, A., CHARLES-DOMINIQUE, P., COCKLE, A., COSSON, J.-F. & MASSON, D. (1996). — Bat communities and deforestation in French Guiana. *Can. J. Zool.*, 74: 1974-1982.

BROWN, K.S., Jr. & HUTCHINGS, R. W. (1997). — Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. Pp. 91-110, *in:* W.F. Laurance & R.O. Bierregaard, Jr. (eds), *Tropical forest remnants. Ecology, management, and conservation of fragmented communities.* The University of Chicago Press, Chicago.

CHARLES-DOMINIQUE, P. (1995). — Interactions plantes-animaux frugivores, conséquences sur la dissémination des graines et la régénération forestière. *Rev. Ecol. (Terre Vie),* 50: 223-237.

CLAESSENS, O., GRANJON, L., DE MASSARY, J.-C. & RINGUET, S. (2002). — La station de terrain de Saint-Eugène: situation, environnement et présentation générale. *Rev. Ecol. (Terre Vie),* Suppl. 8: 21-37.

CONROY, M.J. & NICHOLS, J. (1996). — Designing a study to assess Mammalian diversity. Pp. 41-49 *in:* D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran & M. Forster (eds), *Measuring and monitoring biological diversity - Standard methods for mammals.* Smithsonian Institution Press, Washington D.C.

COSSON, J.-F., PONS, J.-M. & MASSON, D. (1999a). — Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *J. Trop. Ecol.*, 15: 515-534.

COSSON, J.-F., RINGUET, S., DE MASSARY, J.-C., CLAESSENS, O., DALECKY, A. & PONS, J.-M. (1999b). — Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. *Biol. Cons.*, 91: 213-222.

DALECKY, A., CHAUVET, S., RINGUET, S., CLAESSENS, O., JUDAS, J., LARUE, M. & COSSON, J.-F. (2002). — Large mammals on small islands: short term effects of forest fragmentation on the large mammal fauna in French Guiana. *Rev. Ecol. (Terre Vie),* Suppl. 8: 145-164.

DIDHAM, R.K., GHAZOUL, J., STORK, N.E. & DAVIS, A.J. (1996). — Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.*, 11: 255-260.

EISENBERG, J. (1989). — *Mammals of the Neotropics*, volume 1. The University of Chicago Press, Chicago and London. 449 p.

ESTRADA, A., COATES-ESTRADA, R. & MERRIT, D., Jr. (1993). — Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography,* 16: 309-318.

FENTON, M.B., ACHARYA, L., AUDET, D., HICKEY, M.B.C., MERRIMAN, C., OBRIST, M.K. & SYME, D.M. (1992). — Phyllostomid bats (Chiroptera: *Phyllostomidae*) as indicators of habitat disruption in the Neotropics. *Biotropica,* 24: 440-446.

GRANJON, L., COSSON, J.F., JUDAS, J. & RINGUET, S. (1996). — Influence of tropical rainforest fragmentation on mammal communities in French Guiana: early trends. *Acta Oecol.,* 17: 673-684.

GRINDAL, S.D., MORISSETTE, J.L. & BRIGHAM, R.M. (1999). — Concentration of bat activity in riparian habitats over elevational gradient. *Can. J. Zool.*, 77: 972-977.

KALKO E.K.V. (1998). — Organisation and diversity of tropical bat communities through space and time. *Zoology,* 101: 281-297.

KALKO, E.K.V., KRULL, D., HANDLEY, C.O. & SCHNITZLER, H.U. (1999). — Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomatidae). *Biotropica,* 31: 344-353.

KUENZI, A.J. & MORRISON, M.L. (1998). — Detection of bats by mist-nets and ultrasonic sensors. *Wildl. Soc. Bull.,* 26: 307-311.

KUNZ, T.H., TIDEMANN, C.R. & RICHARDS, G.C. (1996). — Observational techniques for small volant mammals. Pp. 122-146, *in:* D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran & M. Forster (eds), *Measuring and monitoring biological diversity - Standard methods for mammals.* Smithsonian Institution Press, Washington D.C.

LAURANCE, W.F. & BIERREGAARD, R.O., Jr. (1997). — *Tropical forest remnants. Ecology, Management, and conservation of fragmented communities.* The University of Chicago Press, Chicago.

O'FARRELL, M.J. & MILLER B.W. (1999). — Use of vocal signatures for the inventory of free-flying Neotropical bats. *Biotropica,* 31: 507-516.

RINGUET, S., CLAESSENS, O., COSSON, J.-F., DE MASSARY, J.-C., GRANJON, L. & PONS, J.-M. (1998). — Fragmentation de l'habitat et diversité des petits vertébrés en forêt tropicale humide: l'exemple du barrage de Petit Saut. *JATBA, Revue d'Ethnobiologie*, 40: 11-30.

SIMMONS, N.B. & VOSS, R.S. (1998). — The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna, part 1. Bats. *Bull. Amer. Mus. Nat. Hist.,* 327: 219 p.

SIEVING, K.E. & KARR, J.R. (1997). — Avian extinction and persistence mechanisms in lowland Panama. Pp. 156-170, *in:* W.F. Laurance & R.O., Bierregaard, Jr. (eds), *Tropical forest remnants. Ecology, Management, and conservation of fragmented communities.* The University of Chicago Press, Chicago.

STOUFFER, P.C. & BIERREGAARD, R.O., Jr. (1995). — Use of amazonian forest fragments by understorey insectivorous birds. *Ecology,* 76: 2429-2445.

TERBORGH, J. (1974). — Preservation of natural diversity: the problem of extinction prone species. *Bioscience,* 4: 715-722.

THOMAS, O. (1928). — The Godman-Thomas expedition to Peru. VII. The mammals of the rio Ucayali. *Ann. Mag. Natl. Hist., Ser.* 10: 249-265.