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LARGE MAMMALS ON SMALL ISLANDS: SHORT TERM EFFECTS OF FOREST FRAGMENTATION ON THE LARGE MAMMAL FAUNA IN FRENCH GUIANA

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RÉSUMÉ

La richesse spécifique en gros mammifères (pour la plupart, de masse corporelle > 1 kg) a été étudiée à Saint-Eugène, Guyane française, dans deux zones adjacentes d'une forêt humide avant et après isolement de l'une d'elles par la mise en eau d'un barrage hydroélectrique. L'état des lieux en 1993-94, avant et pendant la montée des eaux, montre une richesse et une composition spécifiques de gros mammifères similaires entre les deux zones. Avant fragmentation, le peuplement de gros mammifères de Saint-Eugène était relativement complet et comparable à celui d'un site de forêt peu perturbée en Guyane française. Après fragmentation et isolement de l'une des deux zones, devenue une île de taille moyenne, le nombre d'espèces y a diminué d'un tiers tandis qu'il semble inchangé sur la terre ferme. Le suivi après fragmentation (1995-99) de trois îles moyennes supplémentaires (> 20 ha), 22 petites îles (1-10 ha), et 11 îlots (< 1 ha) confirme la perte de richesse spécifique en situation insulaire. Un bilan de l'occurrence des 32 espèces de gros mammifères détectés à Saint-Eugène est dressé pour chaque site, et des résultats préliminaires sur leur abondance globale présentés pour neuf d'entre eux. Le nombre d'espèces présentes sur les îles augmente avec la surface, mais ne semble pas corrélé à la distance d'isolement par rapport à une terre émergée de superficie supérieure. Les îles de moins de 10 ha montrent un peuplement de gros mammifères rapidement appauvri et déséquilibré par rapport à celui des îles de taille moyenne, qui possèdent un peuplement plus riche et plus complexe, comprenant l'ensemble des guildes trophiques, bien que nettement altéré par rapport à la forêt continue. Le peuplement de gros mammifères présents sur les petites et moyennes îles est typiquement composé d'espèces ayant un petit domaine vital et pour la plupart un régime alimentaire généraliste ou herbivore / granivore : les tatous (*Dasypus* spp.), l'Acouchi (*Myoprocta acouchy*), l'Agouti (*Dasyprocta leporina*), le Kinkajou (*Potos flavus*), ainsi que les paresseux (*Choelopus didactylus* et *Bradypus tridactylus*) et les écureuils (*Sciurus aestuans* et *Sciurillus pusillus*). Cependant, les espèces à grand domaine vital, telles que les félins, le Tapir (*Tapirus terrestris*), les pécaris (*Pecari tajacu* et *Tayassu pecari*) et les mazamas (*Mazama americana* et *M. gouazoubira*), exploitent encore les îles, au moins de façon transitoire. Ceci nous amène à discuter du rôle potentiel que pourraient jouer les fragments dans la connectivité entre de plus grands blocs forestiers.

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SUMMARY

In this study, we present data on species richness of large mammals (mostly with body mass > 1 kg) in two contiguous areas at Saint-Eugène, French Guiana, before and after forest fragmentation by flooding. Assessment realized in 1993-94, *i.e.* before and during flooding, showed similar species richness and composition in the two studied areas. Before fragmentation, the large mammal community at Saint-Eugène was comparable to that recorded from a site of pristine forest in French Guiana. After forest fragmentation, one of these zones became isolated (medium-sized island) while the second one remained as a continuous forest. As a consequence, the number of species present on that newly isolated patch decreased of 30 % while it seemed non-affected in the continuous forest. This loss in species richness on the fragmented area was confirmed by a survey conducted in 1995-99 at three additional medium-sized islands (> 20 ha), 22 small-sized islands (1-10 ha) and 11 islets (< 1 ha). Occurrence status of the 32 large mammal species observed at Saint-Eugène is drawn up for all studied sites, and preliminary results on their overall abundance are presented for nine sites. The number of species present in a site was positively correlated to its area, but seemed not to be correlated to its isolation distance from the nearest larger landmass. Islands of less than 10 hectares had a mammal community that was rapidly impoverished and imbalanced in comparison to the one observed on medium-sized islands. The latter presented a mammal community that was richer and more complex, including all trophic guilds, despite it appeared affected in comparison to the continuous forest. Large mammal community on small and medium islands typically included species with small home ranges, and mostly generalist or herbivorous / granivorous feeding habits: armadillos (*Dasypos* spp.), acouchi (*Myoprocta acouchy*), agouti (*Dasyprocta leporina*), kinkajou (*Potos flavus*), sloths (*Choelopus didactylus* and *Bradypus tridactylus*), and squirrels (*Sciurus aestuans* and *Sciurillus pusillus*). However, species with larger home range, as felids, tapir (*Tapirus terrestris*), peccaries (*Pecari tajacu* and *Tayassu pecari*) and brocket deers (*Mazama* spp.) still frequented islands, at least temporarily. We thus discuss the role that fragments may potentially have in connecting larger landmasses.

INTRODUCTION

Habitat destruction and fragmentation are responsible for major losses of biodiversity, especially in tropical forests (Laurence & Bierregaard, 1997; Debinsky & Holt, 2000). From a conservation perspective, it is necessary to understand the consequences of fragmentation for ecosystem changes, both in the short and in the long term. In the numerous research programs on fragmentation, most studies have focused on small vertebrates and plants. With the exception of primates, fewer studies have dealt with large vertebrates, which are often flagship and keystone species (see Rylands & Keuroghlian, 1989; Schwarzkopf & Rylands, 1989; Terborgh, 1992; Andrén, 1994; Offerman *et al.*, 1995; Estrada & Coates-Estrada, 1996; Laurance & Bierregaard, 1997; Debinsky & Holt, 2000; Peres, 2000). This may partly result from the difficulty of distinguishing between effects of fragmentation and overhunting on the large mammal fauna, since both are frequently associated with human influence (Turner, 1996; Richard-Hansen, 1998). In this study, we describe the short-term effects of forest fragmentation on the large mammal fauna at Saint-Eugène, French Guiana, comparing sites before and after flooding. The main objectives of this study are (1) to investigate the effects of forest fragmentation upon species richness, (2) to describe the species composition of insular communities, and (3) to examine overall large mammal abundance on these newly created islands. This approach aimed at understanding the maintenance and establishment of large mammal communities in fragments during the early stages of isolation, and to serve as reference for a long-term survey of the large mammal fauna in this fragmented rainforest.

MATERIALS AND METHODS

STUDY SITES

Field-work was carried out at Saint-Eugène (4° 51' N, 53° 04' W) on the lake created by the Petit Saut hydroelectric impoundment constructed on the Sinnamary River, French Guiana. See Granjon *et al.* (1996), Ringuet *et al.* (1998), Cosson *et al.* (1999b), and Claessens *et al.* (2002) for a detailed description of the study area. Flooding began in January 1994, and resulted in island formation by August 1994, although the water level did not reach its maximum until August 1995 (Cosson *et al.*, 1999b; Ringuet, 2000). Though this area has been exploited for gold near the river banks, especially at the beginning of the twentieth century (Ringuet *et al.*, 1998; Forget, 2002), the human impact on the currently unflooded areas, including the study sites, was relatively low as these were hardly accessible by gold washers before flooding. After fragmentation, the reservoir area and surrounding forest were protected by law against hunting and logging, and no permanent human presence was observed during the study period, until 2000. Nevertheless, a few evidence of hunting has been found, suggesting that some poaching may have occurred during the study period.

Two contiguous areas separated by the river, site 1 and site 2 (see map in Claessens *et al.*, 2002) were sampled before and after flooding, from 1993 to 1999. Site 1 remained a large peninsula (*ca.* 1,000 ha) joined to the mainland, and was chosen as the control site, whereas site 2 became a 28-ha land-bridge island (*sensu* Terborgh *et al.*, 1997) surrounded by several small islands. During and after fragmentation (1994-1999), 36 additional sites were sampled: three medium-sized islands (20-80 ha), 22 small islands (1-10 ha), and 11 tiny islets (< 1 ha). Transect lines in the continuous forest were done at site 1 (two locations noted TF1, and TF2), and at another site in continuous forest north of island 2 (TF3) (see map in Claessens *et al.*, 2002).

METHODS

We focused on the non-flying mid- to large-bodied mammals, size range for individual mass from *ca.* 1 kg to 160 kg –except for the squirrels (< 250 g) and the smallest primates (< 1 kg)– (Emmons & Feer, 1990; Richard-Hansen, 1998; Richard-Hansen *et al.*, 1999; Feer & Charles-Dominique, 2001): primates, carnivores, xenarthrans (anteaters, sloths and armadillos), ungulates (brocket deers, peccaries, and tapir), “large” rodents (Caviomorphs, porcupines and squirrels). Muroid and echimyid rodents as well as marsupials were not studied in our censuses (see Granjon *et al.*, 2002). Animals were identified with reference to Emmons & Feer (1990), but the nomenclature is further based on Wilson & Reeder (1993) (as in Voss & Emmons, 1996; Feer & Charles-Dominique, 2001).

First, using the field station logbook, we reviewed and compiled opportunistic diurnal and nocturnal observations made by biologists primarily engaged in other activities, or in specific mammal censuses, between Sept. 1993 and Dec. 1999. Species occurrence was based on direct (visual) sightings, auditory evidence, and observations of footprints, faeces, recent carcasses, and other evidence of activity (*e.g.*, scratches on tree trunks by felids). The period before and during fragmentation (1993-1994) is referred to as “before fragmentation”, because during 1994, mammal crossings between islands, via the emergent dying forest, were still

observed (Cosson *et al.*, 1999b). The immediate post-fragmentation period (1995-1999) is referred to as “after fragmentation”. Species accumulation curves were constructed from field notes, with cumulative number of person days as the x-axis. Number of person days were calculated as the sum of all productive field days pooled for all observers, *i.e.*, excluding visits with no observation of large mammals, and excluding observations made directly from the camp site (see Voss & Emmons, 1996, p. 39).

Second, we complemented censuses performing line transect sampling (Buckland *et al.*, 1996; de Thoisy, 2000) at nine sites in March-May 1998 (rainy season): three within the continuous forest surrounding the flooded area (TF1 and TF2 on the right side of the river, and TF3 on the left side of the river), three medium-sized islands (number 2, 3, and 58), and three small islands (number 14, 20, and 34). See Claessens *et al.* (2002) for a map of the study area. We used existing trails, and cut additional trails that were left resting during a few days before census. Each transect was censused three to seven times, and the total transect length for each site was calculated as the sum of all censuses (Table I).

TABLE I

Parameters and results of diurnal transect line censuses performed at three continuous forest patches, three medium-sized islands, and three small islands at Saint-Eugène in April-May 1998.

Sites	Continuous forest			Medium-sized islands			Small islands			
	TF1	TF2	TF3	2	3	58	14	20	34	
Number of censuses	3	5	4	6	6	7	5	4	5	
Length of transect (km)	0.9-3.2	0.9	1.5	2.0-2.3	0.9-1.6	0.7-1.2	1.7	1.7	0.9	
Total length (km)	7.0	4.7	6.1	13.7	8.5	7.0	8.5	6.9	4.7	
Total number of encounters	4	2	9	32	19	3	8	9	6	
Number of encounters / 10 km	5.8	4.3	14.7	23.4	22.3	4.3	9.4	13.0	12.9	
Number of encounters for each species										
Rodents	<i>Dasyprocta leporina</i>	2	1	7	12	4	1	4	6	5
	<i>Myoprocta acouchy</i>	-	-	-	8	1	-	-	-	-
	<i>Sciurus aestuans</i>	-	-	-	-	-	1	-	-	-
Primates	<i>Alouatta seniculus</i>	-	-	1	5	3	1	1	-	-
	<i>Pithecia pithecia</i>	-	-	1	3	3	-	-	-	-
	<i>Ateles paniscus</i>	2	-	-	-	2	-	2	-	-
	<i>Cebus apella</i>	-	1	-	-	3	1	-	-	-
	<i>Saguinus midas</i>	-	-	-	-	-	-	3	-	-
Ungulates	<i>Mazama gouazoubira</i>	-	-	-	4	-	-	-	-	-
	<i>Mazama americana</i>	-	-	-	-	2	-	-	-	-
	<i>Pecari tajacu</i>	-	-	-	-	1	-	-	-	-
Carnivores	<i>Eira barbara</i>	-	-	-	-	-	-	-	-	1
Number of species encountered										
		2	2	3	5	8	3	4	2	2

These censuses were made by a single observer (A. D.) at all sites, in the morning (8:00 – 12:00) and afternoon (12:00 – 18:20, mostly after 16:00), walking slowly and stopping frequently (especially when a sound was heard) resulting in a mean speed of 1.2 km.h⁻¹ (sd = 0.3). Because number of observations for each taxon were small, all species were pooled for analysis. We therefore defined encounter rate as the total number of direct sightings (or encounters) per 10 km distance walked (Chiarello, 1999) for all large mammal species combined.

From results of the two methods of survey combined, we obtained a checklist of the large mammal species found at 39 study sites at Saint-Eugène. Species status at each site was defined according to numbers of records of occurrence after fragmentation. They were noted as (1) regularly observed (R) when encountered at least two times at *ca.* one-month interval or more (this class includes resident as well as recurrent visitor species), (2) occasionally observed (O) when encountered once or during only a *ca.* one-month interval (includes occasional visitor species as well as some resident species which were hardly detected), (3) probably extinct (E) when a species was observed before fragmentation but not after, (4) occurrence suspected but not confirmed (?) (*e.g.*, odours of howler monkey's faeces), and (5) never encountered either before or after fragmentation (-).

DATA ANALYSIS

Islands visited less than 10 times were discarded from all data analyses (see Appendix I for minimal number of visits for each site during 1995-1999). Data on species occurrence per site (Appendix I) were used to calculate a similarity index matrix using the Jaccard index:

$$\text{Jaccard Index} = C/(N_i + N_j - C)$$

where N_i and N_j are the number of species at site i and j , respectively, and C is the number of species common to both sites. We coded "present" for the classes O and R, and "absent" for the classes -, E, and ?. In addition, three other control sites were included: sites 1 and 2 before fragmentation (1993-94 census), and the pristine forest of lower Arataye, French Guiana, which includes the field stations of the Nouragues and Saut Pararé. Lower Arataye is only *ca.* 90 km south-east from Saint-Eugène and harbours a complete and well-known mammal fauna (Voss & Emmons, 1996; Feer & Charles-Dominique, 2001). The matrix derived from the similarity indices was used in a hierarchical cluster analysis in order to group sites according to their species composition and richness similarities (for a similar representation, see Chiarello, 1999; Goodman, 1999). In the cluster analysis, we used the Ward minimum variance method, and an Euclidian distance metric.

The relationships between number of species per site on the one hand, and characteristics of area and isolation on the other hand, were estimated using Pearson correlation analyses of transformed data. Number of species, area, and isolation were subjected respectively to square root, logarithmic, and reciprocal transformations (Sokal & Rohlf, 1981). Relationships between encounter rate per site on the one hand, and area and isolation on the other hand were investigated with Pearson correlation analyses performed on untransformed data. Corrected probabilities with the Dunn-Šidák method (sequential Bonferroni tests) were used

for all correlation analyses (Sokal & Rohlf, 1981). Area and distance of isolation values are from Claessens *et al.* (2002). All statistical analyses were performed using SYSTAT 8.0 software (SPSS Inc., 1998).

RESULTS

Thirty-two large mammal species were recorded at Saint-Eugène in 1993-1999 (Appendix I). The large mammal faunal checklist is almost complete, with only eight species missing, in comparison with the undisturbed forest of lower Arataye: *Saimiri sciureus*, *Pteronura brasiliensis*, *Speothos venaticus*, *Herpailurus yagouaroundi*, *Leopardus tigrinus*, *Cyclopes didactylus*, *Priodontes maximus*, and *Cabassous unicinctus* (Feer & Charles-Dominique, 2001).

THE LARGE MAMMAL COMMUNITY BEFORE (1993-94) AND AFTER (1995-99) FRAGMENTATION

Site 1 that remained continuous forest, and site 2 that became a 28-ha island, displayed similar species composition and species richness before fragmentation, with respectively 23 and 22 large mammal species observed after 151 person days of observation (Fig. 1a). Species accumulation curves approached similar asymptotic values (21 species) for both sites after *ca.* 90 person days.

In 1995, after 151 person days, the control site of continuous forest (site 1) exhibited similar species richness after fragmentation as before, with respectively 22 and 23 species, whereas species richness at island 2 declined from 22 to 15 species (Fig. 1a and 1b). Species accumulation curves for continuous forest and island 2 approached asymptotic values after *ca.* 90 effective person days, with respectively 20 and 13 species (Fig. 1b).

In 1996, island 2 showed similar species richness as in 1995 with 12 species after 94 person days and 15 species after 151 person days (Fig. 1c). Sampling effort at site 1 was lower than previously, with only 94 person days. For this sampling effort, site 1 showed a decrease in species richness with 17 species in 1996 (compared to 20 and 21 species for 1995 and 1993-94 respectively), though at a lower extend than site 2 (Fig. 1c).

Although the number of person days on small islands (1-10 ha) and tiny islets (< 1 ha) were too small to compute species accumulation curves for each island and islet, these sites as a whole were nevertheless visited more than 600 times and 420 times, respectively. For comparison, sites 1, 2 and 3 were visited more than 1,000, 700 and 200 times respectively, between 1995 and 1999 (Appendix I). We thus considered that the lower number of species detected on these small fragments was not an artefact of low sampling effort, although we cannot rule out that the number of species for medium-sized islands 48 and 58 (visited > 10 times and > 40 times respectively), may be underestimated.

The cluster analysis based on species richness and composition (Fig. 2) separated a first cluster composed of the control sites (Arataye, sites 1 and 2 before fragmentation, and site 1 after fragmentation) and the medium-sized islands 2 and 3 (cluster A in Fig. 2), from the cluster composed of all other islands (cluster [B + C + D] in Fig. 2). Cluster (B + C + D) can be divided into two groups. The first one, cluster B, contained mostly tiny islets (< 1 ha), with the exception of

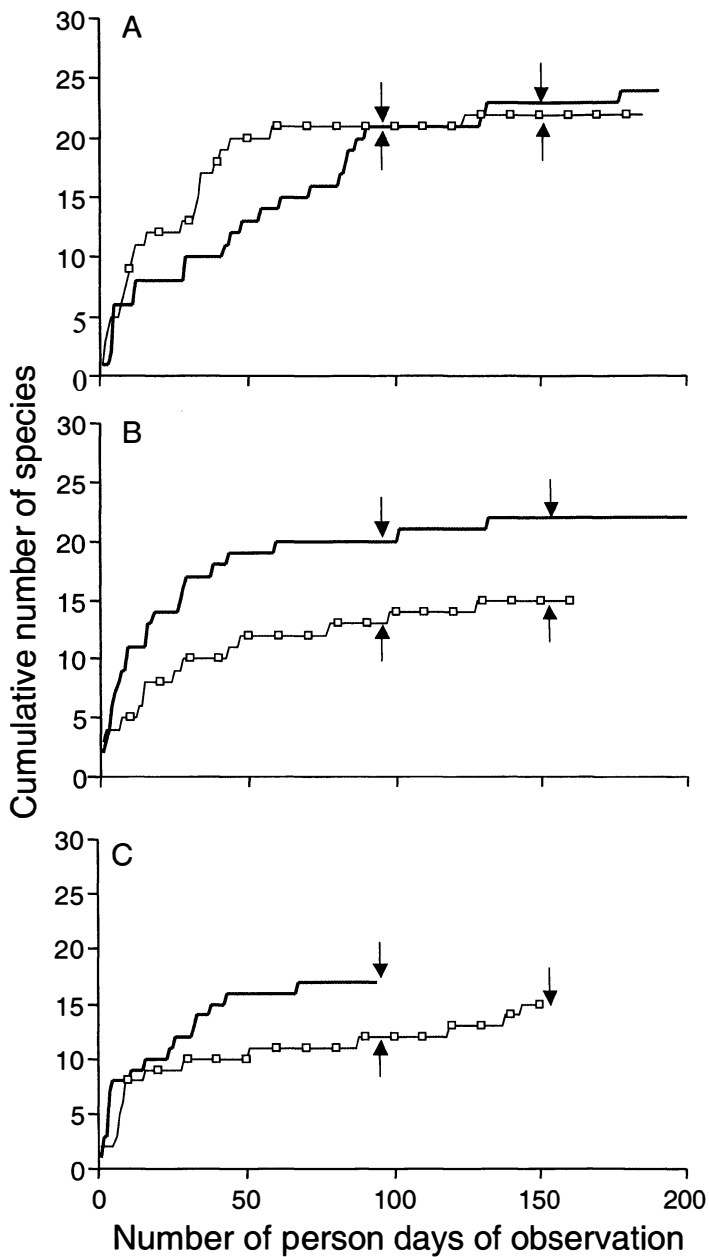


Figure 1. — Cumulative number of large mammal species encountered before and after forest fragmentation at Saint-Eugène, during diurnal censuses at two study sites: site 1 (—), peninsula and site 2 (—□—), island. The two ‘aquatic’ species, *Hydrochaeris hydrochaeris* and *Lontra longicaudis*, are excluded. Arrows indicate 94 and 151 person x days of observations as discussed in text.
 A. — Before and during forest fragmentation (Sept. 1993 – Dec. 1994).
 B. — First year after forest fragmentation (Jan. – Dec. 1995).
 C. — Second year after forest fragmentation (Jan. – Dec. 1996).

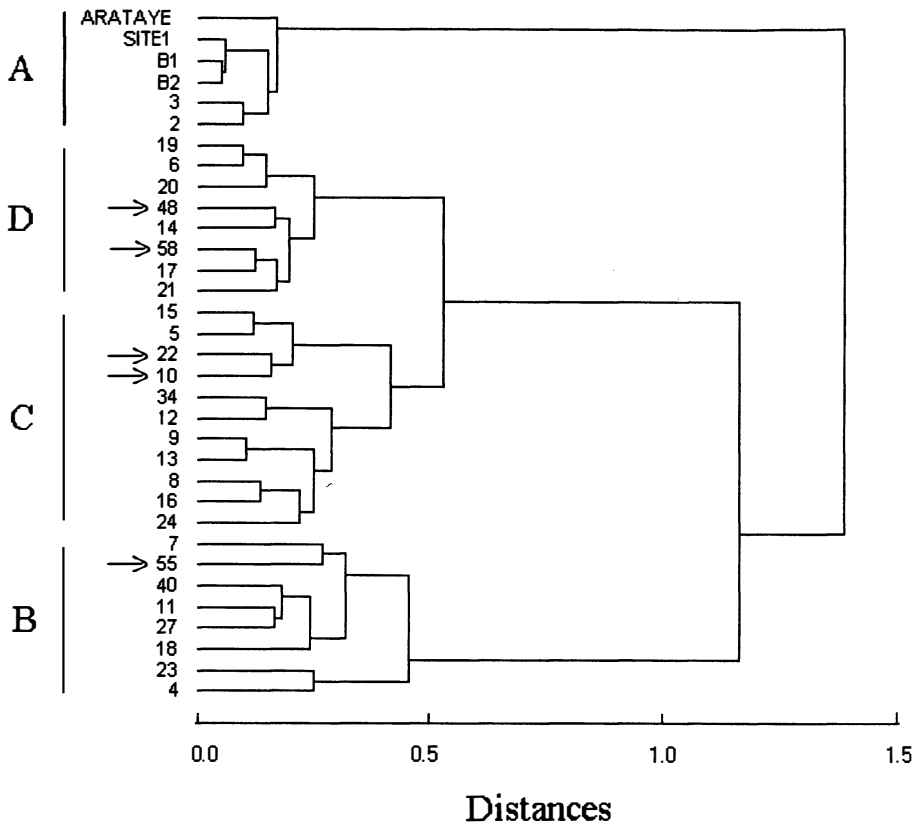


Figure 2. — Hierarchical cluster analysis based on Jaccard similarity indices of the large mammal fauna, for 29 islands (numbered 2 to 58) and continuous forest (site 1) after fragmentation (1995 to 1999), as well as site 1 and site 2 before fragmentation (respectively B1 and B2) (1993 to 1994) and at lower Arataye (Arataye) (Feer & Charles-Dominique, 2001). Islands that are exceptions to the area class are indicated by an arrow (islands 10 and 22: < 1 ha; island 55: 5.4 ha; island 48 and 58: > 20 ha). Capital letters A-D refer to clusters as discussed in text.

island 55 (5.4 ha), and was characterized by a species-poor mammalian fauna. The second one was again separated into two groups: cluster C composed of small islands with a relatively depauperate mammalian fauna, and cluster D composed of islands with a relatively richer mammalian fauna. Note that the two medium-sized islands included in cluster D (islands 48 [40 ha] and 58 [22 ha]) were far less sampled than islands 2 and 3.

Species richness for the 29 study islands was positively correlated with site area ($r = 0.878$, $P < 0.001$), whereas no significant correlation was detected with any of the isolation parameters, *i.e.*, direct distance to the closest landmass ($r = 0.246$, $P = 0.586$), direct distance to the closest landmass of greater area ($r = -0.143$, $P = 0.915$), and minimum cumulative distance over water to a landmass of greater area ($r = -0.059$, $P = 0.997$). The species-area relationship is illustrated in Fig. 3, for the 29 study islands and the mainland.

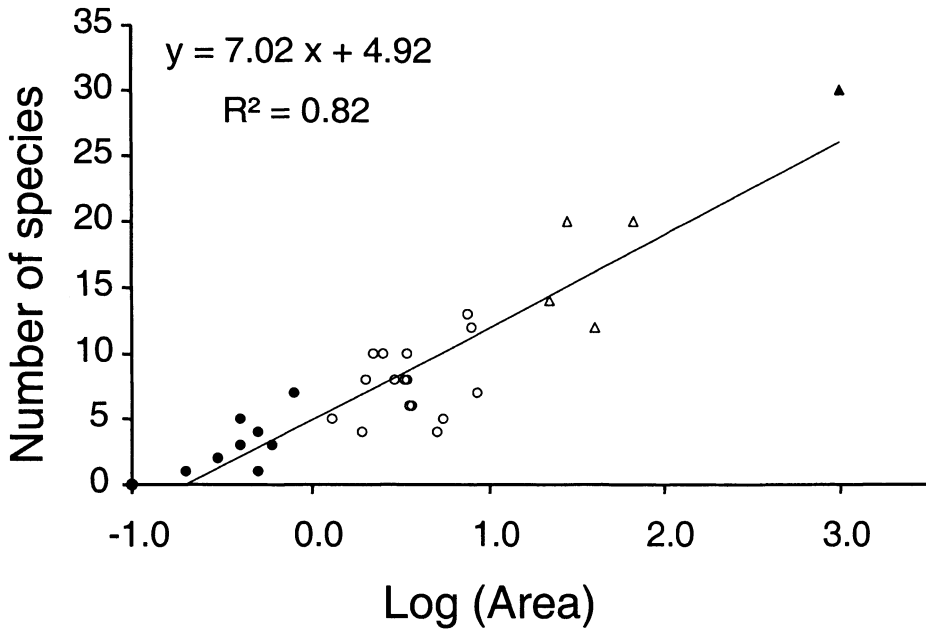


Figure 3. — Species-area relationship deduced from 29 islands and the control site (site 1) under study between 1995 and 1999. Filled circles: tiny islets (< 1 ha), open circles: small islands (1-10 ha), open triangle: medium-sized islands (> 20 ha), filled triangle: continuous forest (site 1).

MAMMALIAN ENCOUNTER RATE AFTER FRAGMENTATION

The 1998 diurnal transect lines comprised a total length of 67 km with 92 encounters (Table I), resulting in a total of 13.7 encounters / 10 km for the whole area. We observed 12 species, the most frequent being the Orange-rumped Agouti (*Dasyprocta leporina*) and the Red Howler monkey (*Alouatta seniculus*) (Table I). For the nine study sites, mammal encounter rate was not significantly correlated with site area ($r = -0.399$, $P = 0.742$), neither with the direct distance to the closer landmass ($r = 0.396$, $P = 0.747$), but was positively correlated with two of the three isolation parameters, namely direct distance to the closest landmass of greater area ($r = 0.807$, $P = 0.034$), and minimum cumulative distance over water to a landmass of greater area ($r = 0.797$, $P = 0.040$). For both medium-sized islands and continuous forest areas, encounter rates exhibited a great heterogeneity between sites (Table I). For instance, both the highest and the lowest values of encounter rate were found within medium-sized islands.

DISCUSSION

LARGE MAMMAL COMMUNITY BEFORE AND AFTER FRAGMENTATION

Before fragmentation, the two forest sites that later either remained continuous forest or became island 2, showed similar large mammal species richness and

composition, and were quite comparable to the pristine forest of lower Arataye. The lack of eight species in the Saint-Eugène inventory (Appendix I) may be attributed to a difference in sampling effort and detectability of the species, since these species are relatively rare in the lower Arataye (Feer & Charles-Dominique, 2001; P.-M. Forget, pers. comm.), some being hardly detectable (Voss & Emmons, 1996), and the two field stations “Nouragues” and “Saut Pararé” have been the foci of long-term ecological studies (Voss & Emmons, 1996; Feer & Charles-Dominique, 2001). This corroborates the fact that previous human settlements near the river banks at Saint-Eugène have had little impact on the present day large mammal fauna list of the study area (Ringuet *et al.*, 1998; Claessens *et al.*, 2002), although this does not imply that previous hunting have had any impact on species abundance (see Richard-Hansen, 1998; Richard-Hansen & Hansen, 1998; de Thoisy & Vié, 1998; Peres, 2000; de Thoisy, 2000). The large mammal community of Saint-Eugène was thus “well balanced”, *i.e.* including all trophic guilds: folivores (browsers and grazers), granivores, frugivores, omnivores, insectivores, and predators.

However, this similarity between the two Saint-Eugène sites was no longer observed after fragmentation occurred. One year after fragmentation, the number of large mammal species on island 2 decreased by one third compared to 1993-94, while the number of species in continuous forest remained stable. Although sampling effort in 1996 for site 1 was relatively low, species accumulation curves suggest that species richness on this peninsula have decreased, although less rapidly and at a lower extent than site 2. This trend needs to be investigated in future years, and may reflect the fact that the peninsula was also affected by forest fragmentation, although we cannot completely exclude an impact of poaching. Similarly to island 2, the other islands censused after fragmentation revealed lower species richness than continuous forest. This corroborates previous studies reporting rapid declines in species richness of small mammals and frugivorous bats following forest fragmentation at Saint-Eugène (Granjon *et al.*, 1996, 2002; Ringuet *et al.*, 1998; Cosson *et al.*, 1999a,b), and of several vertebrate groups in other rainforest sites (Offerman *et al.*, 1995; Turner, 1996; Lynam, 1997; Terborgh *et al.*, 1997; but see Fournier-Chambrillon *et al.*, 2000). We suggest that the effects of fragmentation on the large mammal fauna would have been much stronger if overhunting, logging, and other matrix influences were present (*e.g.*, see Cochrane *et al.*, 1999).

As predicted by the classical species-area relationship of island biogeography theory (MacArthur & Wilson, 1967), we observed a more pronounced loss of mammal species on tiny islets and small islands than on medium-sized islands. Although explanations of the species-area relationship often rely on a dynamic equilibrium in the number of species, island faunas at Saint-Eugène are probably still in disequilibrium. We thus predict further local extinctions both in the short and in the long term, probably not balanced by colonizations, because many islands may be too small to sustain viable populations of most large mammal species (Cosson *et al.*, 1999b). In the literature, the relationship between the number of species S and the area A of a habitat is sometimes expressed as $S = CA^z$, with z typically between 0.1 and 0.4 (Ney-Nifle & Mangel, 2000). Here, our estimates for z were consistently 0.335 ($N = 30$) if we consider the 29 islands and site 1, or 0.377 ($N = 29$) if we consider only islands. In contrast to the area effect on richness, we did not detect any effect of isolation on species richness, as is classically predicted by the MacArthur-Wilson model. However, this may have

resulted either from transitory imbalances of insular mammal communities, or from the fact that the extent of isolation of all islands at Saint-Eugène is quite similar, none being more than 500 m distant from larger landmasses (Claessens *et al.*, 2002). The range of degree of isolation is similarly low in other studies (*e.g.*, Bierregaard *et al.*, 1992). Indeed, according to the criterion of isolation proposed by Terborgh *et al.* (1997), all the islands in this study may be defined as “non far” islands and may therefore share roughly the same influence of isolation on species richness, as far as large mammals are concerned at least. Large mammals, particularly terrestrial species, may be less prone to such isolation effects because they perceive the environment in a coarse-grained manner compared to invertebrates or smaller vertebrates (see Klein, 1989; Powell & Powell, 1987; Malcolm, 1991; Stratford & Stouffer, 1999).

Mammal disappearance during the fragmentation process was documented on island 2, where last observations in the selected species were as follows: Nov. 1993 (*i.e.*, before fragmentation occurred) for *Ateles paniscus*, Jun. 1994 for *Nasua nasua*, Sept. 1994 for *Myrmecophaga tridactyla* (a transient individual) and for *Eira barbara*, and Nov. 1994 for *Cebus apella*. Species loss may be attributed both to sample effects (Laurence & Bierregaard, 1997) as some species were not present when fragmentation occurred (*e.g.*, *A. paniscus* on island 2), and to voluntary escape during or after flooding. Indeed, some terrestrial mammals were seen swimming in the lake (*e.g.*, agouti [P. de Mercey, pers. comm.]), and some arboreal mammals were seen crossing between islands using the emerged crowns of dead trees during the year after flooding (Cosson *et al.*, 1999b). Later, this way of escape became problematic, as falling dead branches offered more sparse and less secure support, and we observed unsuccessful attempts of crossing between islands by monkeys. Loss of individuals may also reveal deaths, as suggested by carcasses found a short time after isolation (*e.g.*, sloths, howler monkeys and armadillos on tiny islets). These extinctions may result from starvation, competition or predation (Fournier-Chambrillon *et al.*, 2000). Indeed, the latter appears to play an important role in the regulation of animal numbers and loss of diversity on newly created islands (Claessens, 2000; Ringuet, 2000).

Species loss on islands resulted in a unbalanced mammal communities. With a few exceptions, the cluster analysis based on species similarity indices in 32 sites groups islets (< 1 ha) separately from small islands (1-10 ha), both separated from larger landmasses. Islets have a depauperate mammalian fauna with zero to seven species, consisting of generalist feeders or folivores / granivores. The mammal community occurring on small islands is mainly composed of species characterized by a small home range, high abundance in continuous forest, and generalist feeding habits, as already found by other authors (*e.g.*, Laurance *et al.*, 1997; Terborg *et al.*, 1997; Cosson *et al.*, 1999b). The basic community on such islands is usually composed of armadillos (*Dasybus* spp.), agoutis (*Dasyprocta leporina*), acouchies (*Myoprocta acouchy*) and pacas (*Agouti paca*). Sometimes the inconspicuous sloths (*Bradypus tridactylus* and *Choloepus tridactylus*) and squirrels (*Sciurus aestuans* and *Sciurillus pusillus*), and the frugivorous kinkajous (*Potos flavus*) were added to these core species. This list is sometimes supplemented by *Mazama* spp., probable occasional visitors. The howler monkey *Alouatta seniculus* was also found on numerous small islands, despite the medium size of its home range, suggesting that this species can persist, at least temporarily, in restricted and degraded habitat thanks to its highly folivorous diet (Julliot & Sabatier, 1993; de Thoisy & Richard-Hansen, 1996). Howler monkeys observed on small islands

were frequently solitary individuals that were probably isolated during flooding. The duration of the presence of such species on these islands may thus not exceed individual lifespans. In contrast to the observations of Terborgh *et al.* (1997) at Lago Guri (Venezuela), howler monkeys at Saint-Eugène were not only found on remote islands, but also on relatively close small islands (six of the 11 small islands and islets on which howlers were observed were situated less than 100 meters away from a larger landmass). We thus did not find any evidence suggesting that howlers had escaped from islands. This difference between Saint-Eugène and Lago Guri may be attributable to a set of confounding factors, *e.g.*, temporal scale, howler abundance and distribution before fragmentation, or predation rate (see Peetz *et al.*, 1992). In addition to the basic community, other species can be found with increasing island area, as other primate species or Collared Peccaries (*Pecari tajacu*), and other visitors such as felids and tapirs (*Tapirus terrestris*). As observed in other studies, species composition in fragments was thus a nested subset of species found in sites of larger area, indicating a deterministic pattern of species loss (see Nilsson, 1986; Blake, 1991; Terborgh *et al.*, 1997; Laurance *et al.*, 1997).

Species regularly observed on islands, such as monkeys (*e.g.*, Guianan saki groups on island 2 [Vié, 1998]), or agoutis and acouchies (with respectively more than 152 and 192 encounters for 342 person days, on island 2 during the 1995-1999 period), were obviously permanent residents. Despite the fact that the aquatic matrix is an unsuitable habitat for most large mammal species, we have direct and indirect evidence of transient visits to islands by several species (Cosson *et al.*, 1999b; Ringuet, 2000; Appendix I). Several species with large home ranges, especially some large carnivores and ungulates, were regularly but not permanently present on islands, and may be classified as recurrent visitors (Ringuet, 2000). A herd of Collared Peccaries monitored by radio-tracking recurrently visited poorly isolated islands (number 13 and 17) during 1995-96 (Judas, 1999). An ocelot was observed 10 times on the relatively well-isolated island 2 between April 1995 and December 1996 and may have been a "temporary resident" on this island (see Ringuet, 2000). Tapirs were frequently observed on different small islands and also swimming in the lake around island 20, while *Mazama* spp. were recurrently observed on some small islands. In addition to recurrent observations, we observed occasional visitations by ungulates, Giant Anteater (*Myrmecophaga tridactyla*), Tayra (*Eira barbara*), small and large felids. These species were encountered or evidence of visitation was found on several islands (faeces and footprints, recently preyed upon vertebrates such as armadillos or the terrestrial turtle *Chelonoidis [Geochelone] denticulata*). These direct and indirect signs were frequently apparent and were not anecdotal. Taken together, these observations clearly show that both large herbivores and top predators with home range requirement too large to allow them to be resident on a given island, may still persist in a fragmented landscape in the very short term. This corroborates observations made a few years after flooding in Venezuela (Terborgh *et al.*, 1997), as well as historical records at Barro Colorado Island (Wright *et al.*, 1994), and large felid movements in the Biological Dynamics of Forest Fragment Project area (Laurance *et al.*, submitted). Only two mammal species more or less restricted to waterside areas were observed at Saint-Eugène. Capybaras (*Hydrochaeris hydrochaeris*) were observed along the shorelines of several islands after flooding. The southern river otter (*Lontra longicaudis*) was present before and after the flooding (first observed in Nov. 1993, and then regularly after flooding, with a burrow on island 5).

No large mammal extinctions were recorded for the Saint-Eugène area considered as a whole (except perhaps for the inconspicuous *Galictis vittata* that was never observed after fragmentation), though communities on individual islands experienced numerous local extinctions. This shows that dispersal and colonization via the aquatic matrix were not sufficient to compensate for local extinctions on islands.

LARGE MAMMAL ABUNDANCE AFTER FRAGMENTATION

Large mammal abundance was investigated after fragmentation for three sites for each of the three area classes: continuous forest, medium-sized islands, and small islands. The overall encounter rate at Saint-Eugène for all large mammal species pooled (13.7 / 10 km) is consistent with what was observed in an Atlantic forest in south-eastern Brazil 10-30 years after isolation (13.1 / 10 km, *i.e.*, 602 encounters for 458.8 km [Chiarello, 1999]), but lower than that found in and around Gatun lake (Panama), either at two peninsulas on the mainland (20.0 and 27.1 / 10 km respectively) or at Barro Colorado Island (42.2 to 70.4 / 10 km) *ca.* 80 years after fragmentation (Glanz, 1990; but see Wright *et al.* [1994] for discussion on the confounding factors resulting in overestimated mammal abundance at BCI).

In contrast to other studies (*e.g.*, Bender *et al.*, 1998; Chiarello, 1999), we did not detect any effect of patch area on encounter rate, since encounter rate greatly varied within some area classes. However, the two highest encounter rate values were for medium-sized islands, and two of the three lowest values were for continuous forest sites. Therefore, despite non-significant evidence for ecological release (*i.e.*, increasing density on islands in response to reduction of competition, predation and / or parasitism, linked to the modification of island communities; Terborgh *et al.* [1997]), our results suggest that this process may occur at Saint-Eugène for large mammals, but that it is not yet fully in evidence (for instance, see Vié, 1998, for evidence of high densities of *Pithecia pithecia* and *A. seniculus* on island 2 at Saint-Eugène). Note that a temporarily increased density of large mammals was observed on the Saint-Eugène peninsula during flooding, as individuals concentrated on the diminishing unflooded area (Granjon *et al.*, 1996), a phenomenon different from ecological release. This temporary concentration of individuals during flooding was also observed for mid- and large-sized mammals on islands situated downstream on the lake, which later exhibited a decrease of animal abundance one year after the beginning of the water inflow (Fournier-Chambrillon *et al.*, 2000). On the other hand, we observed a positive correlation between encounter rate and distance to a larger landmass. This could be explained by two non-exclusive hypotheses: when distance of isolation is weaker (1) a greater proportion of individuals might escape from islands as proposed by Terborgh *et al.* (1997) for vertebrates, and by Claessens (2002) for birds, and (2) predation rate may be increased due to a greater visitation frequency of large predators from surrounding larger forest patches. For instance, island 58, that is close to the mainland, differed from other islands of the same size class in its low encounter rate. However, all interpretations based on encounter rates should be regarded with caution because of design limitations. Indeed, the mode of calculation of encounter rates hides the unequal representation of taxa between sites. Furthermore, the small number of replicates per size class means that it is difficult to make generalization. Moreover, we assumed that large mammal

detectability was similar among the study sites, but this was not investigated. These preliminary results on large mammal abundance need to be tested with more detailed studies (see de Thoisy, 2000).

CONCLUSION

This study assesses the short-term effects of forest fragmentation on the large mammal fauna. Species richness rapidly declined after fragmentation, leading to an unbalanced fauna on islands, whereas species richness of the nearby continuous forest remained similar to that observed before flooding, at least in the very short term. That proved that this decline was not a regional large scale trend induced by some uncontrolled environmental or demographic factors. We also reaffirm previous observations (Bierregaard & Dale, 1996; Terborgh *et al.*, 1997) on the use of such a landscape mosaic by large mammals. Although it is acknowledged that the maintenance of large undisturbed areas of lowland tropical rainforest must be one of the highest priorities for conservation (Thiollay, 1989; Terborgh, 1992), the conservation value of small forest fragments is also debated (Bowman & Woinarsky, 1994; Turner & Corlett, 1996). It is clear that small fragments by themselves cannot maintain a complex large mammal fauna in the long term (Corlett & Turner, 1997). But we showed here that under low or negligible hunting pressure, poorly isolated fragments surrounded by continuous forest were still used by some large mammal species, at least in the very short term, despite the presence of an aquatic matrix that is unfavourable to their movements. Such use of fragmented landscapes may be more frequent when fragments are surrounded by a terrestrial matrix, since some of the terrestrial forest species can use non-forested environments or secondary habitats, at least in some parts of their geographic range (Emmons & Feer, 1990; Bierregaard & Dale, 1996). If such results are confirmed at longer time scales, this would indicate that, without any effect other than fragmentation *per se* like hunting or logging, such fragments may ensure connectivity, for some of the large mammal species, through use as "stepping-stones" (Harris, 1984 cited in Quigley & Crawshaw, 1992; Estrada *et al.*, 1994) between the larger forest patches that are necessary to sustain viable populations.

APPENDIX I

*Occurrence status of 32 large mammal species on 38 islands (numbered 2 to 58) and in continuous forest (site 1) at Saint-Eugène area, between 1995 and 1999. R: regularly observed; O: occasionally observed; E: probably extinct; ?: suspected but not confirmed by visual observation; -: never encountered. * indicates occurrence in the 1993-94 census. Note that (*sp.) or merged cells indicate that an uncertainty remains for precise identification of the species (e.g., large felid, Mazama sp.). For primates, the number in brackets refers to the minimal number of individuals seen after fragmentation. Note that Dasypus spp. includes D. novemcinctus and probably D. kappleri, and that Couendou spp. probably includes C. melanurus and C. prehensilis.*

	Site	site 1	2	3	4	5	6	7	8	9	10	11	12	13	
	Area (ha)	ca. 1,000	28,0	67,0	0,1	2,0	2,2	0,3	3,3	1,3	0,4	0,6	3,4	5,0	
	Number of visits (days / nights)	>1,000 / 73	>700 / 80	>200 / 0	>20 / 0	>50 / 4	>20 / 4	>20 / 0	>20 / 4	>35 / 4	>100 / 1	>60 / 1	>60 / 2	>20 / 0	
	Species	English vernacular names													
Primates	<i>Saguinus midas</i>	golden-handed tamarin	* R	* R(6)	R	-	-	-	-	-	-	-	-	-	E
	<i>Cebus apella</i>	brown capuchin monkey	* R	* E	R(4)	-	-	-	-	E	-	-	-	-	-
	<i>Cebus olivaceus</i>	wedge-capped capuchin monkey	R	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pithecia pithecia</i>	Guianan saki	* R	* R(2 grps)	R(>1pair)	-	-	-	-	-	-	-	-	-	-
	<i>Alouatta seniculus</i>	red howler monkey	* R	* R(4)	R(3)	-	R(1)	R(1)	-	?	-	-	-	?	-
	<i>Ateles paniscus</i>	black spider monkey	* R	* E	R(7)	-	-	-	-	-	-	-	-	-	-
Carnivores	<i>Nasua nasua</i>	South American coati	* R	* E	-	-	-	-	-	-	-	-	-	-	-
	<i>Potos flavus</i>	kinkajou	* R	* R	-	-	R	-	R	-	-	-	-	-	-
	<i>Galictis vittata</i>	grison	-	-	-	E	-	-	-	-	-	-	-	-	-
	<i>Eira barbara</i>	tayra	* R	* E	O	-	-	-	-	-	-	-	-	O	-
	<i>Lontra longicaudis</i>	southern river otter	* -	O	-	-	R	-	-	-	-	-	-	-	-
	<i>Leopardus pardalis</i>	ocelot	(*sp.) O	R	O	-	-	-	-	-	-	-	-	-	-
	<i>Leopardus wiedii</i>	margay	(*sp.) O	* E	O	-	-	-	-	-	-	-	-	-	-
	<i>Puma concolor</i>	puma	(*sp.) O	(*sp.) -	-	-	-	-	-	-	-	-	-	-	-
<i>Panthera onca</i>	jaguar	* R	(*sp.) O	O	-	-	-	-	-	-	-	-	O	-	
Ungulates	<i>Tapirus terrestris</i>	Brazilian tapir	* R	* R	R	-	-	-	-	O	O	O	-	-	O
	<i>Pecari tajacu</i>	collared peccary	* R	* O	O	-	-	-	-	-	-	-	-	-	-
	<i>Tayassu pecari</i>	white-lipped peccary	* R	-	O	-	-	-	-	-	-	-	-	-	-
	<i>Mazama americana</i>	red brocket deer	* R	* R	R	-	-	-	-	-	O	-	-	O	-
	<i>Mazama gouazoubira</i>	grey brocket deer	* R	* R	O	-	O	O	-	O	-	R	-	O	O
Rodents	<i>Sciurus aestuans</i>	Guianan squirrel	* R	* R	R	-	-	-	-	O	-	-	-	-	-
	<i>Sciurillus pusillus</i>	Neotropical pygmy squirrel	* R	* R	R	-	-	O	-	-	-	-	-	-	-
	<i>Agouti paca</i>	paca	* R	* R	R	-	R	R	-	R	R	-	O	R	-
	<i>Dasyprocta leporina</i>	orange-rumped agouti	* R	* R	R	E	O	O	-	O	O	-	-	O	O
	<i>Myoprocta acouchy</i>	red acouchy	* R	* R	R	-	R	R	O	-	-	O	-	-	-
	<i>Hydrochaeris hydrochaeris</i>	capybara	-	-	-	-	R	-	-	-	-	R	R	R	-
	<i>Coendou</i> spp.	porcupines	* O	* O	-	-	-	-	-	-	-	-	-	-	-
	<i>Tamandua tetradactyla</i>	collared anteater	* R	* O	O	-	-	-	-	-	-	-	-	-	-
Xenanthrans	<i>Myrmecophaga tridactyla</i>	giant anteater	* R	* E	-	-	-	-	-	-	-	-	-	-	-
	<i>Dasypus</i> spp.	armadillos	* R	* R	R	-	R	R	R	R	R	-	O	R	R
	<i>Bradypus tridactylus</i>	pale-throated three-toed sloth	* O	* R	-	E	E	O	E	-	-	-	-	-	-
	<i>Choloepus didactylus</i>	southern two-toed sloth	* R	-	-	-	-	O	-	O	-	-	-	-	-

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