

THE SMALL MAMMALS OF AMAZONIAN FOREST FRAGMENTS:
PATTERN AND PROCESS

By

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To my parents

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Chairman: Dr. John F. Eisenberg
Major Department: Wildlife and Range Sciences
(Forest Resources and Conservation)

At a site in the central Amazon approximately 80 km north of Manaus, Brazil, small mammals were censused between October 1983 and March 1989. In total, 19 small mammal species (9 marsupials and 10 rodents) were captured in six habitat types: (i) continuous forest (CF), (ii) CF near clearcut/forest edges, (iii) 100-ha fragment, (iv) 10-ha fragments, (v) 1-ha fragments, and (vi) the matrix of pasture and secondary growth surrounding forest fragments. It is shown that tooth-impressions from live animals can be used to age and distinguish the two Proechimys species at this site: P. cuvieri and P. guyannensis. At the beginning of the research period, most small mammals were much more abundant than in 1982, and during the study, abundances of most taxa declined. The time period during which populations increased in abundance had an unusually pronounced dry season. The pattern of seasonal reproduction switched between the first year of study and the

second. It is suggested that the switch in reproductive behavior was density-dependent, and that resource limitation is a relatively frequent occurrence in this community. Approximately two years after they were isolated from continuous forest, four 10- and four 1-ha fragments exhibited small mammal communities very different from those in continuous forest. Abundances of most taxa, species richness, and biomass were greater in fragments than in CF, and greater in 1-ha fragments than in 10-ha fragments. Arboreal biomass slightly exceeded terrestrial biomass in CF, whereas in 10-ha fragments, and especially in 1-ha fragments, terrestrial biomass exceeded arboreal biomass. Relative to CF, and especially in 1-ha fragments, fragments on average had thicker understory and thinner overstory foliage, and correlated with these vegetation changes, fragments had greater insect biomass from understory tangle-traps and lower insect biomass from overstory pit-fall traps. Models of edge effects independent of insularization per se, including a model more realistic than extant ones, are presented and are found to successfully predict habitat and small mammal community differences between fragments and continuous forest, and between the two sizes of fragments.

CHAPTER 1
GENERAL INTRODUCTION

Ever since Darwin (1859) used the faunas of certain South American archipelagos to shed light on that "mystery of mysteries," the origin of species, studies of insular faunas have been of central importance in evolutionary and biogeographic research (Mayr 1982). Islands have also gained prominence in ecological research, not only because they provide insight into evolutionary processes, but because they provide relatively closed systems with relatively simple faunas. Models of island biogeography, especially the seminal work by MacArthur and Wilson (1967), have in turn served as paradigms for the study of habitat patches and have been extended to problems in patch dynamics, species coexistence, and conservation (reviewed in Simberloff 1974, Gilbert 1980).

The need to understand ecosystem function in habitat patches has become particularly urgent in recent years. A frequent consequence of anthropogenic activities is the reduction of once extensive ecosystems to remnant patches surrounded by human-modified habitat. This is becoming increasingly prevalent in tropical regions, where rates of deforestation are escalating. In many cases, these fragments of forest represent our only hope for preservation of intact tropical ecosystems, and their incredibly rich flora and fauna.

MacArthur and Wilson's (1963, 1967) theory of island biogeography, which suggested that the biota of an island is in dynamic equilibrium between immigration of new species onto an island and extinction of species already present, offers a framework within which predictions concerning population responses to important fragment characteristics such as area, distance to "mainland" habitats, and proximity to other fragments can be made (Diamond 1975a, Simberloff and Abele 1982, Simberloff 1988). However, concurrent with the isolation of fragments, the environment within fragments may often change. In particular, proximity to fragment edges can lead to pervasive changes in fragment communities ("edge effects"). Hence, ecosystem function within fragments may be influenced both by insularization, and the resultant changes in immigration and extinction rates, and by changes in the quantity and quality of habitat within fragments.

In this dissertation, I investigate whether processes dependent on insularization per se were important in structuring the small mammal communities of tropical forest fragments at a site in the central Amazon. I reasoned that the simplest "null" hypothesis would be to suggest that subsequent to the isolation of fragments from surrounding forest, changes in the small mammal community depend solely on changes in the quality of the small mammal habitat and resources in the fragments.

Forest fragmentaion occurred in the late 1970s and early 1980s at this site 80 km north of Manaus, Brazil after a series of cattle ranches were established in the upland primary forest of the area. Several square reserves of 1-, 10-, and 100-ha were set aside prior to

deforestation, and were subsequently isolated from continuous forest as a result of conversion of the surrounding forest to pasture via clearcutting (Lovejoy et al. 1984, 1986). The site provided two important controls to aid in identifying the effects of fragmentation: i) a wealth of continuous, undisturbed forest was available for study, allowing for simultaneous monitoring of fragment and continuous forest communities and ii) communities in fragments in some cases were monitored prior to isolation or shortly thereafter. Initial research on small mammals in the reserves began in February of 1982 (Emmons 1984, Lovejoy et al. 1984) and continued for 5.5 mo. I present results from a second study that began in October 1983 and ran until March 1989.

It is perhaps fitting, given the elementary state of knowledge about species richness in the tropics (Wilson 1988), that the opening (second) chapter focuses on a problem in species identification as a way of introduction to the community under study. Members of the genus Proechimys are the numerically dominant terrestrial small mammal species in many Neotropical forests (Emmons 1982), but it has proven difficult to distinguish sympatric species in the field. In this chapter, I describe a technique whereby teeth impressions are used to distinguish the two species at this central Amazonian site, P. guyannensis and P. cuvieri.

The third chapter examines temporal variation in the abundance of terrestrial small mammals in continuous forest; variation that was unrelated to fragmentation in itself. During nearly seven years of live-trapping, most terrestrial species showed a single peak and decline in abundance. The pattern of seasonal reproductive activity varied with

population density, suggesting density-dependence, and indirectly, resource limitation.

The fourth chapter explores the effects of forest fragmentation on the small mammal community at this site in the central Amazon. Did fragmentation lead to predictable patterns of change in the small mammal community of continuous, undisturbed forest, and did these changes in community structure vary with fragment size? Did patterns of community change suggest that certain processes were more important in driving these changes than others?

In the subsequent three chapters, I attempt to answer the question: why did fragment communities differ from those in continuous forest? In chapters five and six, the effect of fragmentation on two habitat features important to tropical small mammals is examined: vegetation structure and insect biomass. In addition, I test whether the observed effects on vegetation structure and insect biomass can be solely attributed to edge effects. In the seventh chapter, I use an experimental approach to test whether these purely edge-driven habitat changes account for the changes in small mammal communities that occur subsequent to forest fragmentation.

In the final chapter, I conclude by examining some of the implications of my research for attempts to protect these enormously rich ecosystems.

CHAPTER 2
USE OF TOOTH IMPRESSIONS TO IDENTIFY AND AGE
LIVE PROECHIMYS GUYANNENSIS AND P. CUVIERI
(RODENTIA: ECHIMYIDAE)

Introduction

The spiny rat genus Proechimys is among the most abundant and specious of Amazonian rodent genera, yet it is one of the region's taxonomically least understood mammalian groups. In a recent review of the subgenus Proechimys, Patton (1987) used cranial and bacular features to reduce 59 named forms to nine species groups, but he hypothesized that six of the groups were polytypic and cautioned that more detailed work would be required to define the species of Proechimys. Patton and Rogers (1983) and Patton (1987) suggested that the usual morphological approach has met with little success in Proechimys in large part due to age-related variation that obscures geographic patterns and species differences.

Taxonomic work to date within the genus has made use of several characters not easily determined from live specimens, and in no case has it been possible to identify all live individuals (including juveniles) of sympatric species. There is thus a need to develop simple methods to distinguish live individuals of sympatric species. Given the utility of partitioning age related variation (Patton and Rogers 1983), a beginning is to provide relative ages of live individuals. Several authors have utilized tooth wear to age skulls (Moojen 1948, Martin 1970, Fleming

1971, Guillotin 1982_a, Patton and Rogers 1983); however, only pelage characteristics have been used to age live individuals. Fleming (1971) provided the most detailed scheme. Four age classes were defined: juvenile, subadult, young adult, and adult. A more detailed and objective method than his might not only aid in defining sympatric species, but would aid in investigations of population dynamics.

Proechimys guyannensis and P. cuvieri are widely sympatric throughout most of the region north of the Amazon river and north and east of the Rio Negro, and at least in the region north of Manaus and in French Guiana, they are syntopic (Guillotin 1982_a, Malcolm 1990). To date, researchers have not been able reliably to distinguish live individuals (Guillotin 1982_a, Guillotin and Ponge 1984, Emmons pers. comm.); however, the species are easily distinguished based on cranial (Petter 1978, Guillotin and Ponge 1984, Patton 1987), bacular (Patton 1987), or karyotypic (Reig et al. 1979) features. Herein, I describe a simple method by which tooth impressions were used to distinguish and age live individuals. In addition, I examined eye lens weight and reproductive activity as a function of age class.

Materials and Methods

Identification

During the period October 1983 to March 1989, Proechimys spp. were caught approximately 80 km north of Manaus, Brazil on the Biological Dynamics of Forest Fragments Project (BDFFP) (Malcolm 1988, Malcolm 1990, in press). Individuals were live-trapped and/or snap-trapped in several major habitats, including continuous forest, the edge of continuous forest, 1- and 10-ha forest fragments, and 5-year-old

secondary forest. Standard body measurements (total length, tail length, hindfoot length, and ear height) to the nearest mm, body weight to the nearest g, and reproductive status (Malcolm 1988) were determined at first capture of an individual and at recaptures during subsequent trap sessions (where a trap session is the eight or nine consecutive nights traps were set at a site). Impressions of the right maxillary tooth row were collected from 38 skulls from the BDFPP area, from eight skulls from the Balbina dam site (an area some 80 km distant from the BDFPP sites), and from most live animals caught after January 1987 (49 individuals) in the BDFPP area. Skulls were identified to species (Patton 1987) and identifications were confirmed by Dr. Patton (28 *P. guyanensis* and 18 *P. cuvieri*). Eight individuals with collected skulls were missing one body measurement. These missing data were estimated by log-log regression on single best correlates within species. Three skulls had all body measurements missing. Skulls are deposited in the mammal collection of the Instituto Nacional de Pesquisas da Amazônia.

To take the impression, I used modelling clay (plasticene). A 15 by 4 by 2 mm piece of clay was stuck along its long axis to a 60 by 3 by 1 mm piece of aluminum and, by use of the piece of aluminum as a handle, pressed lightly against the tooth row. Two people were needed to take the impression from a live animal; one secured the animal and its rostrum, and the other opened the mouth and took the impression.

Three measurements were taken from the tooth row impressions: the total length of the tooth row, the anterior-posterior length of the occlusal surface of M^1 , and, based on tooth eruption and occlusal surface wear, tooth wear class (figure 2-1). Wear classes 1 through 8

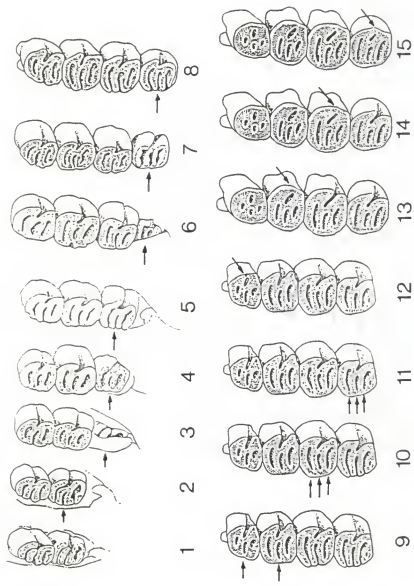


Figure 2-1. Right maxillary toothrow of *Proechimys* illustrating wear patterns and eruption sequence for 15 age classes (see text for complete descriptions of age classes). Age classes 1 - 8 are from Patton and Rogers (1983).

were from Patton and Rogers (1983). I subdivided their age category 9 into three classes (9 - 11), and their category 10 into 4 classes (12 - 15). These new classes were defined as follows: Class 9 - flexi on PM^4 and M^1 isolated; Class 10 - flexi on M^2 isolated; Class 11 - flexi on M^3 isolated; Class 12 - primary flexus on PM^4 isolated or obliterated; Class 13 - primary flexus on M^1 isolated or obliterated; Class 14 - primary flexus on M^2 isolated or obliterated; Class 15 - primary flexus on M^3 isolated or obliterated. Mean cheek tooth length was computed as the length of the tooth row divided by the number of fully occluded teeth in the row (one fully occluded tooth for wear class 1, two for classes 2 - 4, three for classes 5 - 7, four for classes >7).

The extent to which live individuals of the two species could be distinguished was examined for the following sets of measurements: all measurements, body measurements plus wear class, body measurements plus tooth row measurements, and body measurements. For each set, I used a canonical discriminant analysis on log-transformed data to derive a function that maximally discriminated between individuals whose species was known (skulls). Live individuals were subsequently classified into one species or the other using this function, and the F -ratio from an ANOVA comparing means of the canonical variable between the two groups was calculated.

In addition, for each of the sets, I wished to determine which subsets (if any) would equally well distinguish live individuals of the two species. I used a stepwise discriminant analysis on skulls to derive the minimal set (F to enter or leave was set to 0.01), and again

judged the utility of the subset by examination of the F -ratio comparing individuals whose species was not known.

Wear Class as a Measure of Relative Age

Eye lenses from 20 BDFPP individuals with collected skulls were preserved in 10% formalin for at least six months and were blotted dry and weighed to the nearest 0.0001 g. Analysis of variance (ANOVA) was used to examine the relationship between wear class and lens weight.

Results

Identification

F -ratios from ANOVA's on body measurements plus at least one tooth-mold measurement, or subsets of these, were approximately equal and much greater than the F -ratios from the analyses using body measurements alone (table 2-1). Bivariate plots of subset variables are shown in figures 2-2 and 2-3. The plot of mean molar length or M^1 length vs hind foot length did not separate animals in wear classes 1 and 2 (field numbers 1490, 2976, 3379, 3426, 3430, and 3460), but the plots of body measurements vs wear class did. For older animals, the plot of mean tooth length vs hindfoot length separated all but two individuals (field numbers 3276 and 4430). Figure 2-3C suggested that these individuals were P. cuvieri. These results indicate that by taking an impression of the tooth row, most live P. guyannensis and P. cuvieri can be distinguished.

Wear Class as a Measure of Relative Age

Mean eye lens weight generally increased with wear class (table 2-2), suggesting that wear class provided a measure of relative age. Sample sizes were sufficient to compare means among only three wear

Table 2-1. Results from canonical analyses discriminating between known *Proechimys guyannensis* (26 individuals) and *P. cuvieri* (17 individuals). "Best" subsets were determined by stepwise discriminant analysis. Forty-nine live individuals (species unknown) were subsequently classified into one species or the other using the canonical analyses. F-ratios are from analyses of variance (ANOVA) comparing means of the canonical variable between the two groups of live animals.

Variables	Raw canonical coefficients ¹							Multivariate	ANOVA
	WT	BDL	HFL	RAR	ROW	M1	CLASS	F ²	F ³
All	0.82	5.34	8.36	2.20	7.68	17.44	-2.00	83.55 (7,35)	120.73
Best subset	-	-	9.71	-	15.40	16.28	-	179.63 (3,39)	103.93
Body, CLASS	1.85	7.17	9.05	4.30	-	-	-4.02	53.18 (5,37)	99.28
Best subset	-	10.51	11.80	-	-	-	-3.80	84.45 (3,39)	110.46
Body, ROW, M1	-0.33	3.06	7.20	0.98	15.66	16.33	-	86.52 (6,36)	110.68
Best subset	-	-	9.71	-	15.40	16.28	-	179.76 (3,39)	103.93
Body	-2.10	4.39	11.17	5.32	-	-	-	13.38 (4,38)	36.42
Best subset	-	-	10.20	-	-	-	-	48.28 (1,41)	35.53

¹ WT = body weight (g), BDL = head plus body length (mm), HFL = hindfoot length (mm), RAR = ear height (mm), ROW = mean cheek tooth length (mm), M1 = first upper molar length (mm), CLASS = age class.

² Degrees of freedom in parentheses.

³ Degrees of freedom = 1,47.

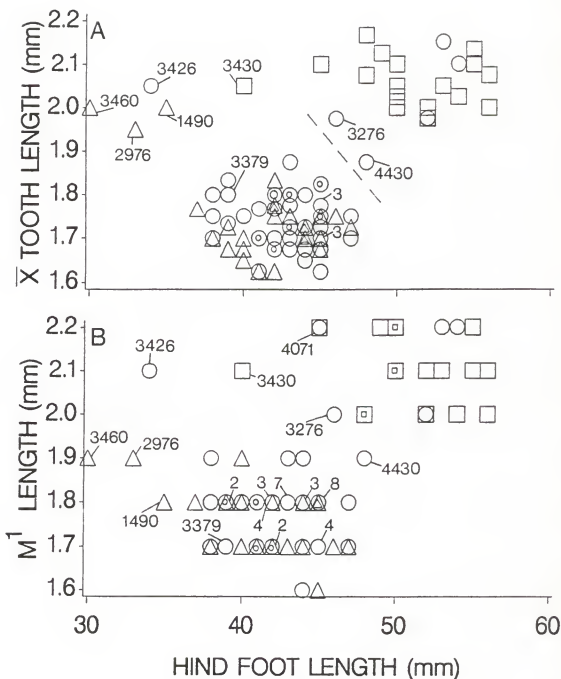


Figure 2-2. Mean anterior-posterior length of teeth in the upper tooth row (Part A) and of the first upper molar (Part B) against hind foot length. Four-digit numbers are field numbers discussed in the text. The dashed line separates *Proechimys cuvieri* (squares) from *P. guyannensis* (triangles). Circles represent impressions taken from live animals (species unknown).

Figure 2-3. Hind foot length (Part A), head plus body length (Part B), and body weight (Part C) against tooth-wear age class. The dashed line separates Proechimys cuvieri from P. guyannensis in age classes 1 - 9. Symbols are as in figure 2-2.

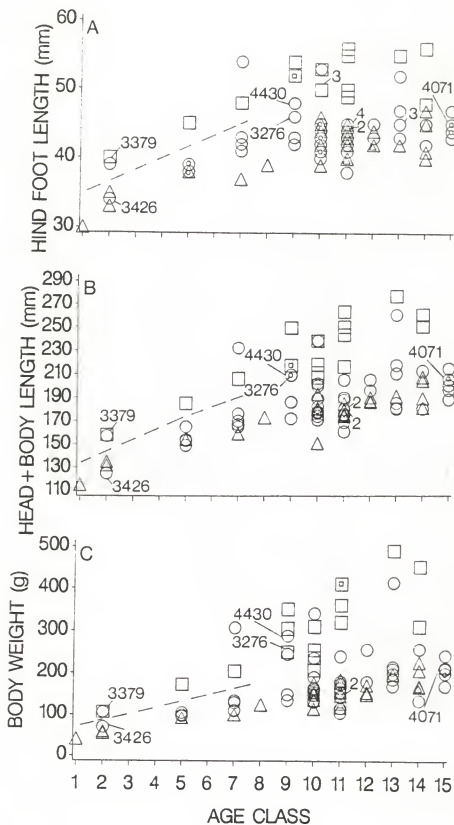


Table 2-2. Wet lens weight, body weight, and reproductive activity of *Proechimys guyannensis* in tooth-wear age classes 1 - 15.

Wear class	Wet lens weight (g) ²		Body weight (g) ¹		Reproductive Activity			
			Male	Female	P/I ³	L/N ⁴	G/N ⁵	S/A ⁶
1				40.0 (1)	0/0	0/0	0/1	0/0
2			69.0 (1)	56.0 ± 2.83 (2)	0/2	0/2	0/2	0/0
5	0.1103	(1)	98.5 ± 9.19 (2)	100.0 ± 4.58 (3)	0/3	0/3	0/0	0/2
7	0.1151	(1)	122.5 ± 16.26 (2)	113.3 ± 15.28 (3)	0/3	0/3	0/2	0/2
8				124.0 (1)	0/1	0/1	0/1	0/0
9				142.0 ± 9.90 (2)	1/1	0/2	0/0	0/0
10	0.1502 ± 0.0217	(5)	165.9 ± 30.84 (8)	184.3 ± 27.30 (6)	3/3	6/6	2/2	2/6
11	0.1584 ± 0.0136	(5)	162.2 ± 48.65 (5)	153.6 ± 25.08 (11)	2/9	0/10	1/5	2/2
12	0.1571 ± 0.0217	(2)		182.6 ± 42.81 (5)	2/2	1/4	0/3	0/0
13	0.1920	(1)	190.0 ± 28.28 (2)	199.5 ± 11.90 (4)	2/2	0/4	2/0	1/1
14	0.2212 ± 0.0198	(4)	230.0 ± 25.24 (3)	160.8 ± 17.19 (4)	2/2	0/4	1/2	0/3
15			185.0 ± 21.21 (2)	216.3 ± 18.04 (4)	4/0	0/2	0/0	1/1

¹ $\bar{X} \pm SD$ (n).

² $\bar{X} \pm SD$ (n).

³ Vagina perforate/imperforate.

⁴ Lactating/non-lactating.

⁵ Gravid/non-gravid.

⁶ Testes scrotal/abdominal.

classes: 10, 11, and 14. ANOVA comparing the three means was significant ($P = 0.015$) and Tukey's Studentized Range Test ($\alpha = 0.05$) indicated significant differences for two of the three of the possible pair-wise comparisons: 10 vs 14 and 11 vs 14.

Reproductive Activity and Pelage Characteristics

Age class 9 was the first with perforate female P. guyannensis, and females were first recorded pregnant, and males scrotal, in age class 10 (table 2-2). After age class 9 or 10, roughly 50% of individuals were perforate, gravid, or scrotal, whereas before age class 8 or 9, none were. A female P. cuvieri was gravid in age class 9, and one scrotal male was recorded in age class 5. Of 22 P. guyannensis with collected skulls and skins, one was in juvenile pelage (age class 2), two were in subadult pelage (age classes 5 and 7), and 19 were in young adult or adult pelage (age classes 8 through 14) (pelage classes sensu Fleming 1971).

Discussion

Given a cheek tooth impression, most live individuals of Proechimys guyannensis and P. cuvieri can be easily distinguished. It appears that the best method for young animals (age classes <7) is to plot hindfoot length or head plus body length vs age class, whereas for older animals, the plot of mean tooth length vs hindfoot length is most useful. The method should be of value in distinguishing sympatric Proechimys spp. whenever they exhibit i) different sized tooth rows, ii) different age-specific body weights, and/or iii) different counterfold patterns. The technique may prove of particular value in distinguishing juveniles,

since color patterns and aristiform characteristics are not available from these animals.

During the course of the research described here, I noticed that P. guyannensis tended to have less hairy tails than P. cuvieri. To test the utility of this character in distinguishing the two species, two biologists ranked 21 skins (13 P. guyannensis and eight P. cuvieri) based solely on tail hairiness. Neither person knew the species of the skins, or even the purpose of the exercise. One person ranked the skins correctly, whereas the other ranked one P. cuvieri incorrectly. Similarly, based on tail hairiness, I correctly determined the identity of seven live individuals (three P. guyannensis and four P. cuvieri). The tooth-impression technique remains of value though, given that it provides a relative age, and that Proechimys spp. frequently lose their tails (for example, some 18% in Fleming's (1970) sample).

In a variety of temperate rodent species, eye lens weight was a better age indicator than other body measurements (references in Malcolm and Brooks 1985). I therefore used eye lens weight as a standard to test whether tooth-wear age class provided a measure of relative age. Gliwicz (1983) also used eye lens weight to age Proechimys; however, no one has tested whether eye lens is a good age indicator for the genus. If eye lens weight does prove to be a reliable measure of age, my results suggest that the tooth wear classes I defined provided a measure of relative age. Data were insufficient to test whether the wear classes were a significant improvement over Patton and Roger's (1983); however, increasing mean eye lens weight after wear class 8 suggested

that this was the case. Certainly, an investigation of variation in age criteria among known-age animals would be of value.

My results are in general accordance with Moojen (1948) in that the molt from juvenile to subadult (adolescent) pelage begins at age class 5. Patton and Rogers (1983) note that the subadult-adult molt is completed by age class 6; however, I captured one age class 7 individual in subadult pelage. These authors suggested that greatest shift in the proportion of mature individuals per age grouping occurs between age classes 7 and 8, in general accordance with my data on reproductive activity. However, there was some evidence that P. brevicauda females on average bred earlier than P. guyannensis; respectively, 57 and 95% of female P. Brevicauda in age classes 7 and 8 were pregnant or parous, whereas none of the P. guyannensis in these age classes had perforate vaginas or were pregnant. Interestingly, males and females in the various tooth-wear age classes had approximately equal body weights (two-way ANOVA [age class by sex] was not significant for sex [$P = 0.11$] nor age class-sex interaction [$P = 0.13$]). Since male Proechimys generally are heavier than females at the same chronological age (Tesh 1970, Gliwicz 1983), wear class thus appears to be weight-specific rather than age-specific.

It is of some interest to ask whether abundance of the two species varied with macrohabitat. Guillotin and Ponge (1984) tentatively suggested that P. guyannensis was more characteristic of open habitats. I trapped in five major habitat types in the BDFFP area: continuous primary forest, the edge of continuous forest, 10-ha primary forest fragments, 1-ha primary forest fragments, and 5-year-old secondary

forest. Respective numbers of individuals of P. guyannensis were 31, 11, 21, three, and five, and respective numbers of P. cuvieri were four, three, one, two, and four. Thus, an increased proportion of P. cuvieri was indicated in edge-dominated or early-successional habitats; P. cuvieri comprised 40% of the captures in 1-ha fragments and secondary forest and only 14% of the captures in continuous forest, its edge, and 10-ha fragments ($P = 0.04$, Chi-square corrected for continuity). Trapping at the Balbina site in riverine forest (<1 km from the Rio Uatumã) yielded only P. cuvieri (da Silva, unpub. data), in marked contrast to trapping in upland continuous forest in the BDFPP area, where only 11% (four of 35) individuals were P. cuvieri. This comparison also suggested that P. cuvieri was relatively more abundant in edge-dominated and early-successional habitats. It will be interesting to see if the proportion of P. cuvieri in the BDFPP area increases as the habitat becomes increasingly fragmented.

CHAPTER 3
SYNCHRONOUS MULTIANNUAL POPULATION FLUCTUATIONS IN AN
AMAZONIAN SMALL MAMMAL COMMUNITY, AND POSSIBLE
DENSITY-DEPENDENT REPRODUCTION

Introduction

Temperate small mammals (especially voles and lemmings) are well known for their dramatic multiannual fluctuations in population density (Krebs and Myers 1974). Several other characteristics seem to vary in concert with density, including body size and shape (Boonstra and Krebs 1979, Mihok and Fuller 1981, Marcström et al. 1990), length and timing of the reproductive season (Krebs and Myers 1974, Wiger 1982), sexual development and growth of young (Krebs and Myers 1974, Myllymaki 1977), and age structure (Zejda 1961, Viro 1974, Wiger 1979, Mallory et al. 1981). Recent observations of synchronous fluctuations among populations of different species of temperate-zone mammals (Marcström et al. 1990) suggest common causation; however, despite considerable research, the reason (or reasons) for the pronounced shifts in population density remain unknown.

Traditionally, rainforests have been thought to be ecosystems of relative climatic stability, both within and between years. As a result of this, and the diverse array of available foodstuffs, vertebrate populations were thought to vary little from season to season and from year to year (eg., Willis 1966). Recent investigations, however, suggest that this view of stability needs to be revised. Many

Neotropical forest ecosystems are markedly seasonal, both with respect to rainfall (Walter 1971) and resource availability (Smythe 1970, Leigh and Smythe 1978, Terborgh 1986). Apparently as a result, reproduction in tropical rodents is usually seasonal (Fleming 1975). In addition, some evidence suggests that variation from year to year in rainfall patterns can lead to variation in resource availability between years, and have dramatic effects on vertebrate populations (Foster 1982). Unfortunately, long-term studies of small mammal populations in tropical forests are rare; only a few investigators have censused populations for more than one year, and apparently only two published studies (Everard and Tikasingh 1973, Emmons 1984) followed a community for three years. Thus, it is unknown if populations of tropical small mammals fluctuate on a multiannual basis, or whether population characteristics, such the intensity and timing of reproduction, vary from year to year.

At a site in the central Amazon, capture rates of four mammalian genera increased dramatically (4- to 25-fold) between a study in 1982 (Emmons 1984) and a study in 1983/84 (Malcolm 1988). Abundances of Oryzomys macconnelli and Proechimys spp. were at their highest at the beginning of the second study, and significantly declined during the following 7 mo (Malcolm 1988). In marked contrast to results from other studies in Neotropical forests, where a peak in reproductive activity is usually reported in the early wet season (Fleming 1973, Guillotin 1982a, Gliwicz 1984, O'Connell 1989), there was little evidence of reproductive activity in the early wet season of 1983, when abundances were at their peak. Instead, reproduction appeared to be starting at the beginning of the following dry season (Malcolm 1988).

Herein, I report on temporal variation in the abundances of small mammals at this Amazonian site during a three-year period (the 7 mo in Malcolm [1988] plus the subsequent 2.5 years). One purpose was to compare patterns of temporal variation within and among taxa. Was the decline in abundance restricted to the first 7 mo, and was it restricted to just a few taxa? A second purpose was to examine rainfall during the period of population increase between Emmons' (1984) study and my own. Foster (1982) noted that years with relatively moist dry seasons had less abundant fruit crops than other years. I reasoned that if the population increase between the two studies was in response to increased fruit availability, then the dry season during the period between the two studies would be an especially dry one. Finally, I wished to determine whether the timing and intensity of reproductive activity varied from year to year, and whether any such variation was correlated with variation in rainfall.

Materials and Methods

Field Methods

Six sites approximately 80 km north of Manaus, Brazil were censused for small mammals between October 1983 and October 1986 (see Malcolm [1988] for results from the first 7 mo of this period). All sites were in undisturbed primary forest; however, two of the sites were close to clearcut. To minimize any edge effect, traplines at these sites were at least 140 m from the clearcut/forest edge and were oriented perpendicular to the edge. Traps at the remaining sites were at least 1 km from clearcut. Five of the sites were on one farm (Fazenda Esteio) and distances between them varied from approximately 800 to 8,500 m.

The remaining site was located on another farm (Fazenda Dimona) and was approximately 27 km from the nearest other site. The 37 mo study was divided into five consecutive 6-7 mo time-periods. All sites were censused during each of the first three time-periods; four were sampled during the fourth time-period; and all six were sampled in the final time-period.

At three of the sites, I centered three parallel traplines within a square 10-ha area, with perpendicular distances of 100 m between adjacent traplines. At the remaining sites, I centered an area measuring 1000 by 860 m within a square 100-ha area. Within each 1000 by 430 m half of the area, I centered four parallel traplines, with perpendicular distances of 200 m between adjacent traplines. Traplines consisted of 15 trap-stations spaced at 20-m intervals and were in the same location from census to census. To lessen biases toward particular size classes of mammals, a trap-station consisted of two different-sized traps: a Tomahawk (14 by 14 by 40 cm) and a Sherman (8 by 8 by 23 cm). The two traps were placed 2 - 4 m apart on the ground. Traps were baited with peanut butter and banana and were set for nine consecutive nights per census. Traps were rebaited daily, and captures were toe-clipped, ear-tagged, measured, and released (Malcolm 1988). Females were classified as lactating and/or gravid or not and, for rodents, vaginal perforation (perforate or imperforate) and testes position (scrotal or abdominal) was noted. Voucher specimens were deposited at the Instituto Nacional de Pesquisa da Amazônia and the United States National Museum of Natural History.

Monthly rainfall for the period January 1981 through October 1988 was available from a site in Manaus' northern outskirts (Fearnside unpubl. data).

Data Analysis

I combined data in each site-by-census combination and, for each taxon, calculated the mean number of individuals per trapline. For each of the two sites not censused during the fourth time period, I combined captures from the third and fifth censuses, and used the average as an estimate of abundance during the missing census. To test for temporal variation in abundance, means from the five time periods were ranked within a site, and a main-effects analysis of variance was performed on the ranks. This test is equivalent to a Friedman's nonparametric block analysis (Luginbuhl and Schlotzhauer 1987). Only taxa represented by at least 25 individuals were tested.

Emmons' (1984) study terminated in July 1982 and mine began in October 1983. Accordingly, I partitioned the rainfall data into seven 12-month periods (September of one year - August of the following), and compared the 1982/83 period with the other six periods. Variation among the seven periods was compared graphically and by use of principal component analysis.

To test for temporal shifts in breeding activity, I defined two seasons a priori: (i) November - April (wet season) and (ii) May - October (dry season). Unfortunately, sample sizes did not permit a finer subdivision. In addition, sample sizes after the dry season of 1985 were insufficient for analysis. Thus, reproductive data were available for two seasons in each of two consecutive year-long periods

(1983/84 and 1984/85). Log-linear analysis (Luginbuhl and Schlotzhauer 1987) was used to test for year and season main effects, and for year-by-season interaction. Patterns of monthly rainfall were compared between the two year-long periods graphically.

Analysis were performed using SAS (Luginbuhl and Schlotzhauer 1987) and statistical tests were judged significant at $P < 0.05$.

Results

Fourteen taxa were captured during the 37 mo study (table 3-1). Of these, eight were represented by at least 25 individuals. The analysis of variance of within-site rankings was significant for three marsupials (Marmosa parvidens, Didelphis marsupialis, and Metachirus nudicaudatus) and two rodent taxa (Oryzomys macconnelli and Proechimys spp.). Duncan's test in all cases indicated higher abundance early in the study than later in the study. Monodelphis breviceadata and Oryzomys capito also declined in abundance through the study, but the ANOVA was not significant. Of the eight taxa, only Marmosa cinerea showed no evidence of a decline in abundance. The total number of individuals per trapline, averaged across the six sites, declined through the study; averages (\pm SD) in the five time periods (in chronological order) were 8.5 (\pm 2.8), 3.2 (\pm 1.3), 3.4 (\pm 1.2), 2.5 (\pm 1.3), and 1.7 (\pm 0.8). ANOVA on within-site rankings of total abundance was highly significant ($P < 0.01$), and according to Duncan's test, the average rank during the first time period was significantly greater than those in other time periods, whereas average ranks did not differ significantly among time periods 2 to 4, and among time periods 2, 4 and 5.

Relative to the other six 12-mo periods, the 12-mo period between Emmons' (1984) visit to the area and my own had unusual rainfall (figure 3-1B). Rainfall was relatively low during the late dry season (September - December), extremely low during what is usually the period of peak rainfall (January and February), and higher than average the following month (March). Principle component analysis confirmed these patterns. Rainfall during the 1987/88 12-mo period was also identified as an "outlier" in the principal component analysis. In contrast to 1982/83, relative to other years rainfall was low in March and extremely high in February and April (hence the large range of values in figure 3-1B for the latter two months).

Significant interaction between yearly and seasonal reproductive activity (as judged by both lactation/pregnancy and vaginal perforation) was found for three taxa: M. cinerea, O. macconnelli, and Proechimys spp. (table 3-2). Very few females showed signs of reproductive activity during the first wet season of the study (when abundances were high), whereas during the following dry season and wet season, most females were reproductively active. In the final dry season, reproductive activity was again at low levels. Thus, the seasonal pattern of reproduction was opposite in the two years. Vaginal perforation showed the same pattern for O. capito, but the test was not quite significant ($P = 0.06$). Some evidence of a "year" main effect was obtained; reproductive activity in the first year of study was lower for O. capito (lactation/pregnancy), O. macconnelli (vaginal perforation and testes position), and Proechimys spp. (testes position) than in the second year. In contrast, more D. marsupialis females were lactating

Table 3-1. Mean number of individuals per trapline (15 trap-stations set for 9 nights) during five time periods, averaged (\pm SD) across six sites in continuous forest. Thirty-three traplines were set during each time period (three or eight per site).

Taxon	Time period										ANOVA ¹
	Oct. - Mar.		Apr. - Oct.		Nov. - Apr.		Aug. - Feb.		Apr. - Oct.		
	83	84	84	84	84	85	85	86	86	86	
<i>Marmosa cinerea</i>	0.250 \pm 0.102		0.181 \pm 0.164		0.146 \pm 0.184		0.236 \pm 0.123		0.396 \pm 0.372		0.98
<i>M. parvidens</i>	0.500 \pm 0.431 ^a		0.174 \pm 0.261 ^b		0.097 \pm 0.153 ^b		0.090 \pm 0.130 ^b		0 ^b		<0.01
<i>M. murina</i>	0.056 \pm 0.136		0.021 \pm 0.051		0.021 \pm 0.051		0.056 \pm 0.101		0		-
<i>Monodelphis brevicadanta</i>	0.285 \pm 0.244		0.306 \pm 0.376		0.236 \pm 0.280		0.076 \pm 0.100		0.083 \pm 0.102		0.27
<i>Bidelphis macrasielis</i>	0.660 \pm 0.490 ^a		0.167 \pm 0.219 ^b		0.306 \pm 0.322 ^{b,c}		0.382 \pm 0.536 ^{b,c}		0.160 \pm 0.212 ^c		<0.01
<i>Metachirus nudicaudatus</i>	0.444 \pm 0.421 ^a		0.319 \pm 0.202 ^a		0.146 \pm 0.255 ^{a,b}		0.104 \pm 0.098 ^{a,b}		0 ^b		0.01
<i>Caluromys philander</i>	0.021 \pm 0.051		0		0.056 \pm 0.136		0		0.056 \pm 0.136		-
<i>Oryzomys capito</i>	1.396 \pm 1.574		0.549 \pm 0.765		0.403 \pm 0.396		0.326 \pm 0.373		0.153 \pm 0.170		0.31
<i>O. macconnelli</i>	1.667 \pm 0.814 ^a		0.333 \pm 0.290 ^b		0.306 \pm 0.359 ^b		0.306 \pm 0.349 ^b		0.111 \pm 0.172 ^b		<0.01
<i>Oecomys paricola</i>	0		0		0.063 \pm 0.068		0		0		-
<i>O. bicolor</i>	0.021 \pm 0.051		0		0.063 \pm 0.105		0.021 \pm 0.051		0		-
<i>Rhipidomys mastacalis</i>	0		0.021 \pm 0.051		0		0.021 \pm 0.051		0		-
<i>Proechimys</i> spp.	3.160 \pm 1.494 ^a		1.083 \pm 0.863 ^b		1.382 \pm 0.518 ^{b,c}		0.910 \pm 0.350 ^{b,c}		0.701 \pm 0.360 ^c		<0.01
<i>Isotrix pagurus</i>	0		0		0.076 \pm 0.135		0		0		-

¹ For each taxon, abundances per trapline per time period were ranked within a site and mean ranks were compared among time periods by use of analysis of variance. Numbers are probability levels from the ANOVA. Small letters in common identify means that did not differ significantly according to Duncan's multiple-range test ($\alpha = 0.05$). Taxa with less than 25 captures (identified by dashes) were not tested.

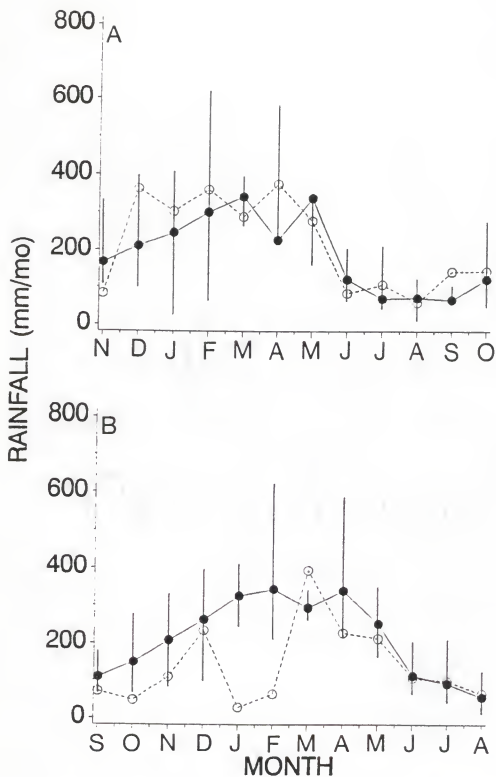


Figure 3-1. Monthly rainfall during 1983/84 (open circles), 1984/85 (closed circles), and five other 12-mo periods after January 1981 (vertical bars = ranges) (Part A), and monthly rainfall during 1982/83 (open circles) contrasted with rainfall during six other 12-mo periods after January 1981 (close circles = means, vertical bars = ranges) (Part B).

Table 3-2. Reproductive characteristics of individuals caught in continuous forest in the wet (November - April) and dry (May - October) seasons of 1983/84 and 1984/85.

Zona	Reproductive status ¹				Vaginal perforation ²				Testes position ³													
	Wet		Dry		Wet		Dry		Wet		Dry		Probability ⁴									
	1983/84	1984/85	1984	1985	Y	S	Y ⁵ S	Y	S	Y ⁵ S	1983/84	1984/85	1984	1985	Y	S	Y ⁵ S					
<u>Marmosa</u>	0:7	5:2	2:1	0:9	0.87	0.81	<0.01	-	-	-	-	-	-	-	-	-	-	-				
<u>ciacra</u>																						
<u>M. parvidens</u>	2:10	1:2	1:4	2:1	0.16	0.44	0.63	-	-	-	-	-	-	-	-	-	-	-				
<u>Bonadelpia</u>	4:2	1:6	0:3	0:1	0.43	0.27	0.16	-	-	-	-	-	-	-	-	-	-	-				
<u>bricoidata</u>																						
<u>Pidelphis</u>	11:1	2:5	1:3	1:5	0.04	0.03	0.12	-	-	-	-	-	-	-	-	-	-	-				
<u>marzagalis</u>																						
<u>Metachirus</u>	0:2	6:3	3:3	3:4	0.57	0.13	0.85	-	-	-	-	-	-	-	-	-	-	-				
<u>andindictus</u>																						
<u>Oryzomys</u>	0:25	4:5	0:3	2:0	<0.01	0.12	0.38	6:19	3:4	3:0	0:1	0.18	0.18	0.06	17:9	6:4	4:11	1:2	0.91	0.07	0.64	
<u>spillo</u>																						
<u>O. macmurtrei</u>	1:20	3:5	3:3	2:6	0.74	0.28	0.07	3:19	8:0	5:1	4:4	0.04	0.45	<0.01	13:8	4:2	1:3	8:1	0.06	0.73	0.10	
<u>Proechimys</u> spp.	2:49	13:25	7:7	2:10	0.95	0.11	<0.01	4:48	19:18	9:5	0:12	0.30	0.65	<0.01	5:36	14:18	7:9	10:4	<0.01	<0.01	0.80	

¹ Lactating and/or gravid : not lactating and/or gravid.

² Vagina perforate : vagina imperforate.

³ Testes scrotal : testes abdominal.

⁴ Probabilities from log-linear tests of year (Y) and season (S) main effects, and year-by-season (Y⁵S) interaction. Prior to the test, 0.5 was added to each cell frequency.

and/or gravid in the first year of study than in the second. Over the two years ("season" main effect), D. marsupialis females were more likely to be lactating and/or gravid in the wet season than in the dry season, and Proechimys spp. males were more likely to be scrotal.

Monthly rainfall varied little between the two year-long periods (figure 3-1A); the maximum difference between monthly rainfall in the two periods was only 150 mm (December). In 10 of the 12 mo, monthly rainfall from the two periods was within the range of values from five other year-long periods.

Discussion

Remarkably, almost all frequently-captured taxa declined in abundance during the 37 mo study, including the smallest (Marmosa parvidens) and largest (Didelphis marsupialis) marsupials in the community, and rodents from two families (Muridae and Echimyidae). Only one species (Marmosa cinerea) showed no evidence of a decline; however, terrestrial traps catch a small proportion of the population of this arboreal species (Malcolm in press), so any conclusions based on terrestrial trapping are suspect. Thus, during the almost 5 years when small mammals were censused in the area, most terrestrial species showed a single, more or less synchronous peak in abundance. The increase in abundance evidently occurred sometime during the 14-mo period between the end of Emmons' (1984) study (July 1982) and the beginning of mine (October 1983), whereas the decline happened over a longer time period (at least 37 mo).

Diets of Amazonian small mammals are to a large extent unknown; however, it appears that all utilize fruit and insects to some degree

(Charles-Dominique et al. 1981, Charles-Dominique 1983). Perhaps the simplest explanation would be to assume that the synchronous population increases were in response to increased fruit availability, possibly in the late wet season/early dry season of 1983. Foster (1982) suggested that plants that flower at the onset of the rainy season require a prolonged drought followed by a sharp, lasting increase in soil moisture, as a stimulus to complete the development of their flowers. Short, moist dry seasons may not allow a sufficient drought period for plants to flower in response to the onset of the rains, and are followed by fruit failures (Foster 1982). In the present study, the dry season of 1982 was pronounced (total rainfall during the period June - August was only 134 mm) and extremely long (except for December, rainfall was low until March 1983). This pronounced dry season immediately followed by heavy rains may have entrained flowering in many canopy tree species, thereby resulting in a bumper fruit crop. Increased plant reproduction could have resulted in an increase in the abundance of insects that feed on plant reproductive parts. Altered rainfall phenology could also have lead to changes in the pattern of leaf flush, thereby influencing populations of foliage-feeding and litter invertebrates.

An alternate explanation is that predation pressure was less during the period of population increase than at other times, as has been argued for vole populations (Angelstam et al. 1984). Predation is likely to be a key source of mortality for many tropical small mammals. However, the predator community in the central Amazon is an especially diverse one, including a host of reptilian, avian, and mammalian predators. It seems unlikely that most predator species were less

abundant or were utilizing different prey during the period of small mammal increase. Similarly, even a key predator could probably not simultaneously influence densities of small mammal species of such diverse sizes, and with such a diverse microhabitat specializations.

This study is the first to report a switch in the seasonal reproductive activity of tropical small mammals from one year to the next. Seasonal reproduction in three, or perhaps four, taxa showed opposite patterns in the first two years of study, and reproductive activity generally was at lower levels during the first year than during the second. Rainfall patterns during the two years were similar, hence the temporal shift in reproduction from one year to the next did not seem to be the result of different resource phenologies in the two years. Rather, it seems more likely that the switch was due to the population peak that occurred just prior to the study. One possibility is that because of peak numbers, resources were at low levels during the wet season of 1983/84, and that as a result, most individuals did not attempt reproduction. A second is that high population density in itself acted as a cue to forego reproduction, perhaps via intraspecific interference. If the adaptive value of this latter response was to avoid reproduction in a period of likely resource scarcity (i.e. high population density usually correlates with resource scarcity), the net effect is the same; individuals were able to respond adaptively to lower resource availability. This in turn suggests that resource scarcity is a relatively frequent occurrence in this community (since selection has occurred), and that competition for resources could be an important process structuring the community (see Hubbell and Foster 1986a).

Similarly, if density in itself acted as a cue to forego reproduction (i.e. decreased reproduction was a density-dependent response), then one could argue that increases in population densities such as those observed here occur relatively frequently. The inter-year switch in seasonal reproductive activity also appears to distinguish these tropical small mammals species from many temperate ones, where reproductive activity is usually restricted to the summer, and to a large extent is controlled by photoperiod (references in Malcolm and Brooks 1985).

In conclusion, yearly variation in tropical animal populations, and the resources upon which they depend, is becoming increasingly apparent. Until long-term studies of populations are conducted, the importance of relatively infrequent events in structuring tropical ecosystems will remain undetermined.

CHAPTER 4
THE SMALL MAMMALS OF TROPICAL FOREST FRAGMENTS I: PATTERN

Introduction

Tropical rainforests, generally recognized as the earth's richest terrestrial ecosystems, are being destroyed at alarming rates. In the late 1970s, approximately 7.6 million hectares, or roughly 1% of the total area, were being lost annually (UNEP 1982). Moreover, in certain regions, the rate of deforestation appeared to be increasing (eg. Fearnside 1982). A direct result of this deforestation has been the extinction of tropical species. Estimates of the number of extinctions expected by the end of the century vary widely, from roughly 15 to 50% of the total number of species present in tropical rainforests (Lugo 1988); however, our ability to derive reasonable estimates is seriously hampered by a lack of information on species richness, a figure that is unknown, even to the nearest order of magnitude (Wilson 1988).

A frequent effect of deforestation is the replacement of large blocks of contiguous forest by networks of forest fragments surrounded by pasture and secondary forests. In order to estimate the rate of loss of tropical species, it will be necessary to examine responses of tropical species and ecosystems to this landscape modification (Lugo 1988). Perhaps more importantly, an understanding of how fragment communities and ecosystems are structured may lead to efficient designs for reserves and reserve clusters, and to methods for the maintenance of

biological diversity and natural ecosystem integrity in human-dominated regions. Studies of fragmentation are thus critically important; they can provide us with empirical information on species loss during fragmentation and with methods to alleviate species loss. Less appreciated, but also important, studies of the less complex ecosystems of fragments and the matrix surrounding them can provide insight into ecosystem function in undisturbed forest (eg. Charles-Dominique 1986).

At a site in the central Amazon, forest fragmentation occurred in the late 1970s and early 1980s after a series of cattle ranches were established 70-90 km north of Manaus, Brazil. Several square reserves of 1-, 10-, and 100-ha were defined prior to deforestation, and were subsequently isolated from continuous forest as a result of conversion of the surrounding forest to pasture via clearcutting (Lovejoy et al. 1984, 1986). The site provided two important controls to aid in identifying the effects of fragmentation: i) a wealth of continuous, undisturbed forest was available for study, allowing for simultaneous monitoring of fragment and continuous forest communities, and ii) in some cases communities in fragments had been monitored prior to isolation. Research on small mammals in the reserves began in February of 1982 (Emmons 1984, Lovejoy et al. 1984) and continued for 5.5 mo. A second study, from which results are presented here, began in October 1983 and ran until March 1989. During the first 7 mo of this second study, I compared terrestrial small mammal communities between 10-ha fragments and continuous forest (Malcolm 1988). One 10-ha fragment (reserve 1202), isolated from continuous forest for approximately 3.5 yr, exhibited a small mammal community very different in composition

from those at six sites in continuous forest, whereas the communities in three other 10-ha fragments and a 100-ha fragment (isolated from continuous forest in all cases for less than a year) were indistinguishable from communities in continuous forest. Thus, any effect of fragmentation in the "oldest" fragment (reserve 1202) stood without replication.

Herein, I report on subsequent censuses of the small mammal communities in these fragments, and in an additional 10-ha fragment, and in four 1-ha fragments. To census the small mammal fauna, I used live-traps, set both on the ground and in the forest canopy (methods of canopy trapping are described in Malcolm in press). This is the first study to intensively census the little-known small mammal fauna of the tropical rainforest canopy.

My questions were three-fold. (i) Did measures of community structure vary with fragment area (given an equal period of isolation from continuous forest), or equivalently, did patterns of community change within fragments vary with fragment area? Area-related variation is predicted both from island biogeography theory (MacArthur and Wilson 1967) and from models of edge effects (Levenson 1981). I compared four measures of community structure among fragments and continuous forest: species abundance patterns, total mammal abundance, species richness, and biomass. (ii) Did the communities of similarly-sized fragments vary as a function of the time that fragments had been isolated from continuous forest? Lovejoy and Orens (1981) suggested that changes in the communities within fragments would be predictable from the length of time a fragment had been isolated. For example, Bierregaard and Lovejoy

(1988) found that capture rates of understory birds were higher in recently-isolated fragments than in continuous forest, and that they subsequently declined to levels below those in continuous forest at 200-400 days post-isolation. (iii) Did fragmentation influence population parameters such as reproductive activity, sex ratio, age structure, and movements? The barrier imposed by the matrix surrounding fragments may lead to altered patterns of population turnover (Bierregaard and Lovejoy 1988), and result in changes in population characteristics. Changes in the habitat/resource base within fragments may also influence individual behavior, and hence population structure.

Materials and Methods

Study Site

The study, part of the Biological Dynamics of Forest Fragments Project (Lovejoy et al. 1984, 1986), took place on three cattle ranches under development in previously uncut forest 80 km north of Manaus, Brazil. Primary forest in the area is upland, or terra firme, on moderately rugged terrain, and is dissected by small creeks that form the headwaters of tributaries of three small rivers: the Cuieiras, the Preto da Eva, and the Urubú. The area is far from large rivers and their associated riverine habitats (várzea and igapó). Most soils are nutrient-poor, yellow, allic latosols of high clay content (Chauvel 1983 cited by Klein 1989). Annual rainfall near Manaus averaged approximately 2200 mm during a 70-year period, with a dry season of <100 mm/mo from July to September (Anon. 1978 cited by Klein 1989).

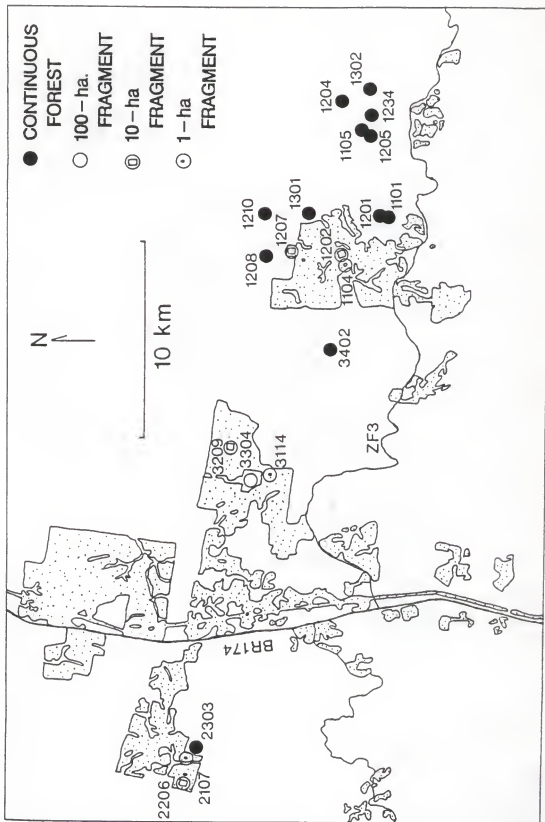
Sampling Schemes

Live traps were used to census small mammal populations in the area during a period of almost six years (October 1983 - March 1989).

Different methods were used in two sampling periods: October 1983 - July 1987 (phase 1) and October 1987 - March 1989 (phase 2). Most effort during phase 1 was devoted to terrestrial trapping, whereas effort was devoted equally to terrestrial and arboreal trapping during phase 2.

Phase 1. Terrestrial traps were used to census 12 continuous forest locations, a 100-ha fragment, four 10-ha fragments, and three 1-ha fragments (figure 4-1). Two of the continuous forest sites (1301 and 2303) were near previously clearcut tracts. To minimize any edge effect, traps at these sites were at least 140 m from the clearcut. Traps at the remaining 10 continuous forest sites were at least 1 km from areas of clearcut. The forest surrounding the fragments was clearcut in the dry season of 1980 (10-ha fragment 1202 and 1-ha fragment 1104), the dry season of 1983 (100-ha fragment 3304, 10-ha fragments 1207 and 3209, and 1-ha fragment 3114), or the dry season of 1984 (10-ha fragment 2206 and 1-ha fragment 2107). The distance from a fragment to the nearest continuous forest ranged from 100 - 1000 m. For one year, the 100-ha fragment (3304) was connected via a 200 m wide corridor to the continuous forest approximately 2 km away. A 300-m wide strip was cut through the corridor in 1984 and isolated the fragment. Fragment 1207 was unique in that three of its four sides were close (approximately 150 m) to continuous forest. A general description of each of the fragments can be found in Lovejoy et al. (1986).

Figure 4-1. Locations approximately 80 km north of Manaus, Brazil censused for small mammals between October 1983 and July 1987 (phase 1). The area of the trail system at a site is identified by the second digit of the four-digit site identification code: 1 = 1 ha, 2 = 10 ha, 3 = 100 ha, 4 = 1000 ha.



Fragments that were isolated in the dry season of 1980 (1202 and 1104) were first sampled at 42 and 60 months post-isolation, respectively; those isolated in the dry season of 1983 (3304, 1207, 3209, and 3114) at 2, 7, 2, and 28 months post-isolation, respectively; and those isolated in the dry season of 1984 (2206 and 2107) at 1 mo prior to and 13 mo post-isolation, respectively.

Each site was delineated by a trail system that encompassed 1, 10, 100, or 1000 ha (figure 4-1). The trap configuration used at a site depended on the area of the trail system. Trap-stations were spaced at 20-m intervals and, except at 1-ha sites, were arranged in lines of 15 trap-stations. At 10-ha sites (i.e. 10-ha fragments and 10-ha trail systems in continuous forest), I centered three parallel traplines within the 10 ha, with a perpendicular distance of 100 m between adjacent traplines. At 100-ha sites, I centered an area measuring 1000 by 860 m within the 100 ha, and within each 1000 by 430 m half of the area centered four parallel traplines, with a perpendicular distance of 200 m between adjacent traplines. I used the same configuration at the 1000-ha site, except that the four traplines were centered in a 1250 by 406 m half of an area measuring 1250 by 812 m, and the perpendicular distance between adjacent traplines was 250 m. The 100-ha fragment and two of the 100-ha continuous forest sites were first sampled with four lines of 30 trap-stations (Malcolm 1988). Thereafter, the sites were sampled in the usual manner, i.e. eight lines of 15 trap-stations per line. At one of the 10-ha sites in continuous forest (1234), I used only two parallel traplines, with 200 meters separating them during one

sample, and 300 meters separating them during the other. At 1-ha sites, I used a six by six grid of trap-stations.

Ten-, 100-, and 1000-ha sites were each sampled on average 4.3 times (range 2 - 6 times), at average intervals of 7.8 mo (range 0.7 - 25.1 mo) (figure 4-2). One-ha sites were sampled twice each, at an average interval of 6.8 mo (range 4.6 - 8.5 mo) (see figure 4-2 for an illustration of the sampling scheme).

Arboreal traps (Malcolm in press) at average heights of approximately 14 m were used to census five of the continuous forest locations, three of the 10-ha fragments (1202, 2206, and 3209), and the three 1-ha fragments (1104, 2107, and 3209) (figure 4-1). The 10-ha fragments were first sampled at 42, 13, and 27 months post-isolation, respectively, and the 1-ha fragments at 60, 13, and 28 mo post-isolation, respectively. At 10-ha sites, trap-stations were again in lines of 15 and were spaced at 20-m intervals. On average, 1.6 parallel traplines were used per site per sample (range 1 - 3), with at least 100 m between adjacent traplines. At 1-ha sites, trap-stations were configured as in phase 2 (see below). Ten-ha continuous forest sites and 10-ha fragments were each sampled on average 3.3 times (range 2 - 6 times), at average intervals of 6.5 mo (range 0.6 - 19.4 mo). One-ha sites were sampled twice each, at an average interval of 6.8 mo (range 4.6 - 8.5 mo) (see figure 4-2 for an illustration of the sampling scheme).

Phase 2. In each of four blocks, five habitats were sampled: (i) continuous forest, (ii) the edge of continuous forest, (iii) 10-ha fragment, (iv) 1-ha fragment, and (v) the matrix surrounding the

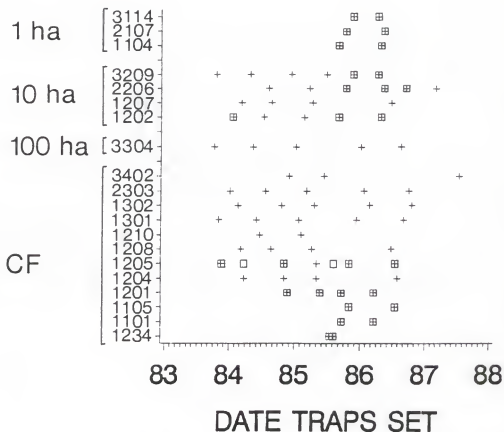


Figure 4-2. Dates at which the sites shown in figure 4-1 were censused (four digit numbers on the ordinate are site identification codes). During a census, traps were usually set for nine consecutive nights. Plus signs represent terrestrial censuses, squares represent arboreal censuses, and squares on top of plus signs represent simultaneous terrestrial and arboreal censuses.

fragments (see figures 6-2 and 6-3). Results from edge and matrix will be presented elsewhere (Chapter 7). In each of the four blocks, I sampled four 1-ha sub-sampling units in continuous forest, four units in the 10-ha fragment, and one unit in the 1-ha fragment. Each block was sampled once during each of three censuses: (i) September 1987 - February 1988, (ii) March 1988 - September 1988, and (iii) October 1988 - March 1989. I divided each 1-ha unit into two 50 by 100 m halves, and established a 100-m long transect in the center of each half. Terrestrial and arboreal trap-stations were placed at 20-m intervals along the transects, to provide 12 terrestrial and 12 arboreal trap-stations per unit. Additional details are provided elsewhere (see Chapter 6).

Trap-stations

To lessen biases toward particular size classes of mammals, a trap-station consisted of two different-sized traps: a Tomahawk (14 by 14 by 40 cm) and a Sherman (8 by 8 by 23 cm). On the ground, the two traps were 2 - 4 m apart, whereas in the trees, the Sherman was placed on top of the Tomahawk. Traps were baited with peanut butter and banana. In addition, arboreal Tomahawks were baited with a cloth sac filled with peanut butter and raisins. Traps were checked each morning and terrestrial traps were rebaited. Arboreal traps were rebaited only when they contained a capture, or were otherwise sprung. During phase 1, traps were usually left open for nine consecutive nights, whereas in phase 2, they were left open for eight consecutive nights. Captured animals were identified, measured, and released (Malcolm 1988). Voucher

specimens were deposited at the Instituto Nacional de Pesquisa da Amazônia and the United States National Museum of Natural History.

In one of the 1-ha fragments sampled in phase 2 (fragment 1112), each station consisted of two steel snap-traps (approximately 9 by 15 cm) instead of two live traps (see Chapter 7). Also, because of extensive damage to the canopy of the fragment during a wind storm in 1987, five of the 12 arboreal stations were at a height of approximately 2 m; the remaining seven were at close to 14 m.

Data Analysis

Analyses were performed using SAS (Luginbuhl and Schlotzhauer, 1987).

Species abundance patterns. Because different methodologies were used in phase 1 and phase 2, and because they covered different time periods, I analyzed the two separately.

For phase 1, I standardized effort by calculating for each census at a site the mean number of individuals captured per trapline. I assumed that the terrestrial grids used at 1-ha sites sampled an area equivalent to 1.2 traplines, and that the arboreal 1-ha grids sampled an area equivalent to 0.8 traplines. These conversion constants are close to those obtained when radii of trapability of 25 - 75 m are assumed (see biomass calculations below). Because arboreal traps during phase 1 were not always set at the same time and place as terrestrial traps, I analyzed the phase 1 terrestrial and arboreal captures separately. If an individual was caught both on the ground and in the trees, it was included in both data sets. I standardized effort in phase 2 by

calculating, for each census within a block-by-habitat combination, the mean number of individuals per 1-ha unit.

To identify and examine major axes of variation in species abundance patterns, I used principal component analysis. Because of the restrictive assumption of multivariate normality, I did not use the analysis to test statistical hypotheses; instead, I used it for its heuristic value. Principal component analysis identified major axes of variation (principal components) in the multidimensional space defined by the original species' abundances (the abundance of each species was represented by one axis in the multidimensional space). In most analyses, the proportion of variance explained by each of the first two components was much greater than that explained by subsequent components; therefore, I examined plots of only the first two principal components. I plotted the position of each site-by-census mean on this plane of maximum variability and the contributions (eigenvectors) of the original species' abundances to the plane. The direction of the eigenvector identified the direction of the species' abundance axis in the plane; census-by-site means that projected highly on the axis defined by the vector had, in general, high abundances of the species. The length of the vector indicated the strength of the correlation between the original species' abundance axis and the axis in the plane. On occasion, I plotted vectors that represented correlations between other site-by-census variables and the principal components. These vectors are interpreted in the same way as species' abundance vectors.

Since total effort varied from site to site in both phase 1 and phase 2 (i.e. number of traplines per site [phase 1] or the number of

1-ha units per site [phase 2]), I used a principal component analyses that was weighted by the number of traplines sampled during the censuses.

To test whether fragmentation affected the abundance of each species, I used standard univariate methods judged significant at $P < 0.05$. For the phase 1 terrestrial data, I excluded censuses prior to May 1985. This omitted censuses early in the study when abundances were high (see Chapter 3) and omitted samples that were obtained shortly after, or shortly before, isolation of 10-ha fragments. In addition, I excluded the 100-ha fragment (because of zero replication in this size class) and the 10-ha fragment 1207 (because of its unique proximity to CP). In the subset, 10-ha fragments (1202, 2206, and 3209) were first sampled at, respectively, 61, 13, and 22 mo post-isolation. I combined all censuses from a site, and calculated the mean number of individuals per trapline. As a non-parametric procedure, I ranked the abundance of each species across the 17 sites, and used ANOVA on the ranks to test for differences among CP (11 sites), 10-ha fragments (3 fragments), and 1-ha fragments (3 fragments). This procedure is equivalent to a Kruskal-Wallis test (Luginbuhl and Schlotzhauer, 1987). Duncan's test with $\alpha = 0.05$ was used as a range test. Only taxa caught at 7 or more sites were tested. For arboreal captures during phase 1, I again ranked abundances of each taxon across all sites, and used ANOVA to compare mean ranks among CP, 10-ha fragments, and 1-ha fragments. Only the four species captured at five or more of the 11 sites were tested.

To test whether fragmentation affected the abundances of taxa captured in phase 2, I combined censuses for each block-by-habitat

combination, ranked mean abundances within a block, and used ANOVA and Duncan's range test to compare mean ranks among CF, 10-ha fragments, and 1-ha fragments. Because data were ranked within a block, the ANOVA was equivalent to a Friedman's test (Luginbuhl and Schlotzhauer, 1987). I analyzed three data sets: arboreal captures, terrestrial captures, and as for the principal component analysis, combined captures. Only taxa captured at five or more of the 12 sites were tested.

Total number of individuals. Terrestrial and arboreal captures were analyzed separately. For phase 1, I excluded fragments 3304 and 1207 and individuals captured prior to May 1985 (see above), and for each site computed the mean number of individuals per trapline. ANOVA and Duncan's test were performed on rank transformed data. For each block-by-treatment combination in phase 2, I computed the mean number of individuals per 1-ha unit, and ranked means within each block. Mean ranks were compared via ANOVA and Duncan's test.

Species richness. To test for differences in species richness among the three treatments, I used only the phase 2 data because effort could be easily standardized. Two measures of richness were calculated: i) the average number of species per census in a 1-ha unit, and ii) the average number of species in a 1-ha unit (censuses combined). As before, data from the 1-ha units in a block-by-habitat combination were averaged (hence the sample size was four per treatment), and ANOVA and Duncan's test were performed on within-block rankings.

Reproductive characteristics, weights, and movements. Population parameters compared among CF, 10-ha fragments, and 1-ha fragments included reproductive activity, sex ratios, and sex-specific body

weights. Captures prior to May 1985 and from fragment 1207 during phase 1 were excluded; otherwise, all data were combined. Females were classified as reproductively active (lactating and/or gravid) or not and, for rodents, vaginas were noted as perforate or imperforate and testes as scrotal or abdominal. Mean body weights, or the shape of the body weight distributions, could differ among habitats. To provide a test that was sensitive to either possibility, for each sex I classified individual body weights into tri-tiles defined from the combined-habitat body weight distribution. Chi-square was used to test for differences among the three treatments. Taxa that, on average, had fewer than five individuals per cell were not tested.

As an additional test, and because of small sample sizes, I combined data from the two fragment types, and compared fragments and CF via Fisher's exact test (sex ratio, reproductive activity, vaginal perforation, testes position) or chi-square (body weight). Fisher's test was performed on taxa with at least 7 observations; body weights were compared for taxa that averaged at least five individuals per cell.

As an approximate measure of the area used by an individual, I used the maximum distance between captures. Because trap configurations differed, I analyzed the phase 1 and 2 data separately. As before, captures prior to May 1985 and phase 1 captures in fragment 1207 were excluded. Because of small sample sizes in 1-ha reserves, phase 1 comparisons were restricted to CF and 10-ha fragments. Because distributions of maximum distances were not normally distributed, and rank-transformations had many ties, differences among treatments were

tested by use of the Median test. The treatments were compared only if they had at least three observations each.

Mammal biomass. In Malcolm (1990), I used distributions of recapture distances to estimate the area that a trapline sampled. The model assumed that during a trapping session an individual used a circular area of radius r such that a trap set within the circle would catch the animal, but a trap set outside it would not. Thus, r was also the radius of the circular area sampled by a trap. The model also assumed that if several traps were placed within the circle, the individual would be caught in at least two of the most distant traps. Given the second assumption, the distribution of maximum distances between recaptures of individuals could be used to calculate r . In Malcolm (1990), I solved for the expected distribution of maximum distances given r and a trapline of t traps, and used least squares to estimate r from observed distributions. I used the same method here for the phase 1 data. The geometry of the trap configuration used in phase 2 was more complex, so I calculated the expected distributions numerically. Again, least squares was used to estimate r from observed distributions. Numerical methods were also used to calculate the area sampled by the 1-ha units used in phase 2.

Distances moved by individuals apparently varied little from treatment to treatment (see Results) so, in order to increase sample sizes, I combined all phase 1 captures after May 1985 (regardless of treatment) and all phase 2 data (regardless of treatment). Values for r used in biomass calculations were means of the phase 1 and 2 estimates, weighted by the respective number of individuals recaptured. Separate

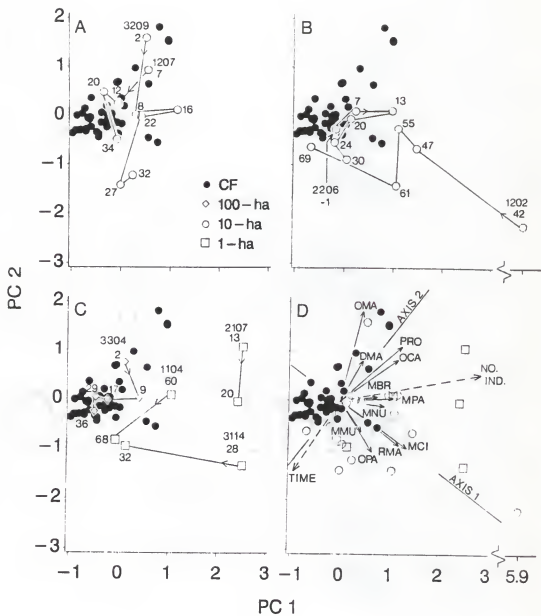
estimates were obtained for terrestrial and arboreal captures. For species that had fewer than four recaptured individuals at one trap height or the other, I used estimates from other species of similar size and arboreality. Estimated \bar{r} values, maximum distances between recaptures, and body weights are shown in Appendix 1. Missing body weights were replaced with the species' mean. As described earlier (see Total Number of Individuals section), only a subset of the phase 1 data was used for biomass comparisons, and data were rank-transformed for analysis. A randomized block design was used to analyze the phase 2 data. Because of large \bar{r} values, and the consequent overlap of trapline and 1-ha sampling areas within a site, biomass of D. marsupialis and P. opossum were not included in the total biomass estimates.

Results

Species Abundance Patterns

Phase 1. Terrestrial trapping yielded 1,434 individuals from 15 taxa (16 species, since the two Proechimys spp. were pooled). Twenty-two individuals could not be identified, either because they escaped, or because of taxonomic problems early in the study (Malcolm 1988), and were excluded. Only taxa with more than 10 captures were included in the principal component analysis: Marmosa cinerea, M. parvidens, M. murina, Monodelphis brevicaudata, Didelphis marsupialis, Metachirus nudicaudatus, Oryzomys capito, O. macconnelli, Oecomys paricola, Rhipidomys mastacalis, and Proechimys spp. The first two principal components, that accounted for 43% of the total variation, were examined (figure 4-3).

Figure 4-3. Principle components one and two from an analysis of individuals captured per terrestrial trapline during phase 1. Censuses in 10-ha fragments 1207 and 3209 (Part A), 10-ha fragments 1202 and 2206 (Part B), 100-ha fragment 3304, and three 1-ha fragments (Part C) are compared with censuses in continuous forest. Lines join censuses from the same fragment; four digit numbers identify the fragment, and one or two digit numbers indicate the number of months post-isolation. In part D, censuses in fragments 1207 and 3304 are excluded, and two major axis of variation discussed in the text (Axis 1 and Axis 2) and eigenvectors of the individual taxa (times three) are shown. Three-letter codes identify taxa (PRO = *Proechimys* spp.; otherwise, the first letter of the genus and the first two letters of the species). Vectors representing correlations (times three) between the total number of individuals caught during a census and the principal component scores, and between chronological time and the principal component scores, are also shown.



Two major axes of variation (identified in figure 4-3D) were apparent. The first separated forest fragment from continuous forest (CF) sites. Variation along this axis among sites was highly correlated with variation in the abundances of: Marmosa cinerea, M. parvidens, M. murina, Monodelphis brevicaudata, Metachirus nudicaudatus, Oecomys paricola, Rhipidomys mastacalis, and to some extent, O. macconnelli (figure 4-3D). All but the last taxon tended to be more abundant in fragments than in CF. The second axis described variation in abundance among both fragment and CF sites of primarily Didelphis marsupialis, Oryzomys capito, O. macconnelli, and Proechimys spp. This second axis was highly correlated with chronological time (figure 4-3D); the seven sessions with highest scores on principal component 2 were all from the first six months of study (except for one session in a 1-ha fragment). This latter axis thus distinguished sessions early in the study when abundances were high from those later in the study when abundances had declined (see Chapter 3). Both axes were correlated with the total number of individuals caught at a site (figure 4-3D).

The small mammal community in the 100-ha fragment (3304) appeared indistinguishable from that in continuous forest, even at three years after isolation (figure 4-3C). Censuses in this fragment early in the study scored highest on the second axis of variation described above, indicating a general decline in small mammal abundances in the fragment over time.

In contrast, by 3 yr post-isolation, three of the four 10-ha fragments showed effects of fragmentation, i.e. communities in general scored highly on axis one described above (figure 4-3A,B). This was

especially true of fragment 1202, which when first sampled at 3.5 yr post-isolation was very different from the sites located in continuous forest, and remained very different thereafter (figure 4-3A). The community in fragment 3209 also was different from that in CF at close to 3 yr post-isolation (32 mo) (figure 4-3B). At 2 or 8 mo post-isolation, communities in this fragment were similar to those in continuous forest. An effect of fragmentation was established at some 27 mo post-isolation, or perhaps slightly earlier. It appeared that by 30 mo post-isolation, fragment 2206 had begun to exhibit a fragmentation effect (figure 4-3B). Earlier samples revealed a community similar to that in CF. Samples from fragment 1207, the fragment close to continuous forest on three sides, remained similar to those in CF even at 34 mo post-isolation (figure 4-3A). Interestingly, as was true of those from the 100-ha fragment and from CF, samples early in the study from 10-ha fragments scored higher on the second axis of variation described above than did later samples.

The small mammal community in 1-ha fragments was in all three cases very different from that in CF, even as early as 13 mo post-isolation (fragment 2107) (figure 4-3C). Again, samples early in the study scored higher on the second axis described above than did late samples. In addition, samples from 1-ha fragments generally had greater numbers of individuals than did samples from 10-ha fragments. Variation among samples from 1-ha fragments was greater than that among samples from 10-ha fragments, which in turn was greater than variation among samples from CF.

Table 4-1. Mean (\pm SD) number of individuals per trapline from terrestrial trapping during May 1985 - July 1987 at 11 sites in continuous forest (CF), three 10-ha forest fragments, and three 1-ha forest fragments, and from arboreal trapping during January 1984 - September 1986 at five sites in continuous forest, three 10-ha fragments, and three 1-ha fragments. One trapline equalled 15 trap-stations (one Sherman and one Tomahawk trap) set for nine nights, except at 1-ha sites (see text for details).

Taxon	Terrestrial traps			Arboreal traps				
	CF ($n = 11$)	10-ha fragment ($n = 3$)	1-ha fragment ($n = 3$)	Probability ¹	CF ($n = 5$)	10-ha fragment ($n = 3$)	1-ha fragment ($n = 3$)	Probability ¹
<i>Harmosa cinctura</i>	0.294 \pm 0.282	0.981 \pm 0.306 ^a	1.111 \pm 0.867 ^a	(0.01)	0.826 \pm 0.967 ^a	4.000 \pm 1.732 ^b	0.625 \pm 0.000 ^a	0.02
<i>H. murina</i>	0.040 \pm 0.113	0.148 \pm 0.032 ^a	0.556 \pm 0.636 ^a	(0.01)	0.036 \pm 0.080	0	0	-
<i>H. parvidens</i>	0.017 \pm 0.040	0.343 \pm 0.205 ^a	0.556 \pm 0.241 ^a	0.02	0	0	0	-
<i>Hemodaphnia brevicornis</i>	0.028 \pm 0.051	0.194 \pm 0.173	0.278 \pm 0.241	0.09	0	0	0	-
<i>Diplophis macropsalis</i>	0.297 \pm 0.395	0.352 \pm 0.140	0.972 \pm 0.867	0.34	0.033 \pm 0.075	0.035 \pm 0.040	0.208 \pm 0.361	-
<i>Phylloclera opacum</i>	0	0.028 \pm 0.046	0	-	0	0	0	-
<i>Metachirius notidensatus</i>	0.163 \pm 0.251 ^a	0.370 \pm 0.175 ^{a,b}	0.972 \pm 0.481 ^b	0.01	0	0	0	-
<i>Calamocera philander</i>	0.030 \pm 0.067	0.028 \pm 0.046	0.139 \pm 0.241	-	2.432 \pm 1.041	0.625 \pm 0.397	0.625 \pm 0.625	0.23
<i>C. lanatus</i>	0	0	0	-	0	0.167 \pm 0.289	0	-
<i>Gezomys capito</i>	0.125 \pm 0.155	0.454 \pm 0.416	3.056 \pm 5.292	0.32	0	0	0	-
<i>G. macconnelli</i>	0.343 \pm 0.398	0.120 \pm 0.125	0	0.11	0	0	0	-
<i>Oecomyia parvicola</i>	0.017 \pm 0.057	0.130 \pm 0.116	0	-	0.071 \pm 0.110	0.035 \pm 0.040	0	-
<i>O. bicolor</i>	0.006 \pm 0.019	0	0.278 \pm 0.241	-	0.510 \pm 1.112	0.069 \pm 0.120	0	-
<i>Hesocorys guianae</i>	0	0.028 \pm 0.048	0	-	0	0	0	-
<i>Rhipidomyia macconnelli</i>	0.006 \pm 0.019 ^a	0.074 \pm 0.128 ^{a,b}	0.278 \pm 0.241 ^b	0.05	0.689 \pm 0.920	1.194 \pm 0.647	1.250 \pm 1.083	0.77
<i>Prochlozeta app.</i>	0.663 \pm 0.383 ^a	0.870 \pm 0.628 ^{a,b}	1.944 \pm 0.867 ^b	0.04	0	0	0	-
<i>Hesocorys hiapidea</i>	0	0	0	-	0.458 \pm 0.538	0.146 \pm 0.171	0	0.26
<i>Loxotritia macconnelli</i>	0	0	0	-	0.161 \pm 0.271	0	0	-

¹ Probability levels from ANOVA on data replaced by ranks. Small letters in common identify mean ranks that were not significantly different according to Duncan's multiple-range test ($\alpha = 0.05$). Bubbles identify taxa that were not tested.

Seven of the 11 tests comparing terrestrial abundances of individual taxa among CF, 10-, and 1-ha fragments were significant (table 4-1). Marmosa cinerea, M. parvidens, and M. murina were significantly more abundant in fragments than in CF, but abundances did not differ significantly between 10- and 1-ha fragments. Metachirus nudicaudatus, R. mastacalis, and Proechimys spp. were significantly more abundant in 1-ha fragments than in CF. Abundances in 10-ha fragments were intermediate, but did not differ significantly from abundances in 1-ha fragments or in CF. O. paricola was significantly more abundant in 10-ha fragments than in 1-ha fragments or CF. Interestingly, nine of the 15 taxa increased in abundance in the sequence: CF, 10-ha fragment, 1-ha fragment, whereas only one (O. macconnelli) decreased (table 4-1). Of the species trapped on the ground, only this latter species was more abundant in CF than in fragments of both sizes. Aside from O. paricola, taxa that could not be ranked in sequence were invariably species that were rarely captured (<11 individuals).

Arboreal trapping during phase 1 yielded 237 individuals of 10 species. Four individuals were not identified and were excluded. Only species with more than 10 captures were included in the principal component analysis: M. cinerea, Caluromys philander, Oecomys bicolor, R. mastacalis, and Mesomys hispidus. Because of small sample sizes, I combined all data for a site, and calculated the mean number of individuals of each species per trapline. Again, the analysis was weighted by the total number of trapline samples at a site. The first two components, which accounted for 76% of the total variation,

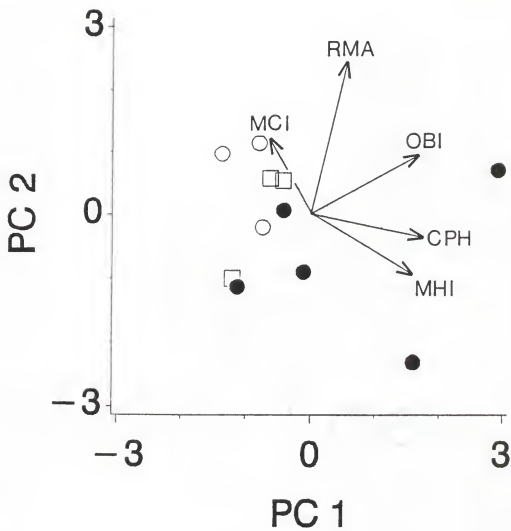


Figure 4-4. As figure 4-3, except that the analysis is based on arboreal traplines, and censuses at a site were combined.

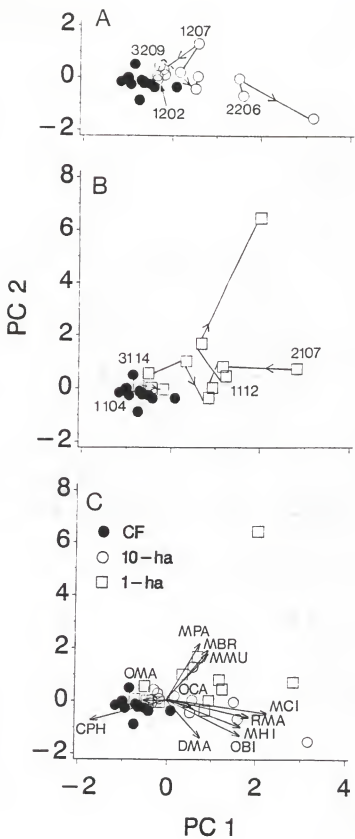
separated fragment from CF sites (figure 4-4). Taxa that loaded highly on this axis were M. cinerea (more abundant in fragments), C. philander, and M. hispidus (less abundant in fragments). Neither principal component separated 10- from 1-ha fragments.

M. cinerea from arboreal trapping was significantly more abundant in 10-ha fragments than in 1-ha fragments or in CF, but abundances in the latter two did not differ significantly. Although not significant, C. philander was more abundant in four of five CF sites than in fragments (table 4-1).

Phase 2. In total, 459 individuals from 18 taxa were caught in the three treatments (CF, 10-ha fragments, and 1-ha fragments). Because terrestrial and arboreal traps were always set at the same place and time, I pooled the two data sets for the principal component analysis. Any individual caught both on the ground and in the trees was represented only once. Only taxa with more than five captures were included in the principal component analysis: Marmosa cinerea, M. parvidens, M. murina, Monodelphis breviceaudata, Didelphis marsupialis, Philander opossum, Caluromys philander, Oryzomys capito, O. macconnelli, Oecomys paricola, O. bicolor, Neacomys guianae, Rhipidomys mastacalis, Proechimys spp., and Mesomys hispidus.

The first two principal components accounted for only 35% of the total variation, but succeeded in distinguishing the three treatment types (figure 4-5). The first axis separated CF from fragment samples. All taxa but C. philander and O. macconnelli loaded positively on this axis, and high loadings were obtained for Marmosa cinerea, Caluromys philander, Oecomys paricola, O. bicolor, Rhipidomys mastacalis, and

Figure 4-5. As figure 4-3, except that individuals (terrestrial and arboreal captures combined) per 1-ha unit between September 1987 and March 1989 (phase 2) are shown. Lines join censuses from the same fragment, except for 10-ha fragment 1202 (censuses not joined). Eigenvectors were multiplied by five.



Mesomys hispidus. The second axis to some extent separated 1- and 10-ha fragments, and was highly correlated with abundances of M. parvidens, M. murina, and M. brevicaudata. In contrast to results from phase 1, communities in all four 10-ha fragments appeared to differ from communities in CF. Fragment 2206 had only just begun to show fragmentation effects in phase 1; however, among the 10-ha fragments sampled in phase 2, it differed most from CF. Fragment 1207, which in phase 1 was indistinguishable from CF, in phase 2 showed effects of fragmentation. Fragment 1202, which in phase 1 was often the fragment least similar to CF, in phase 2 was the fragment most similar to CF. Of the 1-ha fragments, 1104 was most similar to CF in both phase 1 and phase 2. As in phase 1, variability among samples in a treatment was least for CF and greatest for 1-ha fragments.

Tests on the abundances of individual taxa were significant for C. philander and M. hispidus, and nearly significant for D. marsupialis ($P = 0.05$) (table 4-2). Within each block, C. philander was most abundant in CF and least abundant in the 1-ha fragment. M. hispidus was significantly more abundant in 10-ha fragments than in CF or 1-ha fragments and abundances in the latter two treatments did not differ. According to Duncan's test, D. marsupialis was significantly more abundant in 10-h fragments than in 1-ha fragments, and abundance in CF was intermediate. The ANOVA was not significant for M. murina or M. brevicaudata ($P = 0.08$ and 0.09 respectively), but according to Duncan's test, abundances were significantly greater in 1-ha fragments than in CF, and intermediate in 10-ha fragments. As in phase 1, the abundance of many taxa (in this case, seven of 18) increased in the sequence: CF,

Table 4-2. Mean (\pm SD) number of individuals per hectare sub-sampling unit in three habitat types at four sites trapped during October 1987 - March 1989. One unit equalled 12 terrestrial trap-stations and 12 arboreal trap-stations set for eight nights (see text for details).

Taxon	All traps			Prob. ¹
	Continuous forest	10-ha fragment	1-ha fragment	
	(n = 4)	(n = 4)	(n = 4)	
<i>Marmosa cinerea</i>	0.500 \pm 0.180	1.104 \pm 0.878	0.750 \pm 0.167	0.14
<i>M. murina</i>	0.021 \pm 0.042 ^a	0.333 \pm 0.245 ^{a,b}	1.750 \pm 2.872 ^b	0.08
<i>M. parvidens</i>	0	0.125 \pm 0.144	0.083 \pm 0.167	-
<i>Monodelphis brevicaudata</i>	0.104 \pm 0.208 ^a	0.229 \pm 0.080 ^{a,b}	0.833 \pm 0.839 ^b	0.09
<i>Didelphis marsupialis</i>	0.229 \pm 0.356 ^{a,b}	0.208 \pm 0.220 ^a	0 ^b	0.05
<i>Philander opossum</i>	0	0.146 \pm 0.292	0.167 \pm 0.333	-
<i>Metachirus sudicaudatus</i>	0.021 \pm 0.042	0.042 \pm 0.048	0.083 \pm 0.167	-
<i>Caluromys philander</i>	0.958 \pm 0.210 ^a	0.313 \pm 0.185 ^b	0 ^c	<0.01
<i>C. lanatus</i>	0	0.021 \pm 0.042	0.083 \pm 0.167	-
<i>Oryzomys capito</i>	0.146 \pm 0.080	0.083 \pm 0.096	0.417 \pm 0.833	0.52
<i>O. macconnelli</i>	0.104 \pm 0.158	0.021 \pm 0.042	0.083 \pm 0.167	-
<i>Oecomys parvicols</i>	0.042 \pm 0.048	0.250 \pm 0.340	0.583 \pm 0.419	0.33
<i>O. bicolor</i>	0.021 \pm 0.042	0.146 \pm 0.197	0	-
<i>Neacomys guianae</i>	0	0.063 \pm 0.042	0.250 \pm 0.500	-
<i>Rhipidomys mastacalis</i>	0.354 \pm 0.443	1.271 \pm 0.878	1.167 \pm 1.262	0.39
<i>Proechimys</i> spp.	0.313 \pm 0.185	0.479 \pm 0.315	0.333 \pm 0.272	0.39
<i>Neomys hispidus</i>	0.021 \pm 0.042 ^a	0.208 \pm 0.160	0 ^a	<0.01
<i>Isothrix pagurus</i>	0.021 \pm 0.042	0.021 \pm 0.042	0	-

¹ For each taxon, abundances per habitat type (continuous forest, 10-ha fragment, or 1-ha fragment) were ranked within each site and mean ranks were compared among habitat types by use of ANOVA. Numbers are probability levels from the ANOVA. Small letters in common identify mean ranks that were not significantly different according to Duncan's multiple-range test ($\alpha = 0.05$). Dashes identify taxa that were not tested.

Terrestrial traps				Arboreal traps			
Continuous forest	10-ha fragment	1-ha fragment	Prob. ¹	Continuous forest	10-ha fragment	1-ha fragment	Prob. ¹
(n = 4)	(n = 4)	(n = 4)		(n = 4)	(n = 4)	(n = 4)	
0.146 ± 0.080	0.458 ± 0.376	0.417 ± 0.419	0.39	0.500 ± 0.180	0.875 ± 0.738	0.500 ± 0.333	0.75
0.021 ± 0.042 ^a	0.333 ± 0.245 ^{a,b}	0.833 ± 1.106 ^b	0.08	0	0	0.917 ± 1.833	-
0	0.125 ± 0.144	0.083 ± 0.167	-	0	0	0	-
0.104 ± 0.208 ^a	0.229 ± 0.080 ^{a,b}	0.833 ± 0.839 ^b	0.09	0	0	0	-
0.208 ± 0.363 ^{a,b}	0.188 ± 0.185 ^a	0 ^b	0.05	0.042 ± 0.048	0.021 ± 0.042	0	-
0	0.146 ± 0.292	0.167 ± 0.333	-	0	0	0	-
0.021 ± 0.042	0.042 ± 0.048	0.083 ± 0.167	-	0	0	0	-
0	0	0	-	0.958 ± 0.210 ^a	0.313 ± 0.185 ^b	0 ^c	<0.01
0	0	0	-	0	0.021 ± 0.042	0.083 ± 0.167	-
0.146 ± 0.080	0.083 ± 0.096	0.417 ± 0.833	0.52	0	0	0	-
0.104 ± 0.158	0.021 ± 0.042	0.083 ± 0.167	-	0	0	0	-
0.042 ± 0.048	0.083 ± 0.118	0.417 ± 0.319	0.13	0	0.229 ± 0.349	0.167 ± 0.333	-
0	0	0	-	0.021 ± 0.042	0.146 ± 0.197	0	-
0	0.063 ± 0.042	0.250 ± 0.500	-	0	0	0	-
0.063 ± 0.125	0.063 ± 0.080	0.083 ± 0.167	-	0.292 ± 0.323	1.271 ± 0.878	1.083 ± 1.344	0.27
0.313 ± 0.185	0.479 ± 0.315	0.333 ± 0.272	0.39	0	0	0	-
0	0	0	-	0.021 ± 0.042 ^a	0.208 ± 0.160	0 ^a	<0.01
0	0	0	-	0.021 ± 0.042	0.021 ± 0.042	0	-

10-ha fragment, 1-ha fragment (table 4-2). Also as in phase 1, abundances of C. philander and O. macconnelli decreased in the same sequence.

Total Number of Individuals

Averaged across sites, mean abundance per terrestrial trapline (\pm SD) in CF, 10-ha fragments, and 1-ha fragments sampled during phase 1 was, respectively, 1.9 (\pm 0.9), 4.1 (\pm 1.0), and 10.1 (\pm 6.8) individuals. The ANOVA on data replaced by ranks was highly significant ($P < 0.01$). According to Duncan's test on the ranks, abundance per trapline did not differ between 1-ha and 10-ha fragments, but abundance in both sizes of fragments was significantly greater than in CF. Respective means from arboreal trapping were 5.5 (\pm 4.1), 6.3 (\pm 2.0), and 2.7 (\pm 1.3), which according to ANOVA on the rank-transformed data, did not differ significantly ($P = 0.16$). A site in CF (1101) had no arboreal captures; when this site was excluded, the mean for CF became 6.8 (\pm 3.1) and the ANOVA was significant ($P = 0.03$). With this site excluded, Duncan's test indicated significantly fewer arboreal captures in 1-ha fragments than in CF or 10-ha fragments.

Average terrestrial abundance (\pm SD) in the three treatments (CF, 10-ha fragment, 1-ha fragment) in phase 2 was, respectively, 1.2 (\pm 0.6), 2.4 (\pm 1.5), and 4.0 (\pm 2.7) individuals. As in phase 1, ANOVA was highly significant ($P < 0.01$), and according to Duncan's test on the ranks, average abundance per trapline did not differ between 1- and 10-ha fragments, but abundance in both sizes of fragments was significantly greater than in CF. In both phase 1 and 2, means and variances in terrestrial abundance were ranked in the sequence: CF,

10-ha fragment, 1-ha fragment. Average arboreal abundance (\pm SD) in the treatments (CF, 10-ha fragment, 1-ha fragment) was, respectively, 1.9 (\pm 0.4), 3.2 (\pm 2.1), and 2.8 (\pm 1.8), and the ANOVA was not significant ($P = 0.75$). In both phase 1 and 2, arboreal captures outnumbered terrestrial captures in CF and in 10-ha fragments, but the converse was true in 1-ha fragments.

Species Richness

During the nearly six years of trapping, 19 small mammal species were captured (including Proechimys guyannensis and P. cuvieri). Three (P. opossum, C. lanatus, and Neacomys guianae) were never caught in CF, all 19 were caught in 10-ha fragments, and two (Mesomys hispidus and Isothrix pagurus) were never caught in 1-ha fragments (tables 4-1 and 4-2). During an excursion to the area in May of 1990, a specimen of Oecomys regalis (identified by M. Carleton) was captured in a 1-ha fragment, bringing the project total to 20 species, and the 1-ha total to 18. An additional small mammal species (Echimys chrysurus) was observed in the area, but was never trapped. In phase 2, respective mean (\pm SD) number of species per census in CF, 10-ha fragments, and 1-ha fragments were 2.2 (\pm 0.4), 3.4 (\pm 1.4), and 3.5 (\pm 1.7), and respective number of species during the three censuses were 4.2 (\pm 1.0), 6.6 (\pm 1.8), and 6.5 (\pm 3.0). Both ANOVAs were close to significance ($P = 0.08$), and according to Duncan's test, richness in 10-ha fragments was significantly greater than in CF, whereas in 1-ha fragments it did not differ significantly from that in either of the other two treatments. There was little evidence to suggest that the relationship between number of species and number of individuals differed among treatments

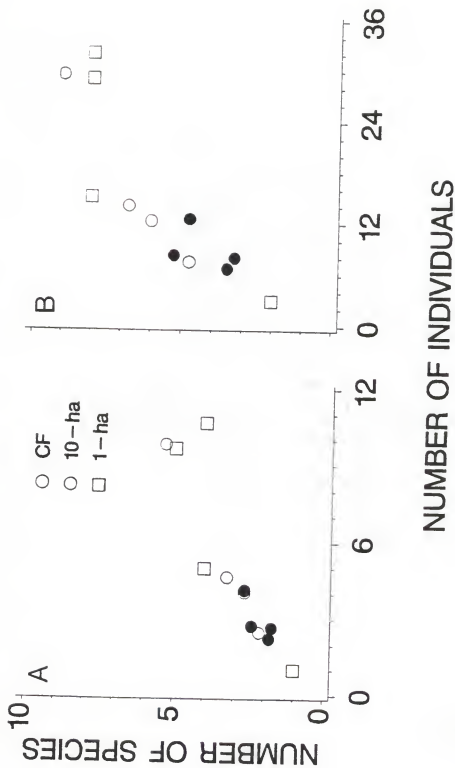


Figure 4-6. Number of species and number of individuals per 1-ha unit in four 1-ha fragments, four 10-ha fragments, and at four sites in continuous forest. In part A, means per census are shown; in Part B, data from the three censuses were combined.

(figure 4-6); analysis of covariance was not significant ($P = 0.68$ in part A, $P = 0.40$ in part B). There was great variability among 1-ha fragments as well as among 10-ha fragments (Figure 4-6). For example, during the three censuses one of the 1-ha fragments yielded two individuals of two species; another yielded 34 individuals of eight species.

Reproductive Characteristics, Weights, and Movements

Only 13% of the 30 tests comparing reproductive activity, sex ratio, and sex-specific body weight distributions among the three treatments, and 2% of the 52 tests comparing the two treatment groupings (CF vs fragments), were significant (table 4-3). Proportionally more female M. murina and O. capito were caught in fragments than in CF and there was also some indication that female M. cinerea and M. brevicaudata were more abundant in fragments (Fisher's test, $P = 0.10$ and 0.06 respectively). Proportionally more female M. cinerea were reproductively active in fragments than in CF, and although not significant, the same was true of M. nudicaudatus and D. marsupialis (Fisher's test, $P = 0.06$). Proportionally more female R. mastacalis had perforate vaginas in fragments than in CF. None of the body weight distributions differed significantly.

Of the 10 taxa recaptured during terrestrial trapping in phase 1, only four had sufficient sample sizes to compare movements in CF and 10-ha fragments (table 4-4). The test was significant for M. cinerea; recaptures of this species on the ground in CF tended to be farther apart than recaptures in 10-ha fragments. Among arboreal captures, there was some evidence that R. mastacalis were recaptured farther apart

Table 4-3. Sex ratio, reproductive characteristics, and body weights of captures during May 1985 - March 1989 in continuous forest (CF) and four 10- and 1-ha fragments. For one of the 10-ha fragments (reserve 1207), only data from phase 2 (October 1987 - March 1989) are included.

Taxon	Sex ratio ¹		Female reproductive status ²		Vaginal perforation ³		Testes position ⁴		Male		Female							
	CF	10-ha	1-ha	CF	10-ha	1-ha	CF	10-ha	1-ha	CF	10-ha	1-ha						
<i>Myrmica cineres</i>	42:31	41:52	9:10	6:24	18:34	6:2*	-	-	-	14/15/16	14/15/12	3/2/4	15/10/6	16/15/19	1/4/4			
<i>M. ruginodens</i>	3:6	6:4	3:3	2:4	2:2	1:2	-	-	-	0/2/1	2/1/2	1/2/0	2/2/2	2/1/1	0/1/2			
<i>M. ruginodens</i>	8:0	15:10	20:36**	0:0	5:3	16:20	-	-	-	4/9/6	5/7/7	4/9/6	0/0/0	3/2/4	12/13/11			
<i>Myrmica brevicornis</i>	2:5	11:5	7:7	2:5	2:3	2:5	-	-	-	1/1/0	4/3/4	1/3/3	1/0/6	2/2/1	3/4/0			
<i>Myrmica ruginodens</i>	18:34	8:10	3:4	15:17	8:2	3:1	-	-	-	5/5/0	3/4/1	1/1/1	12/13/8	2/3/5	1/0/3			
<i>Myrmica ruginodens</i>	0:0	3:5	0:2	0:0	2:3	1:1	-	-	-	0/0/0	1/1/1	0/0/0	0/0/0	2/3/0	0/0/2			
<i>Myrmica ruginodens</i>	5:7	5:8	2:4	1:6	4:4	5:1	-	-	-	2/1/2	1/2/1	0/1/0	4/1/2	2/2/3	0/4/2			
<i>Myrmica ruginodens</i>	39:58	11:9	1:2	19:36	1:8	1:1	-	-	-	13/16/10	2/2/7	1/0/0	18/17/20	4/4/1	0/1/1			
<i>C. lasius</i>	0:0	0:1	0:1	0:0	0:1	0:1	-	-	-	0/0/0	0/0/0	0/0/0	0/0	1/0	0/1			
<i>Myrmica ruginodens</i>	18:6	14:4	10:15*	1:4	0:4	3:12	1:4	3:1	9:4	12:7	11:3	6:5	7/9/3	4/4/6	2/3/4	2/3/1	2/0/2	4/6/5
<i>O. macromellicus</i>	16:7	2:3	0:1	3:14	0:3	1:0	10:7	2:1	1:0	14:3	1:1	0:0	5/6/5	0/1/1	0/0/0	4/6/5	1/2/0	0/0/1
<i>O. macromellicus</i>	3:5	6:9	4:8	1:4	1:8	1:7	2:2	3:5	2:6	3:0	3:3	2:2	2/1/0	1/2/3	1/1/1	2/2/1	2/3/2	2/2/4
<i>O. bicolor</i>	9:10	3:4	0:2	2:7	0:4	0:2	1:8	0:4	1:1	8:2	2:1	0:0	3/3/3	2/0/1	0/0/0	2/4/3	2/0/2	1/7/0
<i>Myrmica ruginodens</i>	0:0	0:4	6:8	0:0	2:1	3:2	0:0	1:3	1:2	0:0	0:0	4:1	0/0/0	0/0/0	2/3/1	0/0/0	1/3/0	2/3/3
<i>Myrmica ruginodens</i>	16:16	34:31	12:10	3:12	6:23	0:10	5:11	4:27	6:4*	13:3	25:10	9:1	4/5/7	10/12/12	6/4/2	4/5/7	13/8/10	2/4/2
<i>Procerosus</i> sp.	44:47	21:27	12:6	9:36	5:10	0:6	11:33	8:19	1:5	24:20	9:7	7:5	14/16/14	6/6/6	5/2/5	17/17/13	7/7/12	2/3/1
<i>Myrmica ruginodens</i>	2:5	5:6	0:0	1:4	2:2	0:0	2:3	2:2	0:0	1:1	0:4	0:0	0/0/2	2/3/0	0/0/0	1/2/2	2/2/2	0/0/0
<i>Myrmica ruginodens</i>	1:1	0:1	0:0	0:1	1:0	0:0	1:0	1:0	0:0	0:1	0:0	0:0	0	0	0	0/1	1/0	0/0

1 Male : Female.

2 Lactating and/or gravid ; not lactating and/or gravid.

3 Vagina perforate ; imperforate.

4 Testes scrotal ; abdominal.

5 For each taxon, individual body weights were classified into 3-tilles defined from the combined sex-specific sample.

* = $P < 0.05$ (Chi-square test [three habitats])

** = $P < 0.01$ (Chi-square test [three habitats]) and Fisher's test (CF vs fragments). Only taxa with an average of five observations per cell were tested.

Table 4-4. Mean (\pm SD (n)) maximum distance between recaptures during two trapping periods: May 1985 - July 1987 (phase 1) and October 1987 - March 1989 (phase 2).

Taxon	Terrestrial				
	Phase 1		Phase 2		
	CP	10-ha	CP	10-ha	1-ha
<u>Marmosa cinerea</u>	51 \pm 29 (12)	18 \pm 20 (12) ¹	10 \pm 14 (2)	25 \pm 9 (12)	-
<u>M. murina</u>	60 (1)	20 \pm 0 (3)	-	36 \pm 26 (5)	35 \pm 21 (2)
<u>M. parvidens</u>	42 \pm 0 (2)	-	-	20 (1)	-
<u>Monodelphis brevicaudata</u>	20 (1)	-	-	40 (1)	10 \pm 14 (2)
<u>Didelphis marsupialis</u>	67 \pm 66 (18)	80 \pm 92 (3)	65 \pm 39 (3)	60 (1)	-
<u>Philander opossum</u>	-	-	-	0 \pm 0 (2)	-
<u>Metachirus nudicaudatus</u>	0 \pm 0 (2)	40 \pm 35 (3)	-	-	54 (1)
<u>Caluromys philander</u>	0 (1)	40 (1)	-	-	-
<u>C. lanatus</u>	-	-	-	-	-
<u>Oryzomys capito</u>	30 \pm 26 (4)	40 \pm 33 (4)	0 (1)	35 \pm 21 (2)	40 \pm 28 (2)
<u>O. macconnelli</u>	47 \pm 45 (4)	30 \pm 14 (2)	40 (1)	-	-
<u>Oecomys paricela</u>	60 (1)	-	40 (1)	54 (1)	20 \pm 28 (2)
<u>Rhipidomys mastacalis</u>	-	-	-	0 (1)	-
<u>Proechimys</u> spp.	29 \pm 29 (11)	43 \pm 62 (7)	-	47 \pm 27 (4)	-
<u>Neotoma hispidus</u>	-	-	-	-	-
<u>Isotrrix parurus</u>	-	-	-	-	-

¹ Means differed significantly (median test, $P < 0.05$).

Arboreal				
Phase 1		Phase 2		
CF	10-ha	CF	10-ha	1-ha
74 ± 68 (16)	43 ± 35 (26)	34 ± 27 (10)	54 ± 30 (20)	37 ± 24 (2)
-	-	-	-	-
-	-	-	-	-
-	-	-	-	-
120 (1)	260 (1)	-	-	-
-	-	-	-	-
-	-	-	-	-
72 ± 49 (29)	40 ± 20 (3)	52 ± 33 (13)	70 ± 17 (8)	-
-	-	-	54 (1)	-
-	-	-	-	-
-	-	-	-	-
20 (1)	80 (1)	-	57 ± 4 (2)	-
50 ± 37 (6)	26 ± 21 (10)	29 ± 23 (7)	43 ± 24 (26)	18 ± 20 (5)
-	-	-	-	-
0 (1)	-	-	60 (1)	-
-	-	-	20 (1)	-

in CF than in fragments ($P = 0.08$). Tests of maximum distances between captures in phase 2 were not significant.

Marmosa cinerea was frequently caught on the ground as well as in the canopy. To test whether fragmentation influenced its vertical use of space, I compared the proportion of individuals caught on the ground vs in the trees among treatments by use of pair-wise Fisher's tests. Only the phase 2 data were used because terrestrial and arboreal effort was matched in both time and space. The tests were not significant; however, the proportion of individuals caught on the ground vs in the trees increased from CF (7 vs 26) to 10-ha fragments (23 vs 46) to 1-ha fragments (5 vs 6).

Mammal Biomass

Comparisons of terrestrial and arboreal biomass among CF, 10-, and 1-ha fragments yielded results qualitatively similar to comparisons of total numbers of individuals among treatments (figure 4-7). ANOVA on the phase 1 terrestrial data replaced by ranks was highly significant ($P < 0.01$), and according to Duncan's test on the ranks, average biomass did not differ between 1- and 10-ha fragments, but abundance in both sizes of fragments was significantly greater than in CF. Mean ranks of the phase 1 arboreal biomass did not differ significantly among treatments ($P = 0.18$), but when the CF site with no arboreal captures was removed, the ANOVA was significant ($P = 0.03$), and Duncan's test indicated significantly fewer arboreal captures in 1-ha fragments than in CF or 10-ha fragments. Although the test of the phase 2 terrestrial biomass was not quite significant ($P = 0.06$), means were in the same sequence as in phase 1. From Duncan's test, biomass in CF and in 1-ha

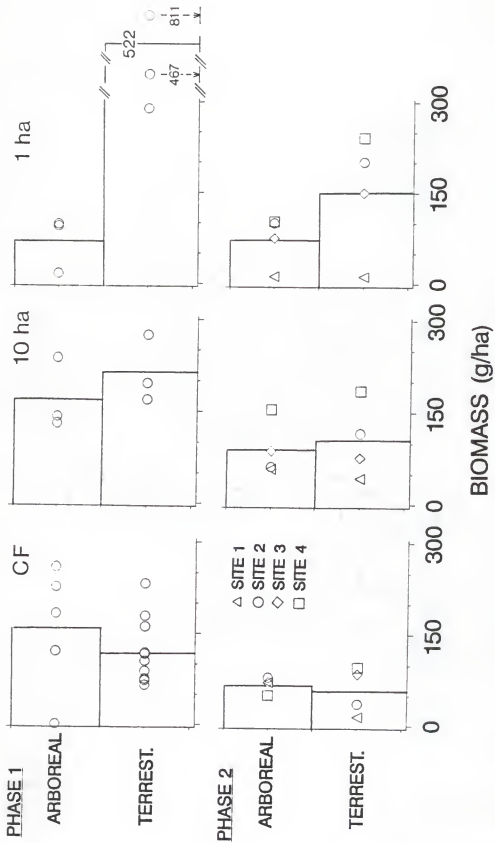


Figure 4-7. Average arboreal and terrestrial biomass in continuous forest (11 sites), four 10-ha fragments, and three 1-ha fragments censused after May 1985 in phase 1, and in each of the three habitats per block censused in phase 2. Histograms are through the overall mean.

fragments differed significantly, but biomass in neither differed significantly from biomass in 10-ha fragments. Phase 2 arboreal biomass did not differ significantly among treatments. In both phase 1 and phase 2, CF arboreal biomass slightly exceeded terrestrial biomass, whereas in 10-ha fragments, the converse was true. In 1-ha fragments, terrestrial biomass greatly exceeded arboreal biomass. Finally, except for arboreal biomass in 1-ha fragments, biomass estimates from phase 1 averaged nearly twice those from phase 2, indicating a continuation of the general decline in abundance observed through phase 1 (Chapter 3).

Discussion

When sampled at <10 mo post-isolation, species abundance patterns in 10-ha fragments were similar to those in continuous forest (CF), but by 20 to 30 mo post-isolation, abundance patterns in two of three fragments no longer fell within the range of variation defined from communities in continuous forest. Instead, communities in these fragments were similar to the community in a 10-ha fragment when it was first sampled at 42 post-isolation. A third fragment sampled soon after isolation exhibited this "effect of fragmentation" at 49 months post-isolation, and perhaps during the previous sample at 34 mo post-isolation. Thus, a replicated "fragmentation effect" appeared to be established in 10-ha fragments by 20 - 49 mo post-isolation. Given this large range of values (20 - 49 mo post-isolation), and the paucity of censuses shortly after isolation in 1-ha fragments, it is difficult to state with assurance whether the timing of community changes in fragments varied with fragment size. However, tabulation of the earliest time post-isolation at which a fragments exhibited unequivocal

effects of fragmentation suggested that small fragments began to differ from CF sooner than large fragments: 13 mo post-isolation for a 1-ha fragment (2107), 27 mo post-isolation for a 10-ha fragment (3209) and >36 mo for a 100-ha fragment (3304).

At >10 mo post-isolation, species abundance patterns in 1- and 10-ha fragments differed from each other. Although few range tests indicated significant differences in abundances between 1- and 10-ha fragments (tables 4-1 and 4-2), in 10 of the 12 range tests that indicated significant differences in abundances among treatments, abundances could be ranked in the sequence: CF, 10-ha fragment, 1-ha fragment. The ranking of treatment means did not follow this sequence for two taxa: arboreal captures during phase 1 of M. cinerea and arboreal captures during phase 2 of M. hispidus. However, only abundances of the first species could be ranked consistently in both trapping periods. Thus, when fragmentation affected the abundance of a species, the effect was more extreme in 1-ha fragments than in 10-ha fragments.

Abundances of most small mammal taxa increased in fragments; 12 of 18 taxa were more abundant on average in fragments than in CF (during both phases 1 and 2), whereas only three (C. philander, Oryzomys macconnelli, and Isothrix pagurus) were generally less abundant in fragments than in CF (during both phases 1 and 2). The comparison was ambiguous for three taxa (D. marsupialis, Oecomys bicolor, and Mesomys hispidus); relative abundance in fragments vs CF switched from phase 1 to phase 2. The greater abundance of most taxa in fragments vs CF resulted in greater total abundance (i.e. the summed abundance of

terrestrial and arboreal individuals), greater total biomass, and greater species richness in fragments vs CF. The relationship between total number of individuals and richness did not appear to vary among habitats, hence increased abundance and biomass in fragments was not the result of the super-abundance of just a few taxa.

Why did fragment communities differ from those of continuous forest? In order to explain the effect in a proximate sense (i.e. in ecological time), one must consider three possible sources of individuals within fragments: i) immigration from populations in continuous forest, ii) immigration from populations in the matrix surrounding fragments, and iii) in situ production. Possibilities i) and iii) are of special importance in island biogeography theory (MacArthur and Wilson 1967). Given constant in situ production (and no immigration from the matrix), increased immigration from CF will decrease the likelihood of population extinction. This is the well-known "distance" effect; populations in habitat "islands" closer to the "mainland" (CF) are less likely to go extinct than populations in islands far from the mainland. Conversely, given a constant rate of immigration from CF, an absolute increase in in situ production (as, for example, from a larger population) will decrease the likelihood of population extinction. This is known as the "area" effect; a larger area, all else being equal, holds a larger population, leading to a decreased likelihood of population extinction.

Sources ii) and iii) above are important in models of edge effects; the altered micro-climate close to the edge will often alter resource/habitat distributions within fragments, and correspondingly, in

situ production. In addition, individuals in the matrix will in some cases wander into fragments. In situ production may also be affected by species interactions, as suggested for example in models of density compensation (MacArthur et al. 1972) and "excess" density compensation (Case 1975, Case et al. 1979). Finally, the nature of emigration from islands may also influence the structure of island communities. Apparently, a barrier to emigration can lead to increased densities on islands ("fence effect" sensu MacArthur 1972). These three simple sources listed above, plus emigration from fragments, give rise to a complex set of possibilities that cannot be untangled without experimental control. However, several of the patterns presented here suggest certain possibilities over others.

The increased average abundances of most taxa with a decrease in fragment area is not as predicted by island biogeography theory. "Excess density compensation" (greater summed species densities on smaller islands) seems unlikely as an explanation. Case et al. (1979) suggest that excess density compensation can occur when overexploitation and/or interference is less on islands than on the mainland. If a mainland guild is overexploiting its resources, then the removal of the more efficient consumers in the guild will lead to higher resource levels, and a greater density of individuals within the guild. Similarly, if guild members are approximately equally efficient, but one or more engage in interspecific and/or intraspecific interference, then a loss of one or more of these dominant competitors will lead to more efficient use of resources by the community, and greater guild density (Case et al. 1979). Both scenarios are more likely when the effect of

insularization decreases species richness within a guild. In the present study, the effect of fragmentation was to increase species richness, hence if the small mammals utilizing a particular forest stratum define a guild in its entirety, the mechanisms become unlikely. Defining a guild is problematic (Adams 1985), for example, insectivorous birds may be utilizing the same resources as many of these largely insectivorous small mammals, and a decrease in their densities could lead to release from overexploitation. However, it seems reasonable to define the terrestrial small mammal species as a guild. All are apparently insectivore/omnivores (Charles-Dominique et al. 1981, Guillotin 1982b, Robinson and Redford 1986), their foraging microhabitats probably differ greatly from other groups of animals, and their nocturnal activity may lead to a predominance of night-active insects in their diet. If they do define a guild in its entirety, decreased abundance of a single terrestrial species (O. macconnelli) can hardly be expected to allow increases in the density of a host of others.

Fonseca (1988) recently suggested that a release from competition explained the lower diversity of small mammals in small fragments (approximately 80 ha) of the Atlantic rainforest. According to his hypothesis, fewer predators in small fragments led to increased densities of D. marsupialis, which through competition for food and nest sites, decreased the species richness of other small mammal species. His hypothesis seems unlikely apply in the present study, because fragmentation did not convincingly influence the density of D. marsupialis; in phase 1, average density was greater in fragments than

in CF, whereas the opposite was true in phase 2. A less abundant or diverse predator community in small fragments may, however, lead to increased densities; a hypothesis that I am unable to evaluate here.

Studies of artificial islands, created by fenced enclosures, have reported higher rodent densities than unenclosed populations, presumably due to reduced dispersal (Krebs et al. 1969, Boonstra and Krebs 1977). Adler et al. (1986) argued that increased isolation of islands could also be expected to lead to decreased dispersal, and in support of the importance of "fence effects", found that island densities of white-footed mice increased with the degree of isolation. MacArthur (1972) argued that, in addition, fence effects should produce a negative correlation between island area and density; hence the greater densities I observed in small vs large fragments could be attributed to fence effects. The study by Adler et al. (1986) included islands of roughly 1 and 10 ha, and isolation distances comparable to mine, but they did not find the expected negative correlation. Note that water must represent a greater barrier to dispersal than the matrix surrounding the fragments that I studied, so fence effects seem even less likely to account for the greater densities in 1-ha fragments. Gottfried (1979) found that densities in woodlot islands surrounded by cornfields decreased with increasing isolation, also suggesting that fence effects were relatively unimportant.

The differential immigration/extinction envisioned in island biogeography theory seems unlikely to account for increased densities on islands, however decreased densities of certain species in the fragments (such as C. philander, and perhaps O. macconnelli and I. pagurus) may

result in part from reduced immigration from CF, and an increased likelihood of population extinction because of small population size. C. philander appears to be a strictly arboreal species (Malcolm in press), hence the lack of a well-developed canopy in the matrix surrounding the fragments may represent a barrier to movements. Results from an excursion to one of the experimental blocks in June of 1989 suggested that events in CF may indeed influence the dynamics of nearby fragment populations of this species. During the course of the visit, I set 12 arboreal trap-stations at one of the continuous forest sites (2-4 stations per 1-ha unit), and captured 12 individuals of Caluromys philander. This capture rate was higher than any obtained previously (the highest capture rate in phase 1 was nine individuals in 15 trap-stations; in phase 2 it was three individuals in 12 trap-stations), and nine of the 12 individuals were young (<125 g). It thus appeared that a particularly successful breeding season had resulted in high population densities in CF. Simultaneous trapping in the 1-ha fragment (reserve 2107) yielded two young individuals. This species was never caught in 1-ha fragments during the 12 censuses of phase 2, hence one possibility is that the individuals in the 1-ha fragment had dispersed from the super-abundant population in CF (some 250 m from the 1-ha fragment). However, arboreality in itself does not necessarily imply a barrier to immigration; R. mastacalis appears to be almost as arboreal as C. philander (Malcolm in press), but it was super-abundant in fragments.

After fragment communities began to differ from those in CF, I obtained little evidence of any sequential changes in the communities of

the fragments correlated with the amount of time that had elapsed since isolation. Remarkably, sequential changes in fragments were instead correlated with chronological time, and mirrored events in CF; in both fragments and continuous forest, overall abundance declined through the study. The general decline in abundance was especially evident when biomass estimates were compared between the two trapping periods; terrestrial and arboreal estimates in phase 1 were almost twice those from phase 2, in fragments and continuous forest alike (the sole exception was arboreal biomass in 1-ha fragments, which was approximately equal in the two periods). In Chapter 3, I argued that high abundances of terrestrial taxa at the beginning of the study resulted from a pulse of resource availability sometime during the previous year, and demonstrated that the population density of most terrestrial taxa declined through the phase 1 trapping. Evidently, the general decline in abundance continued through phase 2, and was not restricted to terrestrial species in continuous forest, but included arboreal populations, and terrestrial and arboreal populations in fragments.

In Malcolm (1988), I argued that the high densities in fragments censused at the beginning of the study were the result of overflow from high densities in CF. When sampled by Emmons in 1982 (Lovejoy et al. 1984), *Proechimys* spp. were absent from the 1980 10-ha isolate (reserve 1202). When trapped in 1984, however, the reserve contained at least 16 individuals (of which the majority were adults). I argued that even if a few individuals were present but not trapped in 1982, it seemed unlikely that the population censused in 1984 arose solely from

reproduction within the reserve. Instead, I reasoned that the population in the reserve must have in part come from the super-abundant populations in the surrounding forest. Similarly, I argued that super-abundant populations early in the study in another 10-ha fragment (1207) resulted in part from invasions from CF. Certainly, if matrix habitat did not represent a barrier to movements (which would seem to be the case, given that high population densities were attained in the 1-ha fragments, an area probably smaller than the home range of many individuals), then high population densities in CF would be expected to overflow into fragments. However, if high densities in fragments early in the study were solely due to immigration from CF, one might expect densities in fragments to increase sometime after those in CF, and decrease earlier; i.e. the range of temporally related variation in abundance would be less in fragments than in CF. In general, the analyses herein provide little evidence of this. Therefore, it seems more reasonable to argue that whatever caused the high densities in fragments (and the subsequent decline) occurred both in CF and in fragments. Certainly, the population increase within CF was not restricted to just a few areas, but was widespread (including sites more than 27 km apart) (Chapter 3). Perhaps the pulse of increased resource availability in forests throughout the region also occurred in fragments.

As discussed above, the habitat surrounding fragments can act both as a barrier to immigration and as a source of immigrants. In the present study, fragments were surrounded by secondary forest, and/or pasture with some arborescent vegetation. Several studies have examined

the terrestrial small mammal communities of Neotropical secondary forests, hence it is possible to examine whether differences in community structure between secondary forest and continuous (primary) forest in these studies in any way resembled differences between fragments and continuous forest in the present study. Two studies used terrestrial trapping to contrast primary forest faunas (similar in species composition to mine) with faunas in secondary forest: Guillotin (1982a) looked at a young (approximately four-year old) secondary forest in French Guyana, and Peterson (in press) examined small mammal succession at a site in Pará during the four months after it was burned. Among species common to my study area, species that they trapped in secondary forest were in all cases ones that I found to be more abundant in fragments than in continuous forest. *Oryzomys macconnelli*, a species that was less abundant in fragments than in continuous forest, did not occur in their secondary forests. Guillotin (1982a) noted that, relative to rodents, marsupials comprised a greater proportion of individuals in secondary forest than in primary forest. Respective percentages in the two forest types were 52% and 16%. Compared with other Neotropical studies, Fonseca (1988) and Stallings (1988) also obtained high capture rates of marsupials relative to rodents (respective percentages of individuals that were marsupials in the two studies were 65 and 83). They attributed this result to the large proportion of their study areas covered in secondary forests. I captured proportionally more marsupials in fragments than in continuous forest: respective percentages of marsupial captures in phase 1 and phase 2 were in 1-ha fragments, 45 and 60%; in 10-ha fragments, 59 and

66%; and in CF, 43 and 43%. Thus, these crude comparisons suggest that differences between secondary forest and CF communities resembled those between fragments and CF, and hence that the matrix may be an important source of immigrants. It is also interesting to note that community structure varied more among fragments of a certain size class than among sites in continuous forest. Variability in community structure in the surrounding matrix, perhaps as a result of variability in vegetation structure, may have contributed to this variability among fragment communities.

The fragmentation effect may also involve resource/habitat changes within the fragments. Certainly, forest structure close to the edge of a fragment differs from that in the interior. Close to the edge, one is faced with a tangle of dense understory, and tree mortality is known to increase close to the edge (Lovejoy et al. 1984). The net effect is presumably a relative increase in foliage biomass and productivity close to the forest floor as one approaches the edge. Perhaps in suite, temperature and humidity vary as a function of distance from the edge (Kapos 1989). This suggests that resources used by small mammals would also vary with distance from the edge. The observation of increased mammalian biomass close to the forest floor relative to biomass in the canopy, and the possible shift in activity of the arboreal *M. cinerea* to close to the ground, could reflect a net downward movement of resources in fragments. The little evidence I obtained of differences in population parameters between fragments and CF suggested that small mammal reproductive activity was greater in fragments than in CF, perhaps reflecting different resource bases in the two habitats.

In conclusion, fragmentation of tropical forests appears to lead to dramatic changes in the small mammal fauna, including a dramatic increase in the abundance of most taxa. Variation in community structure among fragments is partly attributable to fragment size. The simple question, Why this effect of fragmentation?, has a host of potential answers. Results from this study suggest that overflow from the surrounding matrix, coupled with habitat/resource changes within the fragments as a result of edge effects, are important. A decrease in the abundance of some taxa may be explained by island biogeography theory. I turn my attention to these two possibilities in the remainder of the thesis.

CHAPTER 5
EDGE EFFECTS IN CENTRAL AMAZONIAN FOREST FRAGMENTS

Introduction

The creation of abrupt transitions between habitats profoundly affects the environment close to the zone of contact (Ranney et al. 1981, Lovejoy et al. 1986, Harris 1988). Edge effects often give rise to a community characteristic of neither adjacent habitat; some species increase in abundance close to the edge, others decrease (Noss 1983, Yahner 1988). These edge effects have important implications for attempts to preserve ecosystems found on either side of the edge. Small forest fragments may consist of little more than edge-modified habitat (Kapos 1989) and species characteristic of forest "interior" may be lost from the fragments (Levenson 1981). Edge effects may also extend far into either habitat, and in a mosaic of habitat patches and edge, lead to ecosystem modifications on a landscape level (Johnson et al. 1981, Ranney et al. 1981, Janzen 1983, Noss 1983, Alverson et al. 1988, Temple and Cary 1988, Kapos 1989). Edge effects have important theoretical ramifications as well. Attempts to apply island biogeographic theory to habitat islands are inevitably confounded by edge effects; smaller fragments have relatively more perimeter, and hence, on average, present a different environment from larger fragments. The nature of edge effects in habitat fragments of different sizes and shapes may also

influence resource "patchiness" in the fragments, and hence the dynamics of populations (Wiens 1976).

Current descriptive models of edge effects succeed in describing little more than the relationship between perimeter and area. The simplest model is to imagine a strip of edge-modified habitat of width S parallel to the edge (Levenson 1981). A slightly more realistic version is to assume that the magnitude of the edge effect within the strip declines with increasing distance from the edge, perhaps linearly (Laurance 1989) or in a stepwise fashion (Temple and Cary 1988). All of these models consider the effect of only the closest edge. They are incorrect to assume that the magnitude of the edge effect at the center of a circular habitat patch of radius $\frac{1}{2}S$ will be equivalent to the edge effect $\frac{1}{2}S$ units into a forest along a linear edge. The center of the circular patch obviously will be influenced by edge in all directions. Kapos' (1989) results indicated this clearly; the relationship between air temperature or vapor pressure deficit and distance to the nearest edge differed between a 1- and a 100-ha forest fragment.

Thus, edge models to date appear to be overly simplistic. The aims of the present study were to : i) develop a more realistic model of edge effects, and ii) test certain predictions of the model by examining vegetation thickness in Amazonian forest fragments of different sizes.

A Model of Edge Effects

The model supposes that the total edge effect at a point some distance from the edge is the sum of "point" edge effects along the edge. The point edge effect is assumed to be at a maximum (e_0) at the edge and to decline linearly with increasing distance from the edge. At

D_{net} units from the edge and beyond, the point edge effect is zero (figure 5-1A). Thus, the point edge effect (e) as a function of distance from the edge (D) is:

$$(1) e(D) = e_0[1 - (D / D_{\text{net}})] \quad D < D_{\text{net}},$$

$$e(D) = 0 \quad D > D_{\text{net}}.$$

The total edge effect is obtained by integrating (1) over all edge points within a distance of D_{net} units. For example, as a function of the distance (D) to the edge, the total edge effect (E) along a line perpendicular to a linear edge is

$$(2) E(D) = 2 \int_D^{D_{\text{net}}} e_0[1 - (D / D_{\text{net}})] dD$$

$$= e_0 [D_{\text{net}} - 2D + (D^2 / D_{\text{net}})]$$

(figure 5-1B). Notice that equation (2) describes the net edge effect; since the point edge effect is zero at D_{net} and beyond, the total edge effect is also zero past D_{net} . Most measurements (for example temperature or understory thickness) will not be zero past D_{net} , but will assume some constant value >0 . Calling this constant value k , the gross edge effect ($E_1(D)$) along a linear edge is thus:

$$(3) E_1(D) = k + E(D).$$

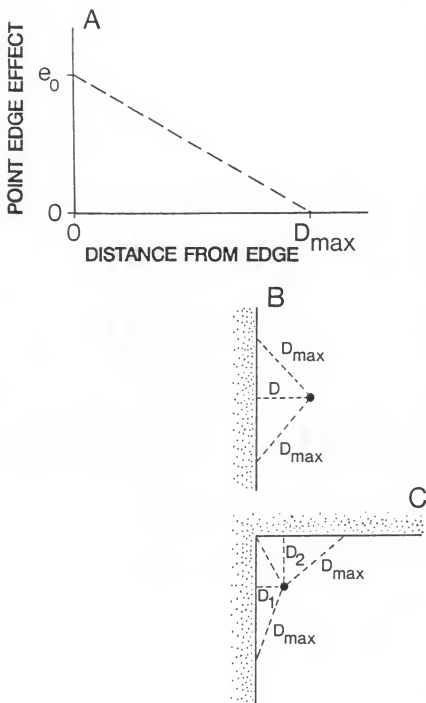


Figure 5-1. The "point" edge effect as a function of distance to the edge (part A). The total edge effect at any point, as for example from a linear edge (B) or from a right-angled edge (C), is obtained by integrating the function over the edge within D_{max} units of the point.

As a further example, consider edge effects in a right-angled edge. The gross edge effect (E_t) at a point D_1 units perpendicular to one edge and D_2 units perpendicular to the other edge is:

$$(4) E_t = k + \int_{D_1}^{D_{max}} e(D)dD + \int_{D_1}^{(D_1^2 + D_2^2)^{\frac{1}{2}}} e(D)dD + \int_{D_2}^{D_{max}} e(D)dD + \int_{D_2}^{(D_1^2 + D_2^2)^{\frac{1}{2}}} e(D)dD$$

(figure 5-1C).

By fitting equation (3) to the relationship between some edge effect and distance from a linear edge, the model can be used to predict edge effects in habitat patches of any size or shape. To test the accuracy of these predictions, I examined understory and overstory foliage thickness in fragmented forest of the Biological Dynamics of Forest Fragments (formerly Minimum Critical Size of Ecosystems) project north of Manaus, Brazil.

Field Methods

At four sites, I measured vegetation structure in three habitats: i) linear edges of continuous, primary forest; ii) 10-ha primary-forest fragments; and iii) 1-ha primary-forest fragments (figure 5-2). A general description of the study site is in Lovejoy et al. (1986). Forest at site 1 was clearcut in July and August 1980 and burned. Thereafter, some areas were maintained as pasture; others were abandoned to secondary forest. Secondary forest was recut in 1987. Forest at sites 2 and 3 was clearcut in August 1983, but never burned or re-cut. Secondary forest was approximately 12 m high at the time of study.

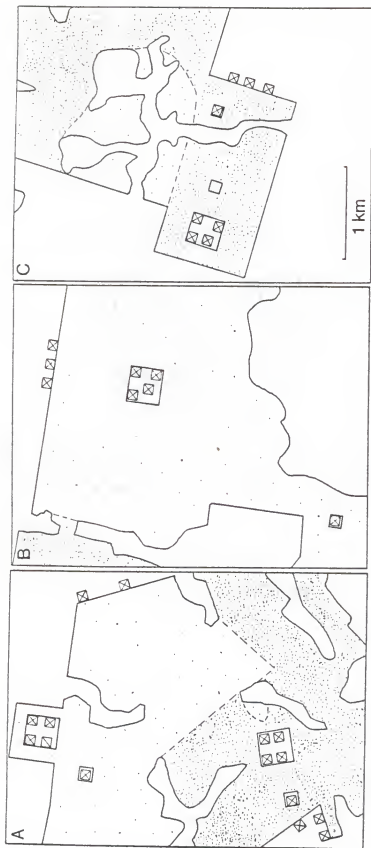


Figure 5-2. Maps of the study sites approximately 80 km north of Manaus (Part A = sites 1 and 2, Part B = site 3, Part C = site 4). At each site, I sampled two or three 1-ha units on the edge of continuous forest, four units in a 10-ha fragment, and one unit in a 1-ha fragment.

Forest at site 4 was clearcut in August and September 1984 and burned. The clearcut area was maintained as pasture thereafter.

Vegetation structure was measured in 1-ha sub-sampling units. At each site, I sampled four units in the 10-ha fragment (16 units in total), two or three units on the edge of continuous forest (11 units in total), and one unit in the 1-ha fragment (four units in total). Units on the edge of continuous forest abutted clearcut along one side and those in 10-ha fragments included fragment corners and linear edge or interior (figure 5-2). A 5-m wide strip completely devoid of vegetation abutted fragment edges, whereas vegetation in the clearcut extended right up to continuous-forest edges. Fragments at site 2 were sampled in October 1987 (three units in the 10-ha fragment) or March 1988 (the 1-ha fragment and one unit in the 10-ha fragment) and continuous-forest edge at site 2 was sampled in October 1988. The remaining units were sampled in March - May 1989.

I modified Hubbell and Foster's (1986b) method to measure vegetation structure. At each point on a 10 m by 10 m grid extending 10 m outside the hectare unit (169 points), a 2.5 m pole was used to make a vertical sighting, and, along the sighting, foliage thickness was scored in six height intervals: 0 - 2, 2 - 5, 5 - 10, 10 - 20, 20 - 30, and 30 - 40 m. Height estimates were periodically checked with a range finder. The first three intervals were scored as 0 (<25% coverage), 1 (25 - <50% coverage), 2 (50 - <75% coverage), or 3 (75% coverage or more). The last three were scored as 0 (<10% coverage), 1 (10 - <50% coverage), 2 (50 - <75% coverage), or 3 (75% coverage or more). Measurements were made by myself or an assistant. To minimize inter-observer bias, we

both measured 299 points, and after each point, discussed any differences in scores. In total, I measured 15 units, he measured 5 units, and we jointly measured 11 units (by alternating pairs of grid rows). The distance to forest edge (defined by uncut, primary-forest trunks) was measured at selected points in each unit, hence the distance to the edge at any point in the unit could be calculated. For some units, a grid row and/or column was on the clearcut side of the edge; these data were excluded from calculations. The following analyses were performed.

Relationship between vegetation thickness and distance. To identify which strata (height intervals) were affected by the edge, for each site on the edge of continuous forest, I calculated the mean score per grid row parallel to the edge, and regressed the means against distance from the edge. Since distances from rows to the edge varied little among units at a site (maximum differences at the four sites respectively were 2, 4, 1, and 2 m), I combined data for the two or three units at a site to provide one mean score and one mean distance per row per site. Regression coefficients (times 10^3) averaged across the four sites (\pm standard error of the mean times 10^3) for the six strata were, respectively, -2.8 (\pm 1.0), -4.3 (\pm 1.0), -1.4 (\pm 1.7), 3.8 (\pm 1.4), 3.8 (\pm 1.4), and 0.9 (\pm 0.7). Therefore, I fitted equation (3) to two data sets: i) the decrease in understory (sum of scores from 0 - 5 m) and ii) the increase in overstory (sum of scores from 10 - 30 m) with increasing distance from the edge. Vegetation thickness in intervals 5 - 10 and 30 - 40 m was variable and showed little relationship with distance from the edge. Data were insufficient to test whether edge effects varied

with time, or with the nature of the habitat abutting the forest. Hence, I combined data from the four sites to fit equation (3).

Since equation (3) described a decreasing edge effect with increasing distance from the edge, I fitted the equation to the overstory data by rotating the data 180° around the line overstory score=7 (i.e., a line parallel to the distance axis). A further 180° rotation returned the data and the fitted curve to the original space.

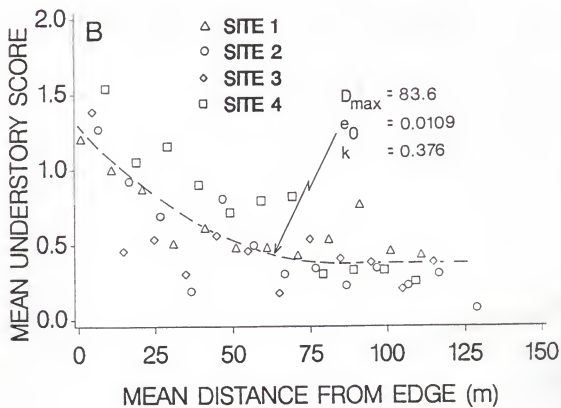
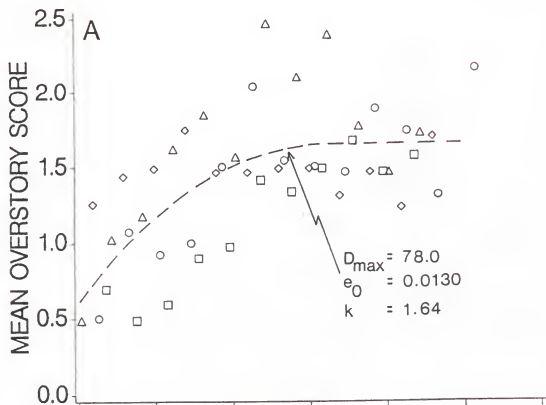
I used the NLIN procedure of SAS (SAS Institute Inc. 1985) to fit equation (3) via the Gauss-Newton method. Note that equation (3) describes a "segmented model" (SAS Institute Inc. 1985); for values of D less than D_{nl} , the equation is nonlinear, and for values of D greater than D_{nl} , the equation is constant.

Edge effects in forest fragments. Observed understory and overstory scores at grid points were compared with scores predicted from the model. Since the fragments were square, integration similar to that in equation (4) was used to calculate predicted scores. To present results graphically, I combined points from a fragment within intervals of predicted scores, and calculated mean observed and predicted scores for points within the interval. Intervals were n -tiles, hence sample size was controlled.

Test Results

Understory and overstory foliage thickness as a function of distance from the edge of continuous forest are shown in figure 5-3. The thickness of understory and overstory foliage varied greatly among the four sites; however, the average thickness was well described by equation (3). The distance at which net edge effects reached zero

Figure 5-3. Mean overstory (10 - 30 m; Part A) and understory (0 - 5 m; Part B) scores in continuous forest against mean distance to the edge. Each symbol represents the mean of 39 (sites 1, 3, and 4) or 26 measurements (site 2; the mean furthest from the edge at site 2 is based on measurements at only 13 points). Fitted curves followed equation (3) (see text).



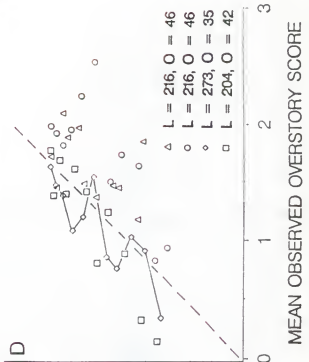
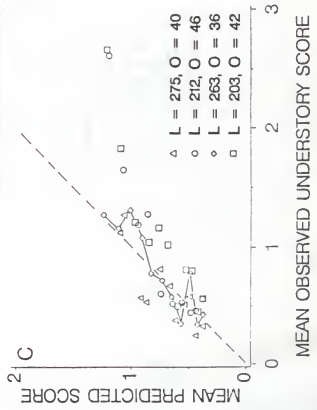
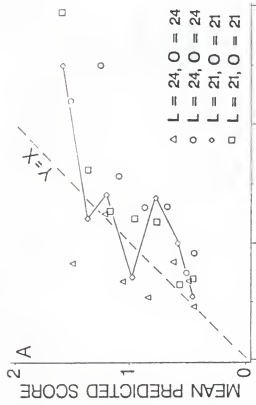
(D_{adj}) was approximately 80 m for both understory and overstory thickness.

Mean predicted and observed understory and overstory scores for 10-ha and 1-ha forest fragments are shown in figure 5-4. Again, observed scores varied widely among the fragments. To examine the success of the model in predicting the average relationship between observed and expected values, for each fragment I regressed mean observed score on mean predicted score, and calculated the mean regression coefficient and mean intercept across fragments. Coefficients should average unity, and intercepts average zero. Mean coefficients (\pm standard error of the mean) for 10-ha and 1-ha understory were, respectively, 1.89 (\pm 0.51) and 1.18 (\pm 0.29) and for overstory were 1.04 (\pm 0.24) and 1.05 (\pm 0.33). Corresponding mean intercepts (\pm standard error of the mean) were -0.47 (\pm 0.28), 0.10 (\pm 0.14), 0.12 (\pm 0.41), and 0.00 (\pm 0.37). Thus, the model predicted average understory and overstory foliage thickness well, except that understory thickness was underestimated close to the edge. Predicted understory thickness at the edge was less than the observed thickness in 7 of the 8 fragments. In both 1-ha and 10-ha fragments, mean overstory thickness was more variable than mean understory thickness.

Discussion

Overstory thickness was predicted reasonably well both near to and far from the edge, but understory thickness close to the edge of fragments appeared to be underestimated. In part, this may reflect differences in types of edges among sites. Secondary vegetation in the clearcut extended right to the continuous forest edge, whereas in

Figure 5-4. Mean predicted understory and overstory scores against observed scores for 1-ha fragments (parts A and B) and 10-ha fragments (parts C and D). Symbols are as in figure 5-3. Lines join means from site 3. Expected scores were calculated using the point edge model shown in figure 5-1 (see text for details). For each site, two sample sizes are given: i) the sample size for the lowest mean predicted score ("L") and ii) the sample size for the other ("O") mean scores.



fragments, a 5-m wide strip devoid of vegetation abutted the edge. Because understory growth on the clear-cut side of the edge will partly shade understory on the forest side, one might expect continuous forest edges to have relatively less understory development close to the edge, as observed.

Because of small sample sizes, I ignored several variables that probably influence the extent of edge effects (and hence the parameters of equation [4]), such as the aspect, soil type, the age of the edge, initial species composition, topography, reach, and the nature of the vegetation on the clearcut side of the edge. Given that edges were formed only 4.3 to 8.8 years before the study, and hence that edge effects had probably not yet reached an equilibrium, one might expect the oldest fragments to have the most damaged overstory and the most developed understory. Interestingly, this was not true among the 8 fragments examined. In general, the oldest fragments (site 1) had the least developed understory and the most developed overstory. One-ha fragments at sites 3 and 4 were severely damaged by windstorms in 1986 and 1987 respectively, whereas the oldest 1-ha fragment remained markedly intact. Evidently, wind damage is highly stochastic. This variability in overstory damage may eventually be accompanied by variability in understory development, since increased understory thickness is probably largely due to increased light levels and decreased root competition from overstory trees.

The effect of the edge on the variables examined in the present study - understory and overstory foliage thickness - is probably determined in large part by physical changes in the edge environment;

increased light penetration and increased exposure to wind respectively. It seems likely that edge effects determined by biological interactions will not be as easily modelled. For example, according to island biogeographic theory (MacArthur and Wilson 1967), isolation of fragments, independent of habitat changes, will lead to changes in communities as a function of fragment size and isolation from other fragments. If these changes due to isolation of fragments in turn influence the nature of edge effects, the model I present would not successfully predict edge effects.

Edge effects will also be influenced by the extent of the habitats that abut at an edge. For example, edge effects along roads or right-of-ways are probably influenced by the width of the deforested strip. The model can easily be modified to account for such influences, by describing a point "gap" effect instead of a point edge effect. For example, the net edge effect in the forest adjacent to a right-of-way strip can be modelled as the sum of the edge effects of each point in the strip. Assume that the point gap effect (e_g) is linear, decreasing, and intersects the distance axis at a . According to a point gap model, the net edge effect (E) D units into the forest perpendicular to a strip of width W is:

$$(5) E(D) = \int_0^W \int_0^{(a^2 - x^2)^{1/2}} e_g(x + D) dy dx$$

This formulation may be useful in modelling edge effects in fragments as a function of the size of clearings that isolate them (Kapos 1989), and

edge effects in and around tree-fall gaps of various sizes (Fletcher et al. 1985, Popma et al. 1988, Barton et al. 1989).

CHAPTER 6
INSECT BIOMASS IN AMAZONIAN FOREST FRAGMENTS

Introduction

Insects are an important food source for many tropical vertebrates. In Malaysian and Australian rain forests, for example, Harrison (1962) estimated that more than 50% of bird and bat species, and 32 - 37% of non-volant mammalian species, were insectivorous, and that an additional 38-39% of non-volant mammal species depended on insects at least in part ("mixed" feeders). Similarly, in the Neotropical faunal region, insectivory is the most common trophic role among birds (Lein 1972) and bats (Wilson 1973), and 29% of non-volant forest mammal species have diets comprised mostly of invertebrates (Robinson and Redford 1986). Given the prominence of insectivory in tropical ecosystems, temporal and spatial variability of insect populations can be expected to have important consequences for ecosystem function.

Increasingly, large blocks of tropical forest are being replaced by fragments in a matrix of pasture and secondary vegetation. Within the fragments, proximity to deforested areas leads to pervasive environmental changes, including changes in air temperature and humidity (Lovejoy et al. 1986, Kapos 1989) and vegetation structure (Chapter 5). The effect on insect communities of tropical forest fragmentation, and concomitant changes in the environment of the fragments, has gone largely unexamined. A few studies in the Neotropics have found greater

insect biomass pasture and secondary forest than in the understory of primary forest (Janzen 1973, Winnett-Murray 1986, Adis 1988) and fragmentation has been shown to profoundly influence butterfly (Lovejoy et al. 1986) and coprophagous beetle communities (Klein 1989).

Certainly, any understanding of vertebrate responses to fragmentation will require detailed information about the resources upon which they depend. This is especially true of attempts to apply island biogeography theory (MacArthur and Wilson 1967) to the study of habitat islands. The importance of differential immigration and extinction in structuring island communities can be evaluated only if habitat and resource differences among islands are known (Simberloff and Abele 1982).

In this study, my purposes were two-fold. First, I wished to determine whether insect biomass differed among five major habitat types in the central Amazon: continuous forest, the edge of continuous forest, 10-ha fragments, 1-ha fragments, and the matrix of second growth and pasture surrounding fragments. Secondly, I tested whether insularization in itself appeared to influence insect biomass in primary forest. I reasoned that the two simplest "null" hypotheses (i.e. hypotheses that accounted for differences in insect biomass among primary forest habitats irrespective of insularization per se) were (i) insect biomass varied solely as a function of proximity to matrix habitat and (ii) insect biomass variation among primary forest habitats was solely due to variation in vegetation structure.

Materials and Methods

Study Area

The study, part of the Biological Dynamics of Forest Fragments Project (Lovejoy et al. 1984, 1986), took place on three cattle ranches under development in previously uncut forest 80 km north of Manaus, Brazil. Primary forest in the area is upland, or terra firme, on moderately rugged terrain, and is dissected by small creeks that form the headwaters of tributaries of three small rivers: the Cuieiras, the Preto da Eva, and the Urubú. The area is far from large rivers and their associated riverine habitats. Most soils are nutrient-poor, yellow, allic latosols of high clay content (Chauvel 1983 cited by Klein 1989). Annual rainfall near Manaus averaged approximately 2200 mm during a 70-year period, with a dry season of <100 mm/mo from July to September (Anon. 1978 cited by Klein 1989). Rainfall measured at four locations on the ranches averaged 3070 mm during 1988, and during the study period (September 1987 - March 1989), averaged <100 mm during October - December 1987 and July 1988 (figure 6-1).

At each of four sites (=blocks), I sampled insects in five major habitat types: (i) continuous forest (=CF), (ii) the edge of continuous forest (=CF edge), (iii) 10-ha forest fragment, (iv) 1-ha forest fragment, and (v) the matrix of pasture and second growth surrounding the forest fragments (figures 6-2 and 6-3). Lovejoy et al. (1986) provided general descriptions of the forest fragments (see reserves 1104, 1202, 1112, 1207, 3114, 3209, 2107, 2206). Matrix habitat at two of the sites (1 and 4) was pasture. Forest surrounding the fragments at site 1 was clearcut in the dry season of 1980, burned, and thereafter

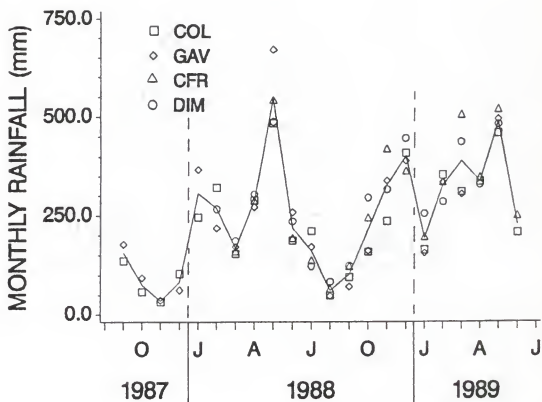
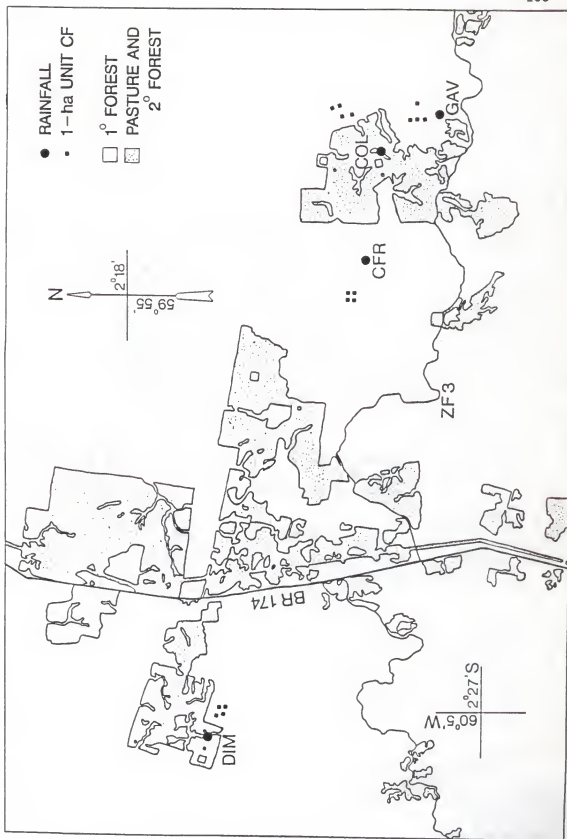


Figure 6-1. Monthly rainfall at four localities approximately 80 km north of Manaus, Brazil. The solid line joins the means. Locations of gauges are shown in figure 6-2.

Figure 6-2. A map of the study area approximately 80 km north of Manaus, Brazil based on an August 1988 Landsat image. One-ha sub-sampling units at four sites in continuous forest (CF) and locations of rainfall gauges are shown. Locations of 1-ha units in other habitats are shown in figure 6-3.



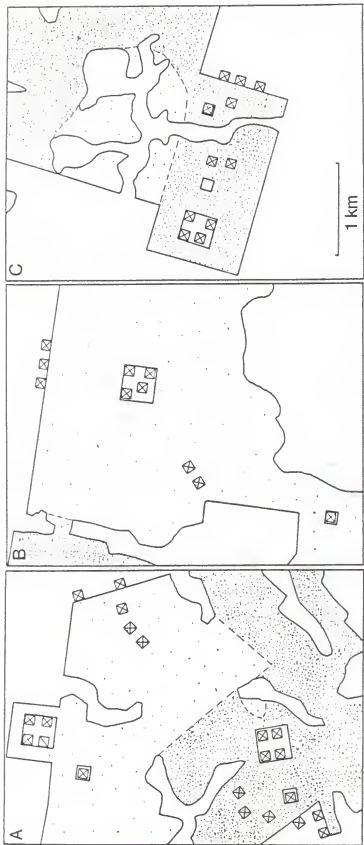


Figure 6-3. Maps of the study sites approximately 80 km north of Manaus, Brazil (Part A = sites 1 and 2, Part B = site 3, Part C = site 4). At each site, I sampled two or three units on the edge of continuous forest, four units in a 10-ha fragment, one unit in a 1-ha fragment, and two or three units in the matrix surrounding fragments. The four units sampled in continuous forest at each site are shown in figure 6-2.

some clearcut areas were maintained as pasture; others were abandoned to secondary forest. Most of the secondary forest close to the fragments was cut and burned in the dry season of 1987, just prior to the study. Forest at site 4 was clearcut and burned in the dry season of 1984 and thereafter clearcut areas were maintained as pasture via periodic removal of secondary vegetation. Secondary vegetation had been most recently cut and burned in the dry season of 1987. Matrix habitat at the other two sites (2 and 3) was secondary forest. The primary forest at these sites was clearcut in the dry season of 1983, but the sites were never burned or recut and the secondary forest was approximately 12 m high at the time of study.

At each of the four sites, I established four 1-ha (100 by 100 m) sub-sampling units in CF (16 units in total), two or three units in CF edge (11 units in total), four units in the 10-ha fragment (16 units in total), one unit in the 1-ha fragment (four units in total), and two or three units in the matrix (11 units in total) (figures 6-2 and 6-3). Units in CF were at least 400 m from the nearest edge, those in CF edge abutted edge along one side, those in matrix were at least 150 m from CF, and those in 10-ha fragments included fragment corners, edge, and in a few cases, fragment interior. The distance from the fragments to the nearest continuous forest ranged from 100 - 800 m.

Each site was sampled for insects once during each of three censuses: (i) September 1987 - February 1988, (ii) March 1988 - September 1988, and (iii) October 1988 - March 1989. Thus, fragments at site 1 had been isolated for seven years prior to first sampling, four years at sites 2 and 3, and three years at site 4. The different

habitats at a site were sampled simultaneously and/or sequentially during each census, so that all habitats were sampled within, on average, a 6-week period (range 3 - 9 weeks). Exceptions were the first census of site 1 (15 weeks), the first census of site 4 (17 weeks), and the second census of site 3 (15 weeks).

Sampling Techniques

In an attempt to provide a comprehensive sample of the insect fauna, I used two trap methods (tangle-traps and pitfall traps) at two heights (understory and overstory).

Tangle-traps. I divided each 1-ha unit into two 50 by 100 m halves, and in the center of each half established a 100-m long transect. Transects were marked at 20-m intervals to provide six points per transect. Transects in units on the edge of continuous forest and on the edge of 10-ha fragments were perpendicular to the edge. I set tangle-traps at three randomly selected points per transect during census 1, and at three of the remaining six points in the unit during census 2. Traps were not set during census 3. Except in matrix habitat, each point had two traps: one at approximately 14-m height (=overstory), suspended 20 cm below a small mammal trap (see Malcolm in press), and another at 0.5-m height (=understory), within 2 m of the tree used to support the mammal trap. I did not set overstory traps in matrix habitat.

Traps were a 20 by 20 cm piece of glass covered on both sides with an approximately 2-mm thick layer of "tangle-trap". Tape along two edges reduced the trap surface to 20 by 17 cm per side. After eight consecutive trapnights, overstory and understory captures from each unit

were removed from the tangle-traps, placed in separate containers, washed in gasoline, and stored in FAA. A few months later, samples were washed in gasoline four more times, dried to constant weight, and weighed to the nearest mg. Insect taxa were not identified; hence, analyses were performed using overall biomass measurements. Because of vagaries of sampling, a few traps were set for less than eight nights. I therefore standardized effort by calculating biomass/trapnight.

Terrestrial pitfall traps. In each 1-ha unit, I established two 100-m long parallel transects, one 20 m from each unit border. Again, transects were marked at 20-m intervals and were situated perpendicular to the forest edge. I set traps at three randomly selected points per transect during census 2 and at the three remaining points during census 1. Pitfall traps were not set during census 1.

I made pitfall traps by burying plastic disposable cups 7 cm below the soil surface. The cups, 7-cm top diameter by 11 cm high by 5-cm bottom diameter, were half filled with a weak soap solution. As bait, a piece of banana was suspended over the cup. To "funnel" captures into the trap, I cut a 7-cm diameter hole in a 25 by 25 cm piece of plywood, placed the top half of a plastic cup flush within the hole, and centered the hole over the pitfall. To prevent rain from entering, I suspended a plastic plate over the hole in the plywood. After three trapnights, I removed captures and replaced the bait and soap solution, and after a further three nights, removed additional captures and the trap. Samples from each census of a 1-ha unit were stored in FAA.

Arachnids and insects (other than larvae) were identified to order (CSIRO 1970), except for spiders and harvestmen (which were lumped) and

whip-scorpions (which were lumped). Other invertebrates were identified to class. In addition, individuals were assigned to one of five size classes: (i) ≤ 5 mm, (ii) 5 - 10 mm, (iii) 10 - 20 mm, (iv) 20 - 35 mm, and (v) 35 - 55 mm. Individuals >55 mm in length were measured to the nearest mm. To estimate biomass, I calculated

$$(1) \quad W = 0.0305 L^{2.62},$$

where \underline{W} = dry weight in mg and \underline{L} = length in mm (Rogers et al. 1976, Winnett-Murray 1986). I used the midpoint of each size class for \underline{L} (except for insects >55 mm in length, where I used the actual length). Total biomass was the summed biomass of all taxa captured. Again, trapping effort was standardized by calculating biomass/trapnight. As a check on the use of equation (1) to estimate biomass, I regressed estimated dry biomass against wet biomass for 24 samples (three samples for each of eight units - see the randomized block experiment described below). Correlation was very high (model with no intercept: $R^2 = 0.98$, $P < 0.01$).

Arboreal pitfall traps. During census 3, I set arboreal pitfall traps at three randomly selected points on the same transects established for tangle-traps, to provide six traps per 1-ha unit. Traps were suspended immediately below small mammal traps. Average trap height in secondary forest was approximately 2 m, whereas in non-matrix habitat it was approximately 14 m. Arboreal pitfall traps were not set in pasture.

Traps consisted of a plastic, disposable cup, 7.5-cm top diameter by 12 cm high by 5.5-cm bottom diameter, half filled with a solution of

soap, 5% alcohol, and water. To support the cup and prevent rain from entering, I constructed plywood boxes 20 by 20 by 4.5 cm high, open on two sides. The cup was placed flush with the bottom of the box in a centered 7.5-cm diameter hole. As bait, a small cloth sac containing banana was suspended over the cup.

Traps at site 2 were set for eight nights, whereas at sites 3 and 4, and at four units in site 1, they were set for six nights. To compare results given this unequal effort, I assumed that capture rate did not vary with the number of nights a trap was set, and controlled for unequal effort by calculating biomass/trapnight. To test the validity of this assumption, I conducted a randomized block experiment at site 1. Within each of eight units, two randomly selected traps were set for four nights, two for six nights, and two for eight nights (=treatment). I drained the insect samples for 5 min, and measured wet biomass to the nearest g. Mean biomass per trapnight did not differ significantly among treatments ($P = 0.14$).

Insects were identified and measured as described for terrestrial pitfall traps.

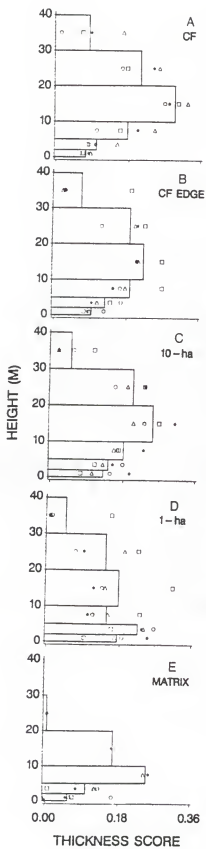
Rainfall. I calculated the amount of rainfall during the trapping periods in the 1-ha units. To control for effort, daily rainfall was weighted by the number of traps set that day. I used rainfall data from the collection location closest to the unit (see figure 6-2 for rainfall collection locations).

Vegetation structure. I measured vegetation structure by use of a modified version Hubbell and Foster's (1986b) method. In 1-ha units other than those in matrix habitat, at each point on a 10 m by 10 m grid

extending 10 m outside the unit (169 points), a 2.5 m pole was used to make a vertical sighting, and, along the sighting, foliage density was scored in six height intervals: 0 - 2, 2 - 5, 5 - 10, 10 - 20, 20 - 30, and 30 - 40 m. Height estimates were checked periodically with a range finder. In matrix units, I scored foliage density at only 36 points: points on the fourth and tenth rows of the 13 by 13 grid, and points between these rows on the second and twelfth columns. Height estimates were periodically checked with a range finder. The first three height intervals were scored as 0 (<25% coverage), 1 (25 - <50% coverage), 2 (50 - <75% coverage), or 3 (75% coverage or more). The last three were scored as 0 (<10% coverage), 1 (10 - <50% coverage), 2 (50 - <75% coverage), or 3 (75% coverage or more). Measurements were made by myself or an assistant. To minimize inter-observer bias, we both measured the first 299 points, and after each point, compared scores and discussed any differences. Data from grid rows and/or columns that were on the clearcut side of the edge were excluded from calculations. To provide a measure of foliage "thickness" in each interval, I recoded non-zero scores by multiplying the number of meters in the interval by the mean percentage corresponding to the score. For example, a score of 1 in the first height interval (0 - 2 m) was recoded as $2 \times 0.375 = 0.75$, a score of 2 was recoded as $2 \times 0.625 = 1.25$, etc.

Among non-matrix habitats, understory (0 - 2 and 2 - 5 m) thickness increased, and overstory (10 - 20 and 20 - 30 m) thickness decreased, with increased proportion of edge in a habitat (figure 6-4). Differences among habitats were not as pronounced in the other two strata. Also, in contrast to the understory and overstory strata,

Figure 6-4. Foliage thickness scores in six height intervals for five habitats: continuous forest (Part A), continuous forest edge (Part B), 10-ha fragment (Part C), 1-ha fragment (Part D), and the matrix surrounding the fragments (Part E). For parts A-D, bars are through the mean of thickness scores from four sites (square = site 1, star = site 2, triangle = site 3, circle = site 4). Bars in part E represent the mean thickness score of sites where the matrix was secondary forest (sites 2 and 3). See text for a description of thickness scores.



vegetation thickness in the 5 - 10 and 30 - 40 m strata showed little relationship with distance from the edge in CP edge (Chapter 5). Therefore, to reduce the number of vegetation variables, I derived two measurements for non-matrix units: understory thickness (sum of the thickness scores in strata 1 and 2 (0 - 5 m)) and overstory thickness (sum of the thickness scores in strata 4 and 5 (10 - 30 m)). In addition to the means for each unit, I calculated the variance among points. The relationship between the mean and variance was strong and linear, so to derive a measure of variability that was "independent" of the mean, I regressed the variance against the mean and used the residuals ($n = 47$ 1-ha units). Finally, I calculated a simple measure of understory and overstory "grain". Neither of the two standard methods was suitable; spectral analysis (Ripley 1978) is not easily applied to measurements from square grids and Greig-Smith's (1952) method is difficult to interpret (Ripley 1978, Diggle 1983). An intuitive method is to use the relationship between surface area and volume. A small relative surface area indicated a coarser grain and vice versa. Each of the strata was visualized as a square array of 169 blocks, where the height of each block was the vegetation thickness at the corresponding grid point. Blocks were 10 by 10 m, hence the volume of a block was 100 times the stratum thickness. Surface area included any surfaces of the blocks not in contact with other block surfaces. The relationship between log-surface area and log-volume was linear, so to render the surface area "independent" of the mean and variance, I used residuals from the multiple regression of surface area on log-mean and variance. In summary, six variables were calculated for each 1-ha

unit: understory and overstory mean thickness, residual variance, and residual surface area.

Data Analysis

Variance in insect biomass among habitats. One-ha units were sub-samples, not replicates, hence I combined data from the hectares in each habitat-by-census-by-site combination and calculated the mean. Because sample size (the number of 1-ha units) varied among means, I used weighted analyses where possible. A three-factor ANOVA (matrix type, habitat, and census) with two repeated measures (habitat and census) was used to analyze the tangle-trap and terrestrial pitfall data and a two-factor ANOVA (matrix type and habitat) with one repeated measure (habitat) was used to analyze the arboreal pitfall data (see Cody and Smith (1987) for examples of these designs). Matrix type at two of the sites was pasture and at the other two it was secondary forest, hence site was "nested" within matrix (Cody and Smith 1987). I conducted two analyses: one with all five habitats, and, because matrix type seemed unlikely to influence samples in continuous forest, one in which continuous forest was excluded. Total biomass was not transformed, whereas biomass of frequently captured taxa (>200 individuals) were square-root transformed. I used non-parametric methods for taxa captured infrequently (20 - 200 individuals). Biomass of rarely captured taxa (<20 individuals) were not analyzed. To test for habitat effects with rainfall as a covariate, I used a block (=site) design (censuses combined).

Tests of hypotheses. According to the first hypothesis, variation in insect biomass among primary forest habitats was solely attributable

to proximity to the edge. The average distance from a 1-ha unit to clearcut decreased in the sequence: CF, CF edge, 10-ha fragment, and 1-ha fragment; hence, a simple prediction from the hypothesis was that it would be possible to rank habitat-specific biomass in the same sequence. I used isotonic regression (Gaines and Rice 1990) to test for the predicted ordering. The test is similar to ANOVA, except that the alternative hypothesis is directional. For taxa that exhibited significant habitat effects (as tested by ANOVA), I removed site effects and used isotonic regression to test the null hypothesis of no habitat effect against one of two alternatives: (i) $\mu_{CF} \leq \mu_{CF\ edge} \leq \mu_{10-ha} \leq \mu_{1-ha}$ (with at least one strict inequality) or (ii) $\mu_{CF} \geq \mu_{CF\ edge} \geq \mu_{10-ha} \geq \mu_{1-ha}$ (with at least one strict inequality). The choice of alternative hypothesis was made a posteriori, so the test was a liberal one.

According to the second hypothesis, variation in insect biomass among habitats was attributable to variation in vegetation structure among habitats. Note that if variation in vegetation structure among habitats is a function of proximity to edge (as suggested in Chapter 5), hypotheses one and two are equivalent. Relationships between insect biomass and vegetation structure were examined using simple and canonical correlation. Canonical correlation finds a linear combination (canonical variable) from each of the two sets of variables (insect biomass and vegetation structure variables), such that the correlation between the two canonical variables (the canonical correlation) is maximized (Luginbuhl and Schlotzhauer 1987). A second set of canonical variables, uncorrelated with the first pair, that produces the second

highest canonical correlation is found, etc. I examined only the first two sets of canonical variables. Because of the restrictive assumption of multivariate normality, I did not use the analysis for statistical testing. The predicted relationship between insect biomass and vegetation structure was tested using simple correlation.

Under the second hypothesis, any relationship between insect biomass and vegetation structure evident among non-isolated (CF and CF edge) habitats should be continuous with the relationship among isolated (10- and 1-ha fragments) habitats, i.e. given identical vegetation structure in an isolated and a non-isolated site, and some relationship between insect biomass and vegetation structure among non-isolated sites or among isolated sites, insect biomass in the two sites should be identical, with no effects attributable to insularization per se. I defined two treatment groups (non-isolated and isolated sites) and tested the hypothesis of equal insect biomass given equal vegetation structure by use of analysis of covariance (ANCOVA). In the special case of a linear relationship, the hypothesis of equal insect biomass given equal vegetation structure was equal to the null hypothesis of no "isolation" effect in ANCOVA. Significant interaction (i.e. a slope effect) could indicate a non-linear, but continuous relationship, or a discontinuity between the two treatment groups.

Analyses other than isotonic regression were performed using SAS/PC (Luginbuhl and Schlotzhauer 1987); isotonic regression was performed using a program supplied by Gaines and Rice. Statistical tests were judged significant at $P < 0.05$.

Results

Tangle-traps

Figure 6-5 depicts mean dry biomass per trapnight for each of the habitat-by-census-by-site combinations. In each matrix type, 1-ha fragments had the greatest understory insect biomass, 10-ha fragments and CF edge were intermediate, and CF had the lowest biomass (habitat effect $P = 0.01$) (table 6-1). Habitat-by-matrix interaction was significant ($P = 0.02$); biomass in the matrix itself varied with matrix type. Biomass in pasture was greater than in all other habitats, whereas biomass in secondary forest only exceeded that in CF. In the analysis of all habitats except CF, habitat ($P = 0.02$) and habitat-by-matrix interaction ($P < 0.01$) were again significant. In addition to the habitat effect and habitat-by-matrix interaction above, biomass in the matrix increased from census 1 to census 2 (habitat-by-census interaction $P = 0.02$), especially in pasture (habitat-by-matrix-by-census interaction $P = 0.05$) (table 6-1). Significant interaction terms could be attributed to the relative changes in matrix biomass; no main effect or interaction terms were significant when matrix habitat was excluded from the analyses. In an analysis of the four primary forest habitats, habitat-by-matrix interaction was no longer significant ($P = 0.18$) and habitat remained significant ($P = 0.04$, isotonic regression $P < 0.01$). The remaining weak interaction was due to higher biomass in fragments surrounded by secondary forest than in those surrounded by pasture.

In the three-way, weighted ANOVA of overstory biomass per trapnight, no main effect or interaction terms were significant, either

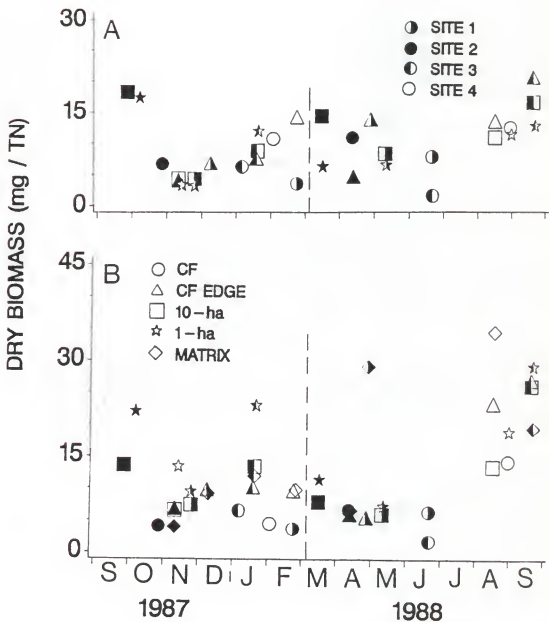


Figure 6-5. Mean dry biomass of insects (mg/trapnight) captured in overstory (Part A) and understory (Part B) tangle-traps vs date the traps were set. Symbol types identify habitat types and symbol shades identify sites. The dashed line separates census one from census two. Means are based on samples from one to four 1-ha sub-sampling units.

Table 6-1. Mean estimated biomass (dry weight in mg/trapnight) for understory tangle-traps during two censuses of five habitats at each of four sites. The matrix at two of the sites was pasture; at the other two it was secondary forest. Prior to calculating means, I removed site effects by computing $\bar{x}_{ijk} = \frac{x_{i.k} + x_{.j.k}}{2}$, where x_{ijk} is the biomass per trapnight during the i^{th} census of the j^{th} habitat at the k^{th} site.

Habitat	Matrix								
	Pasture ($n = 2$)			Secondary Forest ($n = 2$)			Combined ($n = 4$)		
	Census			Census			Census		
	1	2	\bar{Y}	1	2	\bar{Y}	1	2	\bar{Y}
Matrix	9.5 (0.2) ¹	24.3 (3.3)	16.9 (1.7)	4.7 (3.6)	7.2 (0.1)	5.9 (1.7)	7.1 (3.4)	15.8 (10.1)	11.4 (6.5)
1-ha fragment	11.4 (2.2)	5.5 (1.1)	8.5 (1.7)	19.3 (1.4)	14.5 (3.4)	16.9 (1.0)	15.4 (4.8)	10.0 (5.5)	12.7 (5.0)
10-ha fragment	7.0 (1.2)	2.2 (1.8)	4.6 (1.5)	10.3 (2.2)	11.2 (3.7)	10.8 (0.7)	8.7 (2.4)	6.7 (5.7)	7.7 (3.7)
CF ² edge	9.8 (0.7)	6.9 (5.5)	8.3 (2.4)	5.3 (0.3)	10.7 (5.7)	8.0 (3.0)	7.5 (2.6)	8.8 (5.1)	8.1 (2.2)
CF	4.1 (0.1)	2.8 (1.5)	3.4 (0.8)	2.1 (0.3)	-1.6 (12.7)	0.2 (6.5)	3.1 (1.1)	0.6 (7.8)	1.8 (4.2)

¹ Standard deviations are in parentheses.

² CF = continuous forest.

when all habitats were included, or when CF was excluded. As in the analysis of understory biomass excluding matrix habitat, weak habitat-by-matrix interaction ($P = 0.14$ and $P = 0.19$ respectively) was due to higher biomass in fragments surrounded by secondary forest than in those surrounded by pasture (table 6-2).

In continuous forest, overstory insect biomass averaged greater than understory insect biomass. In the other habitats, the converse was true. To compare differences in the ratio of overstory:understory biomass, I regressed overstory biomass against understory biomass, and used ANOVA to analyze deviations from the line $Y = X$. The comparison did not include matrix habitat, because overstory biomass was not measured in matrix habitat. To homogenize variances, I added 5 to each biomass, and log transformed the sums (figure 6-6). A three-way, weighted ANOVA was close to significant for habitat ($P = 0.06$), but not for other main effects or for interaction terms. A one-way ANOVA comparing mean deviations among habitats (censuses combined) was significant ($P < 0.01$, isotonic regression $P < 0.01$). These results thus confirmed the separate analyses on the understory and overstory data; understory biomass increased with increased edge in a habitat whereas overstory biomass changed little, hence the ratio overstory:understory biomass decreased with increasing edge in a habitat. Because matrix habitat was excluded, no interaction terms were significant. Finally, the slightly higher biomass in fragments surrounded by secondary forest than in those surrounded by pasture was true in both the overstory and understory samples, hence habitat-by-matrix interaction was not significant ($P = 0.55$).

Table 6-2. As table 6-1 except that means are from overstory tangle-traps.

Habitat	Matrix								
	Pasture ($n = 2$)			Secondary Forest ($n = 2$)			Combined ($n = 4$)		
	Census			Census			Census		
	1	2	\bar{X}	1	2	\bar{X}	1	2	\bar{X}
1-ha fragment	1.9 (2.5)	3.3 (1.3)	2.6 (0.6)	9.5 (1.7)	3.5 (1.9)	6.5 (0.1)	5.7 (4.7)	3.4 (1.3)	4.5 (2.3)
10-ha fragment	3.0 (2.6)	4.0 (0.3)	3.5 (1.4)	8.3 (4.6)	9.5 (1.2)	8.9 (2.9)	5.6 (4.3)	6.7 (3.2)	6.2 (3.6)
CF edge	9.2 (2.7)	8.0 (2.3)	8.6 (0.2)	0.7 (4.6)	6.6 (8.5)	3.6 (6.6)	4.9 (5.8)	7.3 (5.2)	6.1 (4.8)
CF	5.8 (2.5)	4.5 (1.2)	5.2 (1.8)	1.4 (1.7)	0.2 (9.3)	0.8 (3.8)	3.6 (3.1)	2.4 (5.9)	3.0 (3.5)

Greatest insect biomass, especially in understory traps, was recorded in August and September of 1988, the two driest months of 1988. In contrast, the driest months of 1987 (October - December) were characterized by low insect biomass. In both years, insect biomass was high in September. Rainfall during trapping periods was not a significant covariate in the block analysis comparing understory biomass among habitats ($P = 0.18$), but greater rainfall in a sampling period lead to greater overstory biomass ($P = 0.04$). With rainfall as a covariate, differences in overstory biomass among habitats remained non-significant ($P = 0.13$). Relationships among "adjusted" means (i.e. means corrected for differences in rainfall) were similar to those in table 6-2; CF had lower biomass than the other habitats. In the block analysis on the overstory:understory ratio, rainfall was not significant ($P = 0.11$).

Weighted correlations between insect biomass in non-matrix habitats and the six vegetation variables are shown in table 6-3. The relationship between understory biomass and overstory thickness was strong ($P < 0.01$) and negative; habitats with more open overstories had higher understory insect biomass (figure 6-7A). Not surprisingly (given the negative correlation between overstory and understory thickness), the correlation between understory thickness and understory insect biomass was positive, although not quite significant ($P = 0.07$). The regression between insect biomass and overstory thickness among isolated habitats (1- and 10-ha fragments) was similar to that among non-isolated habitats (CF edge and CF) (ANCOVA $P = 0.26$). None of the correlations between overstory insect biomass and the vegetation variables was

Table 6-3. Weighted correlations between insect biomass/trapnight from tangle-traps and vegetation structure. See text for definitions of insect biomass and vegetation variables.

Vegetation variable	Understory biomass	Overstory biomass	Transformed overstory : understory biomass
Understory thickness	0.46	0.29	0.43
Overstory thickness	-0.69**	-0.29	-0.64**
Understory residual variance	-0.18	0.33	-0.49
Overstory residual variance	-0.06	-0.02	0.01
Understory residual surface area	-0.09	0.06	-0.14
Overstory residual surface area	-0.22	-0.44	0.03

** = Significant at $p < 0.01$.

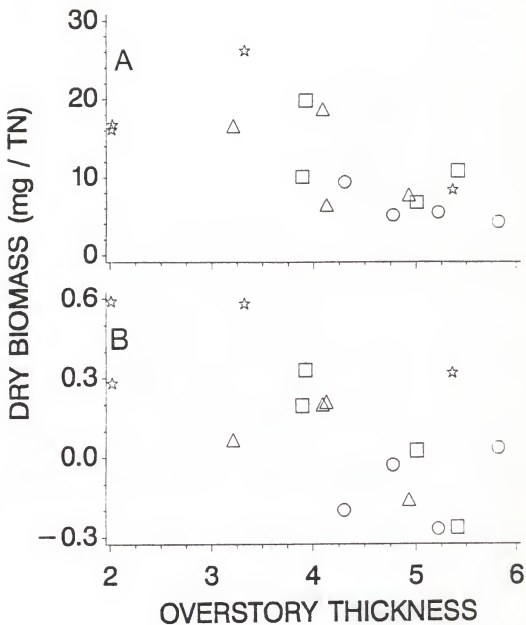


Figure 6-7. Mean dry biomass of insects from understory tangle-traps (Part A) and understory:overstory biomass from tangle-traps (Part B) vs overstory foliage thickness. Understory:overstory biomass are deviations from the line $Y = X$ in figure 6-6.

significant. Analysis of the overstory:understory biomass ratios gave similar results. The ratio decreased with increasing overstory thickness ($\underline{P} < 0.01$, figure 6-7B) and there was some evidence of a decrease in the ratio with decreasing understory thickness and increasing understory variance ($\underline{P} = 0.10$ and 0.06 respectively). These three correlations reflected correlations among the vegetation variables; in addition to the negative correlation between overstory and understory thickness, high overstory thickness was correlated with high understory variance. Again, with overstory thickness as a covariate, insect biomass did not appear to differ between isolated and non-isolated habitats ($\underline{P} = 0.17$).

Terrestrial Pitfall Traps

Total insect biomass for each of the habitat-by-census-by-site combinations is shown in figure 6-8A and census-by-habitat-by-matrix means for frequently-caught taxa are in tables 6-4 and 6-5. Averaged across the 58 1-ha units sampled, the rank order of taxon biomass (mg/trapnight and total number of individuals in parenthesis) was Blattodea (64, 4556), Orthoptera (29, 2681), Diplopoda (28, 172), Hymenoptera (20, 63932), Coleoptera (11, 6559), Dermaptera (9, 1468), Chilopoda (3, 19), Lepidoptera (2, 41), Arachnida (1, 355), Scorpiones (1, 23), Isoptera (1, 9168), larva (1, 75), Annelida (1, 1), Diptera (1, 5611), Gastropoda (1, 7), whip scorpions (<1, 10), mites (<1, 69), Homoptera (<1, 28), Malacostraca (<1, 14), Hemiptera (<1, 2), Diplura (<1, 6), Neuroptera (<1, 2), Archaeognatha (<1, 1), Collembola (<1, 4), and Pseudoscorpiones (<1, 3).

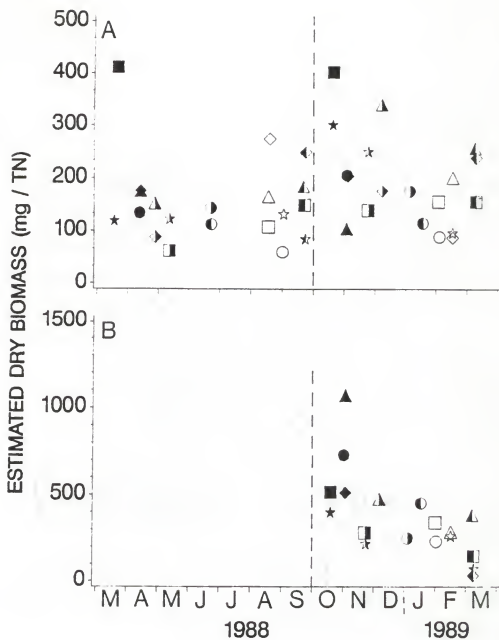


Figure 6-8. As figure 6-5 except that total estimated dry biomass from terrestrial (Part A) and arboreal (Part B) pitfall traps are shown. The dashed line separates census two from census three. See text for biomass estimation.

Table 6-4. Estimated biomass (dry weight in mg/terrestrial pitfall trapnight) (\pm SD) of all captures and taxa with >20 individuals. Prior to calculating means for the total and for each taxon, I removed site effects by computing $\bar{x}_{ijk} - \bar{x}_{i.k} + \bar{x}_{..}$, where \bar{x}_{ijk} is the biomass/trapnight during the i^{th} census in the j^{th} habitat at the k^{th} site.

		Census 2						
Matrix	Taxon	Matrix	1-ha fragment	10-ha fragment	CP ¹ edge	CP		
Pasture (n = 2)	Total	224.3 \pm 107.2	170.2 \pm 17.3	128.1 \pm 8.2	201.6 \pm 15.0	144.9 \pm 83.2		
	Blattodea	28.4 \pm 16.1	92.1 \pm 15.4	42.0 \pm 11.1	102.4 \pm 13.2	48.0 \pm 7.2		
	Coleoptera	7.9 \pm 6.1	14.0 \pm 11.0	6.5 \pm 5.4	11.4 \pm 6.8	18.8 \pm 7.3		
	Dermaptera	2.0 \pm 7.8	14.8 \pm 8.6	5.8 \pm 4.6	22.1 \pm 13.6	6.0 \pm 9.8		
	Diptera	0.6 \pm 0.4	0.4 \pm 0.9	0.8 \pm 0.4	0.6 \pm 0.6	1.4 \pm 0.4		
	Hemiptera	0.2 \pm 0.2	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1		
	Hymenoptera	39.2 \pm 12.6	8.9 \pm 2.9	14.5 \pm 3.8	17.9 \pm 0.6	19.5 \pm 12.9		
	Isopoda	-1.1 \pm 1.9	4.8 \pm 6.8	-0.4 \pm 2.9	2.0 \pm 0.4	0.1 \pm 2.4		
	Lepidoptera	1.5 \pm 0.3	1.3 \pm 0.6	1.9 \pm 0.3	1.3 \pm 0.6	2.6 \pm 1.2		
	Orthoptera	35.1 \pm 4.2	20.5 \pm 0.9	21.9 \pm 1.3	34.8 \pm 0.9	25.4 \pm 5.5		
	Diplopoda	98.4 \pm 68.7	0.6 \pm 21.2	25.4 \pm 13.8	0.5 \pm 21.1	14.3 \pm 40.2		
	Larva	0.8 \pm 0.3	0.5 \pm 0.3	0.6 \pm 0.1	0.7 \pm 0.1	1.3 \pm 0.9		
	Arachnida	1.7 \pm 0.1	1.1 \pm 0.2	0.9 \pm 0.1	2.0 \pm 0.5	1.1 \pm 0.1		
	Scorpiones	1.0 \pm 0.7	3.5 \pm 2.8	1.1 \pm 0.9	1.1 \pm 0.5	1.0 \pm 0.7		
	Secondary forest (n = 2)	Total	206.8 \pm 84.9	95.9 \pm 9.0	274.6 \pm 152.2	174.2 \pm 40.0	117.7 \pm 18.3	
		Blattodea	35.4 \pm 22.4	19.7 \pm 48.1	152.7 \pm 136.1	72.9 \pm 20.6	32.2 \pm 45.1	
Coleoptera		5.4 \pm 5.8	4.4 \pm 0.1	33.6 \pm 0.6	15.9 \pm 5.7	-0.7 \pm 0.7		
Dermaptera		8.7 \pm 2.5	12.8 \pm 5.2	15.7 \pm 1.4	10.0 \pm 8.6	3.4 \pm 0.6		
Diptera		0.6 \pm 1.0	1.3 \pm 0.9	1.2 \pm 0.4	0.7 \pm 0.3	0.1 \pm 0.1		
Hemiptera		-0.1 \pm 0.1	0.5 \pm 0.6	-0.1 \pm 0.1	-0.1 \pm 0.1	-0.1 \pm 0.1		
Hymenoptera		24.6 \pm 37.0	35.1 \pm 18.2	18.1 \pm 8.5	12.8 \pm 6.1	9.5 \pm 16.4		
Isopoda		0.5 \pm 0.5	1.1 \pm 0.4	2.6 \pm 0.5	0.4 \pm 0.4	0.8 \pm 0.7		
Lepidoptera		-0.9 \pm 4.9	0.7 \pm 0.2	8.4 \pm 7.1	-0.8 \pm 2.3	1.1 \pm 0.4		
Orthoptera		62.1 \pm 22.7	3.5 \pm 10.1	20.1 \pm 11.1	25.3 \pm 13.7	26.7 \pm 12.1		
Diplopoda		32.3 \pm 7.6	15.5 \pm 16.2	18.0 \pm 12.6	32.0 \pm 7.2	41.4 \pm 14.0		
Larva		1.0 \pm 0.7	0.6 \pm 0.1	1.4 \pm 0.6	0.5 \pm 0.1	0.5 \pm 0.1		
Arachnida		1.4 \pm 0.7	0.5 \pm 0.1	1.9 \pm 1.5	2.0 \pm 1.1	1.0 \pm 0.3		
Scorpiones		8.6 \pm 11.4	-1.1 \pm 2.3	-1.1 \pm 2.3	1.0 \pm 2.8	0.2 \pm 4.0		
Combined (n = 4)		Total	215.5 \pm 79.6	133.0 \pm 44.4	201.3 \pm 122.1	187.9 \pm 29.3	131.3 \pm 51.6	
		Blattodea	31.9 \pm 16.4	55.9 \pm 51.0	97.3 \pm 101.5	87.6 \pm 22.1	40.1 \pm 27.9	
	Coleoptera	6.6 \pm 5.1	9.2 \pm 8.4	20.0 \pm 16.0	13.6 \pm 5.7	9.1 \pm 12.1		
	Dermaptera	5.4 \pm 6.1	13.8 \pm 5.9	10.7 \pm 6.4	16.1 \pm 11.6	4.7 \pm 5.9		
	Diptera	0.6 \pm 0.6	0.9 \pm 0.9	1.0 \pm 0.4	0.6 \pm 0.4	0.7 \pm 0.8		
	Hemiptera	0.1 \pm 0.2	0.2 \pm 0.4	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1		
	Hymenoptera	31.9 \pm 24.1	22.0 \pm 18.5	16.3 \pm 5.8	15.4 \pm 4.6	14.5 \pm 13.4		
	Isopoda	-0.3 \pm 1.4	3.0 \pm 4.5	1.1 \pm 2.5	1.2 \pm 1.0	0.4 \pm 1.5		
	Lepidoptera	0.3 \pm 3.2	1.0 \pm 0.5	5.2 \pm 5.6	0.3 \pm 1.8	1.9 \pm 1.1		
	Orthoptera	48.6 \pm 20.5	12.0 \pm 11.4	21.0 \pm 6.5	30.0 \pm 9.6	26.1 \pm 7.7		
	Diplopoda	65.4 \pm 55.2	8.0 \pm 17.6	21.7 \pm 11.6	16.3 \pm 22.3	27.8 \pm 29.2		
	Larva	0.9 \pm 0.5	0.5 \pm 0.2	1.0 \pm 0.6	0.6 \pm 0.1	0.9 \pm 0.7		
	Arachnida	1.5 \pm 0.4	0.8 \pm 0.4	1.4 \pm 1.1	2.0 \pm 0.7	1.0 \pm 0.2		
	Scorpiones	4.8 \pm 7.9	1.2 \pm 3.3	0.1 \pm 1.9	1.1 \pm 1.7	0.6 \pm 2.4		

¹ CP = continuous forest.

Census 3

Matrix	1-ha fragment	10-ha fragment	CP ¹ edge	CP
134.5 ± 1.2	175.7 ± 44.5	150.3 ± 75.3	273.3 ± 34.2	135.2 ± 2.3
25.0 ± 40.1	63.9 ± 12.4	51.6 ± 4.2	127.6 ± 75.5	44.8 ± 10.7
12.9 ± 7.5	6.6 ± 0.4	8.1 ± 0.1	18.0 ± 1.4	13.0 ± 6.5
-1.6 ± 0.6	19.7 ± 3.9	8.9 ± 10.1	17.6 ± 4.4	6.0 ± 2.3
1.1 ± 1.1	0.9 ± 0.8	0.8 ± 0.6	1.0 ± 0.5	0.1 ± 0.2
0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
24.1 ± 5.4	19.3 ± 0.6	19.0 ± 1.6	23.0 ± 7.6	14.6 ± 1.2
1.1 ± 0.4	0.8 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	1.8 ± 0.2
1.7 ± 0.1	1.7 ± 0.1	1.8 ± 0.2	1.7 ± 0.1	1.7 ± 0.1
4.7 ± 2.5	13.2 ± 4.2	31.8 ± 34.8	35.7 ± 18.4	52.2 ± 23.1
59.1 ± 47.4	46.1 ± 62.7	7.4 ± 31.2	31.6 ± 65.0	-4.9 ± 13.9
-0.2 ± 0.9	0.1 ± 1.8	4.5 ± 5.3	-0.4 ± 1.1	0.2 ± 1.4
2.5 ± 1.6	-0.1 ± 0.1	1.3 ± 0.7	3.4 ± 1.1	-0.3 ± 1.2
-0.7 ± 2.5	-0.7 ± 2.5	0.7 ± 4.1	8.4 ± 10.4	0.1 ± 1.4
80.6 ± 65.3	189.6 ± 50.1	239.1 ± 133.4	139.7 ± 149.0	119.8 ± 22.9
19.6 ± 31.6	68.4 ± 28.6	141.0 ± 121.8	38.3 ± 46.2	45.5 ± 15.3
2.2 ± 9.3	34.1 ± 34.3	13.2 ± 0.4	5.7 ± 10.7	3.3 ± 14.6
19.4 ± 6.9	12.6 ± 3.2	7.6 ± 0.9	6.6 ± 0.2	4.5 ± 9.1
0.6 ± 0.1	0.6 ± 0.1	0.8 ± 0.2	1.1 ± 0.2	0.7 ± 0.2
0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
17.0 ± 15.0	11.2 ± 8.5	14.8 ± 16.1	5.8 ± 9.8	49.3 ± 49.3
0.5 ± 0.2	0.5 ± 0.2	2.8 ± 0.6	0.7 ± 0.4	0.9 ± 0.2
3.8 ± 2.9	1.3 ± 0.6	3.5 ± 2.6	0.1 ± 2.4	0.1 ± 2.4
39.0 ± 3.9	23.7 ± 23.3	24.2 ± 3.1	18.2 ± 15.4	32.5 ± 7.1
80.7 ± 6.9	-9.0 ± 26.4	16.5 ± 25.3	60.5 ± 71.9	-9.5 ± 27.1
0.2 ± 0.9	2.3 ± 3.2	1.2 ± 1.6	0.3 ± 1.0	0.1 ± 0.2
1.1 ± 0.1	0.9 ± 1.3	2.1 ± 0.7	1.1 ± 0.1	1.6 ± 0.7
2.1 ± 1.9	0.9 ± 0.1	2.9 ± 2.3	0.9 ± 0.1	0.9 ± 0.1
157.6 ± 46.2	182.7 ± 63.0	194.7 ± 102.2	206.5 ± 117.2	127.5 ± 16.0
22.3 ± 29.7	66.2 ± 18.2	96.3 ± 87.3	83.0 ± 72.6	45.2 ± 14.0
7.6 ± 9.3	20.3 ± 25.4	10.7 ± 3.0	11.9 ± 9.4	8.1 ± 10.8
8.9 ± 12.7	16.1 ± 5.1	8.3 ± 5.9	12.1 ± 6.8	5.3 ± 5.5
0.8 ± 0.7	0.7 ± 0.5	0.8 ± 0.4	1.1 ± 0.3	0.4 ± 0.4
0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
20.5 ± 10.1	15.2 ± 6.8	17.9 ± 9.4	14.4 ± 12.2	31.9 ± 34.8
0.8 ± 0.5	0.7 ± 0.2	1.8 ± 1.2	0.8 ± 0.3	1.3 ± 0.6
2.7 ± 2.0	1.5 ± 0.4	2.7 ± 1.8	0.9 ± 1.7	0.9 ± 1.7
21.9 ± 19.9	18.5 ± 15.0	28.0 ± 20.6	27.0 ± 17.1	42.4 ± 18.0
69.9 ± 30.3	18.6 ± 50.6	11.9 ± 23.8	46.0 ± 58.4	-7.2 ± 17.8
0.1 ± 0.8	1.1 ± 2.5	2.8 ± 3.7	-0.1 ± 1.0	0.1 ± 0.8
1.8 ± 1.2	0.4 ± 1.0	1.7 ± 0.7	2.2 ± 1.5	0.7 ± 1.3
0.7 ± 2.4	0.1 ± 1.7	1.8 ± 3.0	4.6 ± 7.4	0.4 ± 1.0

Table 6-5. As table 6-4 except that data from the two censuses are combined.

Matrix	Taxon	Habitat					
		Matrix	1-ha fragment	10-ha fragment	CP ¹ edge	CP	
Pasture (n = 2)	Total	179.4 ± 54.2	173.0 ± 30.9	139.2 ± 41.7	237.4 ± 24.6	140.1 ± 40.4	
	Blattodea	26.7 ± 28.1	78.0 ± 13.9	46.8 ± 3.4	115.0 ± 44.4	46.4 ± 5.8	
	Coleoptera	10.4 ± 6.8	10.3 ± 5.3	7.3 ± 2.7	14.7 ± 2.7	15.9 ± 6.9	
	Dermatpeta	0.2 ± 3.6	17.2 ± 2.3	7.4 ± 2.7	19.8 ± 4.6	6.0 ± 6.1	
	Diptera	0.8 ± 0.8	0.6 ± 0.9	0.8 ± 0.1	0.8 ± 0.5	0.7 ± 0.3	
	Homoptera	0.2 ± 0.1	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± <0.1	<0.1 ± 0.0	
	Hymenoptera	31.7 ± 3.6	14.1 ± 1.1	16.8 ± 1.1	20.5 ± 3.5	17.0 ± 7.0	
	Isoptera	<0.1 ± 0.7	2.8 ± 3.4	0.2 ± 1.5	1.4 ± 0.2	1.0 ± 1.3	
	Lepidoptera	1.6 ± 0.1	1.5 ± 0.3	1.9 ± 0.1	1.5 ± 0.3	2.1 ± 0.6	
	Orthoptera	19.9 ± 3.3	16.8 ± 2.5	26.8 ± 18.0	35.3 ± 9.6	38.8 ± 14.3	
	Diplopoda	78.8 ± 10.7	23.3 ± 42.0	16.4 ± 22.5	16.0 ± 22.0	4.7 ± 13.2	
	Larva	0.3 ± 0.6	0.2 ± 1.0	2.5 ± 2.6	0.1 ± 0.6	0.7 ± 0.3	
	Arachnida	2.1 ± 0.8	0.5 ± 0.1	1.1 ± 0.4	2.7 ± 0.8	0.4 ± 0.5	
	Scorpiones	0.1 ± 1.6	1.4 ± 0.2	0.9 ± 2.5	4.7 ± 5.0	0.5 ± 1.1	
	Secondary Forest (n = 2)	Total	193.8 ± 75.1	142.7 ± 24.5	256.8 ± 142.8	156.9 ± 94.5	118.7 ± 2.3
		Blattodea	27.5 ± 27.0	44.1 ± 38.4	146.8 ± 129.0	55.6 ± 33.4	38.9 ± 30.2
		Coleoptera	3.8 ± 7.6	19.2 ± 17.2	23.4 ± 0.1	10.8 ± 2.5	1.3 ± 7.0
Dermatpeta		14.0 ± 4.7	12.7 ± 4.2	11.7 ± 0.2	8.3 ± 4.4	4.0 ± 4.8	
Diptera		0.6 ± 0.6	0.9 ± 0.4	1.0 ± 0.3	0.9 ± 0.1	0.4 ± 0.0	
Homoptera		<0.1 ± 0.1	0.3 ± 0.3	<0.1 ± 0.1	<0.1 ± 0.1	<0.1 ± 0.1	
Hymenoptera		20.8 ± 26.0	23.1 ± 4.9	17.4 ± 3.8	9.3 ± 7.9	29.4 ± 32.8	
Isoptera		0.5 ± 0.3	0.8 ± 0.3	2.7 ± 0.5	0.5 ± 0.4	0.8 ± 0.5	
Lepidoptera		1.4 ± 3.9	1.0 ± 0.2	6.0 ± 2.3	-0.4 ± <0.1	0.6 ± 1.4	
Orthoptera		50.5 ± 13.3	13.6 ± 16.7	22.2 ± 7.1	21.8 ± 0.9	29.6 ± 9.6	
Diplopoda		56.5 ± 7.3	3.2 ± 21.3	17.3 ± 19.0	46.3 ± 39.6	15.9 ± 6.5	
Larva		0.6 ± 0.1	1.4 ± 1.6	1.3 ± 1.1	0.4 ± 0.5	0.3 ± 0.1	
Arachnida		1.2 ± 0.3	0.7 ± 0.6	2.0 ± 1.1	1.6 ± 0.6	1.3 ± 0.5	
Scorpiones		5.3 ± 6.7	-0.1 ± 1.1	0.9 ± 2.3	0.9 ± 1.4	0.5 ± 1.9	
Combined (n = 4)		Total	186.6 ± 54.1	157.8 ± 28.7	198.0 ± 109.5	197.2 ± 73.1	129.4 ± 26.4
		Blattodea	27.1 ± 22.5	61.0 ± 30.6	96.8 ± 94.2	85.3 ± 46.9	42.6 ± 18.3
		Coleoptera	7.1 ± 7.0	14.8 ± 11.6	15.4 ± 9.5	12.7 ± 3.1	8.6 ± 10.2
	Dermatpeta	7.1 ± 8.7	15.0 ± 3.8	9.5 ± 2.9	14.1 ± 7.6	5.0 ± 4.6	
	Diptera	0.7 ± 0.6	0.8 ± 0.6	0.9 ± 0.2	0.9 ± 0.3	0.6 ± 0.2	
	Homoptera	0.1 ± 0.2	0.1 ± 0.2	<0.1 ± <0.1	<0.1 ± 0.1	<0.1 ± 0.0	
	Hymenoptera	26.2 ± 16.4	18.6 ± 6.0	17.1 ± 2.3	14.9 ± 8.2	23.2 ± 20.7	
	Isoptera	0.2 ± 0.5	1.8 ± 2.3	1.5 ± 1.7	1.0 ± 0.6	0.9 ± 0.8	
	Lepidoptera	1.5 ± 2.3	1.2 ± 0.3	3.9 ± 2.7	0.6 ± 1.1	1.4 ± 1.3	
	Orthoptera	35.2 ± 19.4	15.2 ± 9.9	24.5 ± 11.5	28.5 ± 9.6	34.2 ± 11.3	
	Diplopoda	67.6 ± 14.9	13.3 ± 29.5	16.8 ± 17.0	31.1 ± 31.4	10.3 ± 10.7	
	Larva	0.5 ± 0.4	0.8 ± 1.3	1.9 ± 1.8	0.3 ± 0.5	0.5 ± 0.3	
	Arachnida	1.7 ± 0.7	0.6 ± 0.4	1.6 ± 0.9	2.1 ± 0.9	0.9 ± 0.7	
	Scorpiones	2.7 ± 5.0	0.6 ± 1.0	0.9 ± 2.0	2.8 ± 3.7	0.5 ± 1.3	

¹ CP = continuous forest.

The weighted, three-way ANOVA on total biomass was not significant for main effects or interaction terms, either when all five habitats were tested ($P = 0.26$ for matrix, otherwise $P \geq 0.40$), or when CF was excluded ($P = 0.19$ for matrix, otherwise $P \geq 0.30$). Nor was multivariate analysis of variance on the eight frequently caught taxa (>200 individuals) significant for main effects or interaction terms (all five habitats, Wilk's Lambda P always > 0.30). Degrees of freedom were insufficient for a multivariate test of a matrix effect, and for a test excluding CF. Univariate, three-way ANOVA on each of the eight taxa yielded the following significant results: matrix and matrix-by-habitat-by-census for Diptera (all habitats $P = 0.03$ and $P = 0.04$, respectively); matrix for Hymenoptera (all habitats $P = 0.04$); habitat (CF excluded $P = 0.03$, isotonic regression $P = 0.02$) and matrix-by-habitat (all habitats $P = 0.02$, CF excluded $P < 0.01$) for Dermaptera; and matrix-by-habitat for Coleoptera ($P = 0.04$). Of the 112 F -statistics (2 tests with 7 statistics for 8 taxa), only 7% were significant.

As a non-parametric test of habitat effects and habitat-by-matrix interaction, for infrequently-captured taxa (Homoptera, Lepidoptera, Diplopoda, larva, mites, and Scorpiones) I ranked biomass within sites, and used two-way (habitat by matrix) ANOVA on the ranks. Homopterans were more abundant in matrix habitat and 1-ha fragments than elsewhere (all habitats $P = 0.06$, CF excluded $P = 0.04$, isotonic regression $P = 0.10$), but their relative abundance in matrix and 1-ha fragments varied with matrix type (matrix-by-habitat interaction, all habitats $P = 0.03$, CF excluded $P < 0.01$). Lepidoptera were more abundant in 10-ha

fragments (CF excluded $P = 0.02$, isotonic regression $P = 0.16$). Tests for other taxa were not significant. To test for matrix effects, I calculated mean biomass/trapnight/site. For taxa other than Lepidoptera, the range of values at pasture sites (sites 1 and 4) overlapped with those at secondary forest sites (sites 2 and 3). Estimated Lepidoptera biomass per trapnight at the two pasture sites averaged 0.44 and 0.03 mg, and at the two secondary forest sites averaged 3.37 and 3.06 mg.

Highest total insect biomass was obtained in the late dry season - early wet season of 1988 (August - December). Rainfall during the trapping sessions again proved to be of little value as a covariate. In a block design comparing total biomass among all five habitats, or one comparing habitats except CF, rainfall was not significant. Similarly, rainfall was not a significant covariate in MANOVA comparing biomass of frequently caught taxa among habitats.

The following correlations between terrestrial insect biomass and vegetation structure were significant: (i) total, Blattodea, and Arachnida biomass increased with increasing variance in understory foliage thickness; (ii) total and Coleoptera biomass decreased with increasing overstory grain; and (iii) Dermapteran biomass increased with increasing understory thickness and decreased with increasing overstory thickness (table 6-6). Canonical correlation provided corroborative results: the first "insect" canonical variable was highly correlated with total, Blattodea, and Arachnida biomass, and the first "vegetation" canonical variable was highly correlated with understory variance (the first set of correlations above). The second canonical correlation

Table 6-6. Weighted correlations between insect biomass/terrestrial pitfall trapnight and vegetation structure and between each set of variables and their first and second canonical variables. See text for definitions of vegetation variables.

	Understory thickness	Overstory thickness	Understory residual variance	Overstory residual variance	Understory residual surface area	Overstory residual surface area	Insect CV ¹ 1	Insect CV 2
Total biomass	0.36	0.21	0.68**	0.38	0.14	-0.54*	0.72	-0.04
Blattodea	0.31	0.35	0.73**	0.38	0.06	-0.45	0.78	-0.13
Coleoptera	0.30	-0.11	0.14	0.02	0.18	-0.59*	0.07	0.10
Dermaptera	0.62*	-0.60*	0.08	0.32	0.01	-0.30	0.30	0.73
Diptera	0.13	-0.19	0.23	-0.01	0.31	-0.32	0.13	0.13
Hymenoptera	-0.05	0.11	-0.02	0.10	0.06	-0.02	-0.06	-0.11
Isoptera	0.11	0.23	0.34	0.14	0.17	-0.20	0.28	-0.07
Orthoptera	-0.38	0.16	<0.01	-0.16	0.22	0.06	-0.19	-0.36
Arachnida	0.13	0.12	0.65**	0.45	0.15	-0.18	0.73	-0.05
Vegetation CV 1	0.34	0.29	0.80	0.55	-0.07	-0.23	0.99	-
Vegetation CV 2	0.82	-0.78	-0.35	0.24	-0.27	-0.17	-	0.94

¹ CV = Canonical variable.

* $P < 0.05$.

** $P < 0.01$.

corroborated the third set of correlations; the "insect" canonical variable was correlated with Dermaptera biomass, and the "vegetation" variable was positively correlated with understory thickness and negatively correlated with overstory thickness (table 6-6). Two of the relationships are shown in figure 6-9: total biomass vs understory variance and Dermaptera biomass vs understory thickness. Recall that among frequently captured taxa, only Dermaptera showed evidence of variation in biomass with habitat. As predicted, Dermaptera biomass varied with understory and overstory thickness. Analysis of covariance comparing isolated (1- and 10-ha fragments) and non-isolated (CF edge and CF) habitats was not significant ($P = 0.16$, figure 6-9).

Arboreal Pitfall Traps

Total insect biomass/trapnight is shown for each habitat-by-site combination in figure 6-8B. Insect biomass was highest at the first site sampled (in late October/early November of 1989) and declined thereafter; each subsequent site mean was less than the proceeding one. Averaged across the 52 1-ha units sampled, the rank order of taxon abundance (mg/trapnight and total number of individuals in parenthesis) was Lepidoptera (192, 7797), Diptera (106, 41803), Coleoptera (43, 6277), Blattodea (19, 844), Hymenoptera (11, 2870), Orthoptera (6, 62), Neuroptera (3, 114), Larva (1, 548), Mantodea (<1, 1), Arachnida (<1, 18), Dermaptera (<1, 2), Isoptera (<1, 4), Pseudoscorpion (<1, 2), and Homoptera (<1, 1).

A two-way, weighted ANOVA on total biomass was significant for habitat when secondary forest was excluded ($P < 0.05$, isotonic regression $P < 0.01$), and close to significant when CF was also excluded

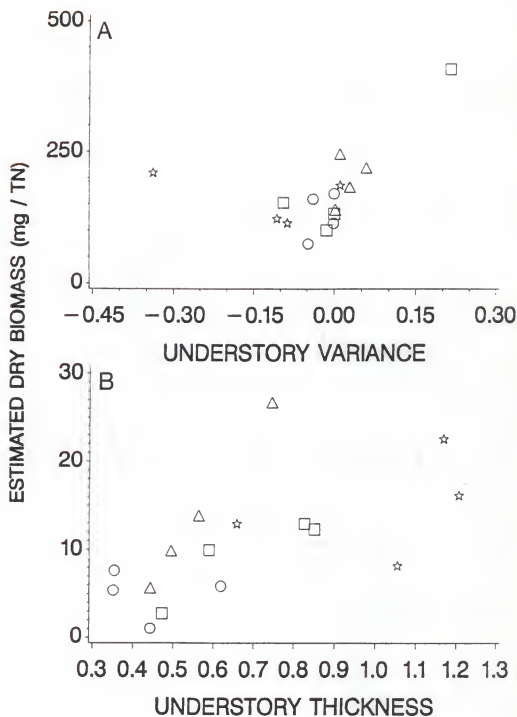


Figure 6-9. Total biomass from terrestrial pitfall traps vs residual understory foliage variance (Part A) and Diptera biomass from terrestrial pitfall traps vs understory foliage thickness (Part B). See text for biomass estimation and for explanations of vegetation variables. Symbols are as in figure 6-6.

($P = 0.06$), but was not significant for matrix effects or habitat-matrix interaction. Highest biomass/trapnight was obtained in CF edge, followed by CF, 10-ha fragments, and 1-ha fragments (table 6-7). Matrix and habitat-matrix interaction were not significant for any of the frequently caught taxa, and habitat was significant only for Diptera ($P < 0.01$ [matrix excluded] and $P = 0.04$ [matrix and CF excluded]). Diptera biomass increased with decreasing proportion of edge (isotonic regression $P < 0.01$). However, among 1-ha fragments, 10-ha fragments, and CF edge, all frequently-caught taxa but Hymenoptera were least abundant in 1-ha fragments and most abundant in CF edge (table 6-7). Again, as a non-parametric test of habitat effects and habitat-matrix interaction, I ranked biomass of infrequently-captured taxa (Orthoptera, Neuroptera, and larva) within sites, and used two-way (habitat by matrix) ANOVA on the ranks. Habitat was significant for larvae, either when matrix habitat was excluded, or when both matrix and CF habitat were excluded ($P = 0.01$ and $P = 0.02$ respectively). As with Diptera biomass, larva biomass increased with decreasing proportion of edge (table 6-7). Habitat-by-matrix interaction was significant for Neuroptera ($P < 0.01$); fragments surrounded by pasture had more Neuroptera than other habitats, whereas the opposite was true for fragments surrounded by secondary forest (table 6-7). For the three infrequently-captured taxa, ranges of means at pasture sites overlapped with those at secondary forest sites.

To compare insect biomass in secondary forest with that in the other habitats, I used a randomized block ANOVA, and included data from only those sites where the matrix was secondary forest. Again, for

Table 6-7. Estimated biomass (dry weight in mg)/arboreal pitfall trapnight (\pm SD) of all captures and taxa with >20 individuals. Prior to calculating means for the total and for each taxon, I removed site effects by computing $\bar{x}_{jk} - \bar{x}_{.k} + \bar{x}_{.j}$, where \bar{x}_{jk} is the biomass/trapnight in the j^{th} habitat at the k^{th} site.

Matrix	Taxon	Habitat			
		1-ha fragment	10-ha fragment	CF ¹ edge	CF
Pasture ($\bar{n} = 2$)	Total	325.0 \pm 50.5	398.6 \pm 59.0	468.3 \pm 114.8	328.4 \pm 5.2
	Lepidoptera	192.1 \pm 40.8	223.2 \pm 8.5	266.6 \pm 61.5	116.9 \pm 29.2
	Diptera	56.8 \pm 4.3	92.7 \pm 53.3	98.6 \pm 16.7	139.9 \pm 40.9
	Coleoptera	39.0 \pm 1.8	43.6 \pm 0.2	53.7 \pm 13.4	37.8 \pm 15.1
	Blattodea	10.0 \pm 7.5	12.5 \pm 5.0	25.5 \pm 5.6	24.4 \pm 8.1
	Hymenoptera	21.1 \pm 18.4	13.4 \pm 4.8	14.4 \pm 17.2	1.0 \pm 5.9
	Orthoptera	1.7 \pm 4.7	6.2 \pm 1.8	8.2 \pm 4.6	5.9 \pm 1.7
	Neuroptera	4.7 \pm 0.8	5.5 \pm 2.2	-0.5 \pm 4.0	1.5 \pm 1.0
	Larva	0.6 \pm 0.4	1.3 \pm 0.1	1.5 \pm 0.9	1.0 \pm 0.4
Secondary forest ($\bar{n} = 2$)	Total	143.3 \pm 61.9	240.9 \pm 33.4	635.8 \pm 192.3	501.2 \pm 97.0
	Lepidoptera	154.8 \pm 13.9	126.8 \pm 48.3	326.2 \pm 201.6	191.1 \pm 139.4
	Diptera	-30.0 \pm 40.8	8.0 \pm 35.7	171.2 \pm 10.5	238.7 \pm 66.0
	Coleoptera	-7.3 \pm 33.5	63.7 \pm 58.0	105.7 \pm 1.7	12.1 \pm 26.2
	Blattodea	11.8 \pm 11.1	18.1 \pm 2.9	12.3 \pm 17.1	30.1 \pm 3.1
	Hymenoptera	12.4 \pm 7.4	11.2 \pm 0.8	11.3 \pm 1.8	15.0 \pm 6.4
	Orthoptera	0.2 \pm 7.1	10.9 \pm 12.0	2.4 \pm 1.3	8.6 \pm 6.2
	Neuroptera	1.6 \pm 1.4	1.9 \pm 1.2	5.2 \pm 2.6	2.6 \pm 0.1
	Larva	-0.1 \pm 1.1	0.5 \pm 0.3	1.6 \pm 1.2	2.3 \pm 0.2
Combined ($\bar{n} = 4$)	Total	234.6 \pm 115.1	319.7 \pm 99.1	552.0 \pm 161.5	414.8 \pm 114.4
	Lepidoptera	173.5 \pm 32.9	175.0 \pm 62.5	296.4 \pm 126.4	154.0 \pm 92.7
	Diptera	13.4 \pm 55.4	50.3 \pm 61.4	134.9 \pm 43.5	189.3 \pm 72.6
	Coleoptera	15.9 \pm 33.0	53.6 \pm 35.4	79.7 \pm 31.0	25.9 \pm 22.9
	Blattodea	10.9 \pm 7.8	15.3 \pm 4.6	10.9 \pm 12.9	27.2 \pm 6.0
	Hymenoptera	16.7 \pm 12.5	12.3 \pm 3.1	12.9 \pm 10.2	8.0 \pm 9.5
	Orthoptera	0.9 \pm 5.0	8.6 \pm 7.5	5.3 \pm 4.4	7.3 \pm 4.0
	Neuroptera	3.1 \pm 2.0	3.7 \pm 2.5	2.3 \pm 4.2	2.0 \pm 0.8
	Larva	0.2 \pm 0.8	0.9 \pm 0.5	1.5 \pm 0.8	1.6 \pm 0.8

¹ CF = continuous forest.

infrequently captured taxa, I used a two-way ANOVA on ranks within sites. Habitat was close to significant for total biomass ($P = 0.06$) and significant for Diptera ($P < 0.01$), Neuroptera ($P = 0.03$), and Larva ($P < 0.01$). In general, biomass in secondary forest was similar to that in 1-ha fragments and lower than that in CF edge and CF (table 6-8).

Rainfall was not a significant covariate in the one-way block analysis on total biomass, either when matrix habitat was excluded, or when both matrix and CF habitats were excluded ($P > 0.46$). Similarly, multivariate tests of the biomass of frequently caught taxa were not significant with rainfall as a covariate ($P > 0.44$). In a test including all five habitats (sites 2 and 3 only), rainfall was not a significant covariate for total biomass, or for biomass of each of the five frequently captured taxa.

Weighted simple correlation between insect biomass and vegetation variables yielded the following significant relationships: (i) Coleoptera biomass increased with increasing understory variance and grain and (ii) Hymenoptera biomass increased with increasing understory thickness and increasing overstory variance in foliage thickness (table 6-9). The first canonical correlation corroborated the first relationship; "insect" canonical variable one was highly correlated with Coleoptera biomass and the first "vegetation" variable was correlated with understory foliage variance and grain. The second insect canonical variable contrasted Hymenoptera biomass with total biomass and the biomass of the other taxa. Hymenoptera biomass increased with increasing understory thickness, decreasing overstory thickness, and increasing understory grain, whereas for other taxa and for total insect

Table 6-8. As table 6-7 except that data are from the two sites where matrix habitat was secondary forest.

Taxon	Habitat				
	Secondary forest	1-ha fragment	10-ha fragment	CP ¹ edge	CP
Total	269.8 ± 35.2	232.2 ± 70.7	329.8 ± 42.1	724.7 ± 183.5	590.1 ± 105.8
Lepidoptera	185.2 ± 40.3	179.4 ± 24.0	151.4 ± 58.3	350.8 ± 191.5	215.7 ± 149.4
Diptera	43.5 ± 3.6	9.7 ± 41.7	47.6 ± 36.6	210.9 ± 9.6	278.4 ± 65.1
Coleoptera	23.4 ± 11.3	17.3 ± 30.6	88.3 ± 60.8	130.3 ± 4.5	36.7 ± 23.4
Blattodea	8.6 ± 1.6	13.9 ± 11.5	20.1 ± 3.3	14.4 ± 16.7	32.2 ± 3.5
Hymenoptera	7.4 ± 0.6	9.6 ± 7.2	8.4 ± 0.6	8.4 ± 1.9	12.2 ± 6.5
Orthoptera	1.2 ± 3.0	1.9 ± 4.3	12.6 ± 12.8	4.1 ± 2.9	10.3 ± 5.4
Neuroptera	0.1 ± 1.1	0.1 ± 1.1	0.4 ± 0.9	3.6 ± 2.9	1.0 ± 0.3
Larva	0.5 ± 0.8	0.4 ± 0.8	1.0 ± 0.1	2.1 ± 1.4	2.9 ± 0.4

¹ CP = continuous forest.

Table 6-9. As table 6-6 except that correlations are for insect biomass/arboreal pitfall trapnight.

	Understory thickness	Overstory thickness	Understory residual variance	Overstory residual variance	Understory residual surface area	Overstory residual surface area	Insect CV ¹ 1	Insect CV 2
Total biomass	-0.12	0.31	0.32	0.25	0.14	-0.24	0.21	0.64
Blattodea	-0.22	0.41	0.23	0.09	-0.06	-0.02	0.25	0.48
Coleoptera	0.00	0.26	0.68**	0.12	0.26	-0.55*	0.67	0.61
Diptera	-0.39	0.37	0.11	-0.05	0.19	0.06	-0.13	0.59
Hymenoptera	0.58**	-0.30	-0.03	0.50*	-0.35	-0.08	0.28	-0.63
Lepidoptera	0.05	0.13	0.20	0.38	0.01	-0.23	0.19	0.40
Vegetation CV 1	0.41	0.18	0.68	0.31	-0.21	-0.41	0.96	-
Vegetation CV 2	-0.59	0.53	0.42	-0.21	0.58	-0.34	-	0.76

¹ CV = Canonical variable.

* $p < 0.05$.

** $p < 0.01$.

biomass, the opposite was true. The second canonical correlation thus described differences in biomass observed among the various habitats; biomass of Hymenoptera increased with increased proportions of edge in a habitat, whereas the opposite was true for other taxa and for total biomass (figure 6-10). With understory thickness as a covariate, there was little evidence to suggest that isolated and non-isolated habitats differed (figure 6-10A, $P = 0.32$; figure 6-10B, $P = 0.76$).

Discussion

Fragmentation of once continuous forest had a profound effect on the spatial variability of insect biomass in this study. Evidence of significant differences among habitats was obtained for: total biomass from understory tangle-traps, Dermaptera, Homoptera, and Lepidoptera biomass from terrestrial pitfall traps, and total biomass from arboreal pitfall traps. The abundance of most taxa captured in arboreal pitfall traps varied with habitat type, but significant differences among habitats was obtained only for Diptera, Larva, and Neuroptera.

Perhaps most importantly, insect biomass varied among primary forest habitats as a function of the proportion of edge-modified forest in a habitat. Recall that the average distance from a 1-ha sub-sampling unit to the matrix interface decreased in the sequence: CF, CF edge, 10-ha fragment, and 1-ha fragment, hence the proportion of edge-modified forest in a habitat presumably increased in the same sequence. In most cases, when significant variation in insect biomass was found among habitats, habitat-specific means also could be ranked in this sequence (as tested by isotonic regression). This was true for total biomass from understory tangle-traps, Dermaptera biomass from terrestrial

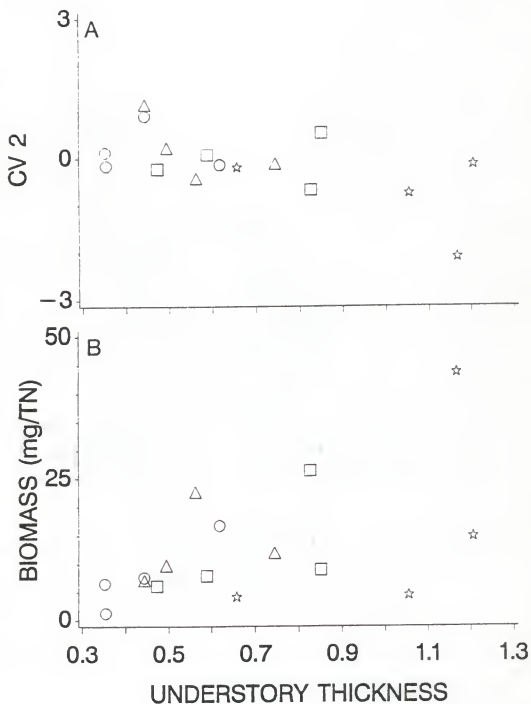


Figure 6-10. Insect canonical variable 2 (Part A) and Hymenoptera biomass (Part B) from arboreal pitfall traps vs understory foliage thickness. See text for biomass estimation and definitions of the canonical variable and understory thickness.

pitfall traps, and total and Diptera biomass from arboreal pitfall traps. Moreover, variation in biomass of these taxa was correlated with understory and/or overstory thickness; vegetation variables that appeared to vary according to a simple edge model (Chapter 5). Simple correlation between total and Diptera biomass from arboreal pitfalls and understory or overstory thickness was not significant; however, in the canonical correlation analysis, total biomass and the biomass of all taxa except Hymenoptera correlated highly and positively with understory thickness and negatively with overstory thickness.

With understory or overstory thickness as a covariate, I found little evidence of differences in biomass between "isolated" primary forest (1- and 10-ha fragments) and "non-isolated" primary forest (CF edge and CP), a result of theoretical importance. Attempts to apply island biogeographical theory (MacArthur and Wilson 1967) to habitat "islands" are inevitably confounded by the action (and perhaps interaction) of both edge effects and immigration/extinction in structuring fragment communities (see Chapter 5). The recent study by Webb and Hopkins (1984, see also Hopkins and Webb 1984) is illustrative. Contrary to predictions from island biogeographic theory (MacArthur and Wilson 1967), these authors found that as the area of heathland patches decreased, beetle diversity and abundance increased. They attributed this result to edge effects from a richer and more abundant beetle community in the surrounding matrix. However, for species "typical" of heathland, diversity decreased with island area, as predicted by island theory. These authors also compared communities at the edge of large patches with those at the center. Total beetle diversity and abundance

was greater at the edge, whereas heathland species diversity was greater at the center.

The measurement of insect biomass in CF edge in the present experiment provided information critical to tests of "null" models of edge effects, i.e. models of edge effects independent of island effects. CF edge and fragment edges share many environmental features in common, however the potential for immigration of CF species may differ radically between the two. CF edge therefore provides a control for changes in community structure resulting solely from environmental changes. The more closely environmental conditions along the edge approximate those in fragments, the more effective the control will be. In the present study, insect biomass in primary forest fragments could be predicted from vegetation structure in continuous forest and its edge (the "mainland"), hence I found little reason for invoking island processes such as density compensation (MacArthur et al. 1972, Case 1975, Case et al. 1979), differential immigration/extinction (MacArthur and Wilson 1967), or "fence" effects (Krebs et al. 1969) to explain variation in insect biomass among habitats. It may not always be possible to find habitat features correlated with the abundances of taxa of interest (or correlations obtained may be irrelevant); however, if taxon abundance in "mainland" communities, or in large islands, is measured at various distances from matrix habitat, "null" edge models can be constructed (see, for example, Chapter 5). Unfortunately, in the present study I did not measure insect biomass in CF edge as a function of distance from the edge. These models offer additional hope for extricating island processes from edge processes. In the study by Webb and Hopkins (1984)

for example, measurements in very large heath patches of the increase in heath species diversity with increasing distance from the edge could be used to predict "null" diversities in small patches.

Contrary to the predicted ranking, both terrestrial and arboreal pitfall traps captured more Lepidoptera in CF edge than in other habitats. However, the result was significant only for terrestrial pitfall traps (which captured the taxon infrequently) and not for arboreal pitfall traps (which captured huge numbers). One explanation of the possible greater abundance in CF edge may be that the CF and matrix Lepidopteran faunas are distinct, and that the CF fauna has largely disappeared from fragments. High biomass in CF edge might represent overflow from both CF and matrix communities. Isotonic regression also failed to support the hypothesis of ranked abundances of Homoptera; however, the assumption of normality was severely violated, rendering the test suspect. Inspection of means in table 6-5 generally supported the ranking: CF, CF edge, 10-ha fragment, 1-ha fragment.

It is important to note that the trapping methods I used provided only relative measures of abundance, and that they captured a biased sample of the actual arthropod community. In particular, the use of bait as an attractant allowed the possibility of an additional source of error (Southwood 1978). In addition, variation in capture rates will reflect variation both in insect density and in activity levels. However, captures rates by vertebrate predators also may depend on both densities and activity levels of prey (Redford and Dorea 1984), hence a distinction between increases in relative abundance due to increases in

absolute abundance and increased activity levels may be largely irrelevant.

The few data available indicate that insect biomass is greater in the overstory of tropical forests than in the understory (Wolda 1982), a result corroborated by a comparison of overstory and understory tangle-traps in the present experiment. Also, biomass from arboreal pitfall traps in continuous forest was nearly four times that from terrestrial pitfall traps, although comparisons of these very different trap types is suspect. The net effect of fragmentation appeared to be an increase in the proportion of insect biomass close to the ground; biomass from understory tangle-traps in fragments was greater than that from traps in CF, whereas the opposite was true for arboreal pitfall traps. This change in the spatial distribution of insect prey may have important consequences for vertebrate predators, and at least in part may account for more frequent observations of canopy bird and mammal species close to the ground in forest fragments (Bierregaard and Lovejoy 1989, Malcolm 1988, Chapter 4). If insectivorous species are resource limited, then the shift in prey distributions in fragments may eventually lead to decreases in the densities of canopy predators, and to a superabundant understory predator fauna.

Differences in the distribution of prey biomass among habitats also appear to be correlated with other characteristics of the insect community relevant to an insect predator. For example, Winnett-Murray (1986) conducted visual sampling of understory insects in several habitats in Costa Rica, including pasture and early successional scrub, woodland edge, and woodland. As in the present study, she found that

biomass was highest in open habitats, intermediate in woodland edges, and least in woodland. In addition, she found that several estimates of temporal and spatial variability of insect populations were higher in forest than in more open habitats, and that insects in the forest were more likely to be in concealed microhabitats. She reasoned that predators in more open habitats would be more likely to find not only more prey, but more prey of the same types from place to place and from month to month. Klein (1989) noted that changes in the insect community may lead to "ripple effects". For example, a depauperate dung and carrion beetle community could lead to second-order changes in mite dispersal, which may in turn trigger third-order changes in populations of dung- and carrion-breeding flies.

Edge correlated increases in the biomass of understory insect taxa in fragments and along the edge of CF may in part result from overflow from the adjacent matrix habitat, and in part from localized increases in populations within the forest. A more abundant fauna close to the ground in open habitats than in other habitats was found in the present study and has been reported in several other studies (Janzen 1973, Adis 1982, Winnett-Murray 1986). Increased abundance in the matrix is perhaps in response to the increased volume and productivity of understory vegetation and to an increased proportion of actively growing tissues (Janzen 1973). Similarly, increases within the forest may be due to increased foliage productivity close to the edge. The importance of the two, i.e. external versus in situ increases, most likely varies from taxon to taxon. Data from understory tangle-traps in general suggested that increases along the edge resulted in large part from in

situ increases; despite large differences in biomass in the two types of matrix habitat, there was little evidence of a matrix effect among non-matrix habitats, or of matrix-by-habitat interaction. In contrast, the matrix effect was significant for Diptera and Hymenoptera from terrestrial pitfall traps, but matrix-by-habitat interaction was not, indicating greater biomass in primary forest abutting pasture sites, and in the pastures themselves, than in primary forest abutting secondary forest, and in the secondary forests themselves. These matrix effects presumably resulted from overflow of populations in the matrix into the adjacent forest. More mobile taxa will presumably overflow more than less mobile taxa. Also, one might expect in situ production to decrease as taxon size increases. For example, a 60-m wide belt of increased insect abundance in continuous forest close along the edge would probably only trivially increase the edge populations of most insectivorous mammals.

Similarly, a less abundant overstory insect fauna along edges may result in part from decreased production of insects at the edge and in part from fewer arboreal insects in the adjacent matrix. Decreased production at the edge is expected from a decreased resource base; wind damage results in less foliage at the edge. If overflow from adjacent "intact" canopy is important, then one might expect relatively greater edge populations in CF edge than in fragment edge, a result not predicted by simple edge models (Chapter 5). In general, recolonization by overstory species seems much less likely in fragments than in CF edge.

Insect abundance in continuous forest has been observed to peak in the early wet season (Robinson and Robinson 1970, Willis 1976, Wolda 1978, Gradwohl and Greenberg 1982, Levings and Windsor 1982, Smythe 1982, Wolda 1982, Winnett-Murray 1986) during the period of maximum leaf flush (Smythe 1982, Wolda 1982), although dry season peaks can apparently result from influxes from open habitats (Winnett-Murray 1986) and the timing of seasonal peaks may vary with the severity of the dry season (Janzen 1973). As Wolda (1978) notes, however, variation between years can be greater than variation within years. In the present experiment, variation in insect biomass from site to site and from habitat to habitat within a site appeared to be of greater magnitude than variation from season to season. I obtained some evidence of biomass increases in the late dry season (tangle-traps) and early wet season (pitfall traps) of 1988; however, the present experiment was poorly designed to investigate seasonal effects. Habitats at a site were sampled infrequently, and each trap type was set for, at most, slightly more than one year.

In conclusion, fragmentation of tropical rainforest appears to have a profound effect on insect biomass. Understory biomass increased in edge-modified forest, whereas arboreal biomass decreased, and these edge effects could be predicted from the structure of the forest vegetation along the edge. Extensive habitat/resource changes along the edges of fragments will likely have important consequences for ecosystem function within fragments, and will complicate attempts to apply island biogeography theory to the study of tropical forest fragments.

CHAPTER 7
THE SMALL MAMMALS OF TROPICAL FOREST FRAGMENTS II: PROCESS

Introduction

Attempts to test the utility of island biogeography theory (MacArthur and Wilson 1967) in predicting insular community structure are complicated by covariation between island area and habitat characteristics. As MacArthur and Wilson (1967) note, the carrying capacity of an island, a parameter of central importance in models of stochastic extinction (MacArthur and Wilson 1967, Goel and Richter-Dyn 1974, Wright and Hubbell 1983), will likely be determined not only by area, but by the quantity and quality of available habitat. It is well known that species richness is often correlated with measures of habitat diversity (references in Simberloff 1974, Dueser and Brown 1980). As islands decrease in size, habitat diversity often decreases, and several authors have argued that the depauperate nature of island communities results in part from a lack of suitable niche space (eg. Bowman 1961, Johnson et al. 1968, McNab 1971, Dueser and Brown 1980, Simberloff and Abele 1982, Jarvinen and Haila 1984, Wilbur and Travis 1984, Stevens 1986, Zimmerman and Bierregaard 1986). In many cases, habitat characteristics and resource abundances on islands have been found to differ from those on the mainland (Allan et al. 1973, Janzen 1973, Abbott 1976, Morse 1971, 1973), but few studies have compared habitat quality between mainland and island sites (Diamond 1975b). If proximity

to the edge of an island influences habitat quality (so called "edge effects"), as must often be the case, the inevitable result is that changes in habitat quality accompany changes in island size. Smaller islands have a greater perimeter:area ratio, and hence have relatively more edge-modified habitat. Edge effects may be particularly important in the case of habitat "islands", where the habitat surrounding a given patch is suitable for many plant and animal species that may "invade" the edges of the patches, thereby influencing communities in the patches. In forest fragments, edge and interior conditions often differ markedly from each other, and a consideration of perimeter:area ratios and other simple models of edge effects have proven useful in understanding the relation between community structure and fragment size (Gates and Gysel 1978, Levenson 1981, Ranney et al. 1981, Whitcomb et al. 1981, Lovejoy et al. 1986, Yahner 1988). Determination of habitat island resource characteristics and carrying capacities are required in order to test the role of immigration and extinction in structuring island or fragment communities.

In the central Amazon, fragmentation of the rainforest leads to profound changes in the communities of birds (Bierregaard and Lovejoy 1988, 1989), insects (Klein 1989, Chapter 6), primates (Schwarzkopf and Rylands 1989) and small mammals (Chapter 4), and some of the variability in community structure among small (1- and 10-ha) forest fragments can be attributed to fragment size. At the same time, proximity to the forest edge leads to pervasive environmental changes within the fragments; temperature close to the edge increases, humidity decreases, the thickness of understory (0 - 5 m height) vegetation increases,

canopy tree mortality increases, and the thickness of overstory (10 - 30 m) vegetation decreases (Lovejoy et al. 1984, 1986, Kapos 1989, Chapter 5). Also, understory insect biomass increases and overstory insect biomass decreases with increasing proximity to an edge (Chapter 6). In Chapter 4, I argued that these edge-induced changes in the habitat/resource base of fragments might account for the greater abundance and richness of the small mammals in fragments than in continuous forest, independently of any island-biogeography effects per se. On the other hand, the rarity of some species in fragments may be attributable to reduced immigration and an increased likelihood of population extinction, as predicted by island theory, although edge-induced loss of suitable habitat is a possible alternative explanation.

Herein, I use an experimental approach to test whether differential immigration/extinction is an important process in structuring the small mammal communities of these small tropical forest fragments. I reasoned that the simplest "null" hypothesis (i.e. a hypothesis that accounted for differences in small mammal communities between forest fragments and continuous forest irrespective of insularization per se) was that small mammal community structure varied solely as a function of (i) proximity to matrix habitat and (ii) variation in the habitat/resource base among habitats. In one experiment, I used the edge of continuous forest as a control of edge-induced modifications of community structure. In two other experiments, correlations between community structure in fragments and in the surrounding matrix were examined.

Materials and Methods

A general description of the study site is provided in Chapter 4.

Experiment 1: The Edge of Continuous Forest

In each of four blocks, small mammals were trapped in 1-ha (100 by 100 m) sub-sampling units in four major habitat types: i) continuous forest (CF), ii) CF edge, iii) 10-ha fragment, and iv) 1-ha fragment. In total, 16 units in CF (four per block), 11 units in CF edge (two or three per block), 16 units in a 10-ha fragments (four per fragment), and four units in 1-ha fragments were sampled (see figures 6-2 and 6-3). Units in CF edge were censused in the same way as units in the other habitats (see Chapter 4); 12 terrestrial and 12 arboreal trap-stations were set for eight consecutive nights during each of three censuses. In all units but one (fragment 1112), a trap-station consisted of a Tomahawk and a Sherman live-trap (see Chapter 4).

I tested whether differences between the small mammal communities of continuous forest and fragments could be attributed solely to: i) differences in proximity to clearcut, and ii) differences in habitat/resource levels. If variation in habitat/resource levels among habitats is edge-driven (i.e. is a function of proximity to clearcut), then the two possibilities are equivalent. Notice that in both hypotheses, the degree to which a habitat was isolated from neighboring primary forest was immaterial; if a fragment site and a continuous forest site were equally proximate to clearcut (hypothesis 1), or if their habitat/resource states were identical (hypothesis 2), then their small mammal communities were expected to be identical.

Proximity to clearcut varied systematically among habitats; the average distance from a 1-ha unit to clearcut decreased in the sequence: CF, CF edge, 10-ha fragment, 1-ha fragment. Units in CF were at least 400 m from clearcut, units in CF edge abutted clearcut on one side, units in 10-ha fragments abutted clearcut on one side (five units), two sides (nine units), or were in the fragment interior (two units), and units in 1-ha fragments abutted clearcut on four sides. Thus, a simple prediction from the first hypothesis was that it would be possible to rank community characteristics in the same sequence. I standardized effort within each block-by-habitat combination by averaging across the 1-ha units, and computed the abundance of each mammalian taxon, total abundance, terrestrial biomass, and arboreal biomass (see Chapter 4, phase 2, for additional details). Abundances from the four habitats were ranked within a site, and statistical tests were performed on the ranks. For biomass, I used a randomized-block ANOVA. Two statistical tests were used to test whether the observed ranks were in the predicted sequence. First, I used Duncan's multiple range test to test whether any incorrect rankings among means from the four habitats were significant. Second, I used isotonic regression (Gaines and Rice 1990), which is similar to ANOVA, except that the alternative hypothesis is directional. The null hypothesis of no habitat effect was tested against one of two alternatives: (i) $\mu_{CF} \leq \mu_{CF \text{ Edge}} \leq \mu_{10\text{-ha}} \leq \mu_{1\text{-ha}}$ (with at least one strict inequality) or (ii) $\mu_{CF} \geq \mu_{CF \text{ Edge}} \geq \mu_{10\text{-ha}} \geq \mu_{1\text{-ha}}$ (with at least one strict inequality). According to the prediction, any differences from Duncan's test would also be significant when tested by

isotonic regression. The choice of alternative hypothesis was made a posteriori, so the test was a liberal one.

In a second test of the first hypothesis, a simple model of edge effects was evaluated. According to the model, the total "edge effect" at a point in primary forest some distance from clearcut is the sum of "point" edge effects along the clearcut/forest edge (see Chapter 5 for details). The point edge effect is assumed to be a maximum (e_0) at the edge and to decline linearly with increasing distance from the edge, such that at D_{max} units from the edge and beyond, the point edge effect is zero. The total edge effect at a point is obtained by integration of this linear function over all edge points within D_{max} units of the point. For example, as a function of the distance (D) to the edge, the total edge effect (E) along a line perpendicular to a linear edge is

$$(1) \quad E(D) = k + 2 \int_D^{D_{\text{max}}} e_0 (1 - [D / D_{\text{max}}]) dD$$

$$= k + e_0 (D_{\text{max}} - 2D + [D^2 / D_{\text{max}}])$$

In Chapter 5, I fitted this equation to data obtained along linear edges and used the resulting parameter estimates to predict edge effects in 10- and 1-ha fragments. I used the same method here. Unfortunately, only two species (Marmosa murina and Monodelphis brevicaudata) provided sufficient data to fit equation (1). Other species were rarely captured in CF edge.

In each 1-ha unit in CF edge, data from the two six-station traplines running perpendicular to the edge were used. I divided the six traps per trapline into three groups: the two traps closest to the edge, the two in the middle of the trapline, and the two farthest from the edge, and for each group combined all data from CF edge and calculated the mean abundance of each taxon and the mean distance from the trap-stations to the edge. Equation (1) was fitted to the three points obtained, except that k was assumed a priori to equal the abundance observed in CF (hence only two parameters, D_{III} and a_0 were estimated by the fit). Given the three parameter estimates, and the exact locations of trap-stations within fragments, I could calculate an average expected abundance of each of the two species in the two sizes of fragments. Expected and observed abundances were compared graphically.

To test the second hypothesis, namely that small mammal community structure depended solely on habitat/resource levels, I used vertical stratification of foliage as a measure of habitat/resource levels. At each point on a 10 m by 10 m grid extending 10 m outside each 1-ha unit (169 points), vegetation was scored in six height intervals and scores were recoded so that they represented vegetation thickness (see Chapter 6). From these data, I derived two variables for each unit: understory thickness (the mean of the summed thickness scores in strata 1 and 2 [0 - 5 m]), and overstory thickness (the mean of the summed thickness scores in strata 4 and 5 [10 - 30 m]). Measurements were averaged across the units within a block-by-habitat combination. The use of only two variables to represent the "habitat/resource base" is simplistic;

however, given the small sample sizes (only four replicates of each of the four habitat types), I wished to keep the number of independent variables small. Also, these two measurements (or ones similar to them) have been found to correlate with mammal community structure (August 1983, Nitikman and Mares 1987, Fonseca 1988, Stallings 1988), and to correlate with other habitat features important to small mammals, including the quantity of fallen timber (unpublished data). I reasoned that the understory and overstory measurements would also successfully measure tree-fall abundance, a quantity that in previous work (unpublished) in CF was correlated with the abundance of some mammal taxa, because tree-falls result in decreased overstory density and, with time, in increased understory density. Insect biomass (a major food resource for small mammals) also correlates with understory and overstory thickness (Chapter 6), and I assumed that other resource variables would as well.

I defined two habitat groups: non-isolated primary forest (CF and CF edge) and isolated forest (10- and 1-ha fragments), and tested for correspondence between the two in the relationships between small mammal abundance and vegetation thickness. According to the second hypothesis, any relationship between mammal abundance and vegetation thickness evident in one group should be continuous with the relationship in the other group, i.e. given equal vegetation values in the two groups, and some relationship between vegetation structure and mammal community structure within a group, the mammal community should be identical in the two groups. I used analysis of covariance (ANCOVA) to test for differences between non-isolated and isolated forest mammal abundance,

with vegetation thickness as a covariate. In the special case of a linear relationship, the hypothesis of equal mammal abundance given equal vegetation was equivalent to the null hypothesis of no isolation (= group) effect in the ANCOVA. A significant isolation effect in the ANCOVA would thus lead to rejection of the second hypothesis. Significant interaction (i.e. a slope effect) could indicate a non-linear but continuous relationship, or a discontinuity between the two treatment groups. To derive a multivariate test of the hypothesis, I used canonical covariance weighted by the number of 1-ha units sampled in a habitat. Canonical correlation finds a linear combination (canonical variable) of each of the two sets of variables (mammal species' abundances and vegetation thickness) such that the correlation between the two canonical variables is maximized (Luginbuhl and Schlotzhauer 1987). I reasoned that if the second hypothesis was true, canonical axes of correlation evident among non-isolated sites would predict the small mammal communities of isolated sites and *vice versa*. To test this prediction, I performed separate canonical analyses on the non-isolated sites and on the isolated sites. The resulting mammal and vegetation coefficients were used to calculate the positions of the excluded sites (respectively, the isolated and the non-isolated sites) in the same canonical space. According to the hypothesis, sites not included in the canonical analysis would fall on the axis of correlation defined from the other sites.

Experiment 2: Matrix Habitat

In addition to the four major habitat types discussed above, in each block (= site) I censused the matrix surrounding the fragments.

Matrix habitat was censused for eight consecutive nights three times during October 1987 - March 1988, and trap-stations were arranged in 1-ha sub-sampling units (see Chapter 6). Two or three units were sampled per site (see figure 6-3). Matrix habitat at two of the sites (1 and 4) was pasture. At site 1, forest surrounding the fragments was clearcut in the dry season of 1980 and burned, and thereafter some clearcut areas were maintained as pasture; others were abandoned to secondary forest. Most of the secondary forest close to the fragments was cut and burned in the dry season of 1987, just prior to the study. Forest at site 4 was clearcut and burned in the dry season of 1984; thereafter clearcut areas were maintained as pasture by periodic removal of secondary vegetation. Secondary vegetation had been most recently cut and burned in the dry season of 1987. Matrix habitat at the other two sites (2 and 3) was secondary forest. Primary forest at these sites was clearcut in the dry season of 1983, but never burned or recut. Secondary forest was 4 - 4.5 yr old when first censused for small mammals, and was approximately 12 m high. In pasture sites, I used only terrestrial trap-stations, whereas in secondary forest sites, both terrestrial and arboreal (approximately 1.8 m high) trap-stations were used.

My purposes were two fold. First, unlike islands, forest fragments are surrounded by an environment that is potentially habitable by terrestrial mammals. Clearly, if a species is equally or more abundant in matrix than in CF, matrix habitat cannot be viewed as a barrier to immigration from CF into fragments. We should expect "island effects" only for species less abundant in matrix than in CF. Abundances were

compared between matrix and CF by use of median tests and t -tests. Of course, species may be locally abundant in matrix close to CF, but decrease in abundance with increasing distance from CF. Therefore, at three sites (1, 2, and 4), units were 150, 350, and 550 m from CF, and at site 3, units were 150 and 350 m from a 100 ha fragment (see figure 6-3). To test whether small mammal community structure in the matrix varied with distance from CF, I looked for correspondence between within-site rankings of mammalian abundance and within-site distance rankings.

Secondly, if mammalian abundance in primary forest edge is determined in part by abundance in the matrix, variation in mammalian abundance among matrix sites will result in variation in abundance among edges. Because small fragments include proportionally more edge-modified habitat than large fragments, abundance in the matrix should most closely approximate abundance in small fragments. To examine this hypothesis, I first tested whether small mammal abundance varied among matrix sites. The most obvious feature that varied among matrix sites was vegetation volume. I therefore correlated total mammalian abundance with total vegetation thickness, and used principal component analysis to examine correlations between species abundance patterns and vegetation thickness. Vegetation thickness in the matrix was measured as in other habitats, except that only with 36 points were sampled per unit (see Chapter 6). As a measure of vegetation volume in a unit, I took the mean of the summed thickness scores in strata 1 - 6. To compare the small mammal communities in matrix with those in the

abutting primary forest, I regressed total small mammal abundance in fragments and CF edge against total abundance in the surrounding matrix.

Experiment 3: Immigration

Two experiments were designed to obtain estimates of the rate at which small mammals immigrated into forest fragments. In one experiment, I repeatedly defaunated a 1-ha fragment (fragment 1112 at site 2) and simultaneously monitored small mammal abundances in the secondary forest surrounding the fragment. The reserve was defaunated (=censused) three times, at intervals of 6 or 7 mo. During a first trapping session of a census, traps were set and configured as described previously; 12 terrestrial and 12 arboreal trap-stations (arranged in two traplines) set for 8 nights. Because of extensive damage to the canopy of the fragment in a windstorm in 1987, only seven of the arboreal stations were at a height of approximately 14 m; the remaining five stations were at approximately 1.8 m. Each trap-station consisted of two 9 by 15 cm steel snap-traps, baited with banana, raisins, and peanut butter. Terrestrial traps were 2 - 4 m apart, whereas arboreal traps were 30 cm apart. Three to five days later, I set traps for an additional 8 - 10 consecutive nights. In addition to the original two traplines, during this second session I set three more: one between the original two, and one along each of the reserve edges parallel to the original traplines. Thus, 30 terrestrial and 30 arboreal trap-stations were used, configured in a grid with 5 rows and 6 columns (row spacing was 25 m, column spacing was 20 m). During this second session, each terrestrial and arboreal trap-station consisted of only one snap-trap,

and arboreal snap-traps on the additional lines were at 1.8 m (arboreal traps on the original lines were at the same height in the two sessions). Simultaneously with the second session of trapping, I used snap-traps to census mammals in the secondary forest surrounding the reserve. Trap-stations were spaced at 20 m intervals in lines. Each trap-station had one terrestrial and one arboreal (1.8 m height) snap-trap baited with banana, raisins, and peanut butter, and was set for eight consecutive nights. In total, 66 trap-stations in secondary forest were set per census. All traplines but one were perpendicular to CF, and traps averaged 220 m from CF (range: 0 - 680 m). Traps were at the same location from census to census. Evidence of differential recolonization among taxa was obtained by comparing abundances in census 1 with those in the subsequent two censuses. Only one reserve was defaunated, hence statistical tests were not performed.

In a second experiment, I examined the extent to which matrix habitat presented a barrier to small mammal movements by contrasting homing of individuals through matrix and through CF. In primary forest along one side of a long (2.3 km), narrow (150 - 350 m wide) strip of pasture, I set 107 terrestrial trap-stations, 45 understory trap-stations (1.8 m height), and 45 arboreal trap-stations (14 m height) for 8 or 9 consecutive nights in June 1988. Traps were arranged in four traplines so that the distance from a trap-station to forest on the other side of the strip was approximately constant within a trapline (distances were 250, 300, 310, and 360 m) (figure 7-1). Captures were fitted with an FM transmitter and were released the day they were captured either: i) in primary forest on the other side of the strip, or

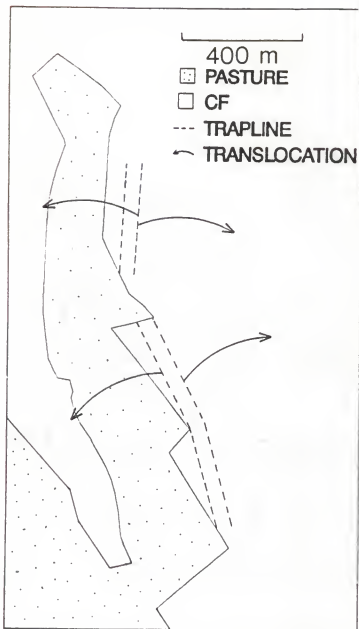


Figure 7-1. A narrow strip of pasture used in experiment three to contrast homing of individuals through pasture with homing through contiguous forest (CF). Individuals captured on the traplines were fitted with a radio-collar and released in forest on the other side of the strip, or an equal distance away, but in forest on the same side of the strip.

ii) an equal distance away but in primary forest on the same side of the strip (see figure 7-1 for examples of release sites). Thereafter, I attempted to locate each radio-tagged animal once nightly between 2000 and 2400 h. If an animal released on the other side of the strip was not found near its release point or near its capture location, I searched for it along the entire perimeter of the pasture. However, if an animal released on the same side of the strip was not found close to one of the traplines, I rarely searched for it.

Results

Experiment 1: The Edge of Continuous Forest

Total abundance, terrestrial and arboreal biomass, and abundances of each of the taxa captured in the four habitats are listed in table 7-1. Of the 19 taxa, eight provided general support for the predicted ranking: seven were less abundant in CF than in 1-ha fragments, while abundances in CF edge and 10-ha fragments were intermediate, and one (Caluromys philander) was more abundant in CF than in 1-ha fragments, while abundances in CF edge and 10-ha fragments were intermediate. Significant variation in means among habitats was indicated for six taxa (Duncan's test). The ranking of only one (Mesomys hispidus) was contrary to that predicted; this species was significantly more abundant in 10-ha fragments than in either CF edge or 1-ha fragments. Also, except for M. hispidus, when Duncan's test was significant, isotonic regression was significant, i.e. the hypothesis of no treatment effect was rejected in favor of one of the one-sided alternatives. Variation in terrestrial biomass and total abundance among treatments was in the

Table 7-1. Mean number of individuals per 1-ha sub-sampling unit averaged (\pm SD) across four sites. At each site, four units in continuous forest, two or three units in continuous forest edge, four units in a 10-ha forest fragments, and one unit in a 1-ha forest fragments were sampled three times for eight consecutive nights during October 1987 - March 1989. One unit equalled 12 terrestrial trap-stations and 12 overstory trap-stations.

Taxon	Continuous forest ($\bar{x} = 4$)	Continuous forest edge ($\bar{x} = 4$)	10-ha fragment ($\bar{x} = 4$)	1-ha fragment ($\bar{x} = 4$)	Probability ¹
<i>Harmosa cinerea</i>	0.500 \pm 0.180	0.764 \pm 0.450	1.104 \pm 0.878	0.750 \pm 0.167	0.37
<i>H. parvirens</i>	0	0.042 \pm 0.083	0.125 \pm 0.144	0.083 \pm 0.167	-
<i>H. murina</i>	0.021 \pm 0.042 ^a	0.500 \pm 0.264 ^b	0.333 \pm 0.245 ^{a,b}	1.750 \pm 2.872 ^b	0.06
<i>Monodelphis breviceaudata</i>	0.104 \pm 0.208 ^a	0.486 \pm 0.448 ^{a,b}	0.229 \pm 0.088 ^{a,b}	0.833 \pm 0.839 ^b	0.16
<i>Didelphis marsupialis</i>	0.229 \pm 0.356 ^{a,b}	0.111 \pm 0.091 ^{a,b}	0.208 \pm 0.228 ^a	0 ^b	0.12
<i>Philander opossum</i>	0	0	0.146 \pm 0.292	0.167 \pm 0.333	-
<i>Metachirus anticandidatus</i>	0.021 \pm 0.042	0.028 \pm 0.056	0.042 \pm 0.048	0.083 \pm 0.167	-
<i>Caluromys philander</i>	0.958 \pm 0.210 ^a	0.236 \pm 0.233 ^b	0.313 \pm 0.185 ^b	0 ^c	<0.01
<i>C. lanatus</i>	0	0.125 \pm 0.250	0.021 \pm 0.042	0.083 \pm 0.167	-
<i>Oryzomys capito</i>	0.146 \pm 0.080	0.083 \pm 0.106	0.083 \pm 0.096	0.417 \pm 0.833	0.86
<i>O. macconnelli</i>	0.104 \pm 0.158	0.125 \pm 0.095	0.021 \pm 0.042	0.083 \pm 0.167	0.51
<i>Oecomys paricola</i>	0.042 \pm 0.048	0.250 \pm 0.356	0.250 \pm 0.340	0.583 \pm 0.419	0.43
<i>O. bicolor</i>	0.021 \pm 0.042	0	0.146 \pm 0.197	0	-
<i>Neacomys guianae</i>	0	0.139 \pm 0.167	0.063 \pm 0.042	0.250 \pm 0.500	0.22
<i>Rhipidomys mastacalis</i>	0.354 \pm 0.443 ^{a,b}	0.181 \pm 0.189 ^b	1.271 \pm 0.878 ^a	1.167 \pm 1.262 ^a	0.03
<i>Proechimys</i> spp.	0.313 \pm 0.185	0.250 \pm 0.106	0.479 \pm 0.315	0.333 \pm 0.272	0.53
<i>Neotoma hispidus</i>	0.021 \pm 0.042 ^a	0.028 \pm 0.056 ^a	0.208 \pm 0.160 ^b	0 ^a	0.01
<i>Isothrix pagurus</i>	0.021 \pm 0.042	0	0.021 \pm 0.042	0	-
Total number of individuals	2.9 \pm 0.8	3.3 \pm 1.5	5.1 \pm 3.0	6.6 \pm 4.5	0.17
Terrestrial biomass ² (g/ha)	58 \pm 39 ^a	98 \pm 23 ^{a,b}	105 \pm 61 ^{a,b}	151 \pm 100 ^b	0.09
Arboreal biomass ² (g/ha)	68 \pm 13	45 \pm 26	91 \pm 45	73 \pm 42	0.24

¹ Mean abundances per 1-ha unit were ranked within each site and mean ranks were compared among habitat types by use of ANOVA. Probabilities are from ANOVAs comparing mean within-site rankings among habitat types and small letters in common identify mean ranks that were not significantly different according to Duncan's multiple-range test ($\alpha = 0.05$). Dashes identify taxa that were not tested.

² Average biomass was compared among habitats by use of a randomized-block ANOVA.

sequence predicted, and for the latter, both Duncan's test and isotonic regression were significant (table 7-1).

Abundances of Marmosa murina and Monodelphis brevicaudata in CF edge (and, for comparison, in matrix habitat [see experiment 2] and in CF) are shown as a function of distance to the clearcut/forest edge in figure 7-2. The edge model (equation 1) provided a reasonable fit to the observed decline in abundance with increasing distance from the edge. Both species attained abundances characteristic of CF at close to 100 m from the edge (respective D_{95} values were 102 and 78 m). Predicted abundances in 10- and 1-ha fragments were within 1.1 standard errors of the observed abundances, except for abundance of M. brevicaudata in 10-ha fragments (5.9 standard errors) (figure 7-3).

In the ANCOVAs comparing abundances and biomass between non-isolated and isolated habitats, understory was a significant covariate for M. brevicaudata, Oecomys paricola, terrestrial biomass ($P < 0.01$), and M. murina ($P = 0.04$), and was close to significant for Neacomys guianae ($P = 0.07$). Overstory was significant for M. brevicaudata, O. paricola, and terrestrial biomass ($P < 0.01$), and was close to significant for Caluromys philander ($P = 0.05$), M. murina, and Neacomys guianae ($P = 0.06$). There was little evidence to suggest that "adjusted" abundance or biomass differed between non-isolated and isolated habitats (treatment effect P values were always >0.19), or to suggest that isolation-type and vegetation thickness interacted (interaction P values were always >0.18). To illustrate, I plot terrestrial biomass vs understory and overstory thickness (figure 7-4). The relationship was strong (as understory thickness increased, or

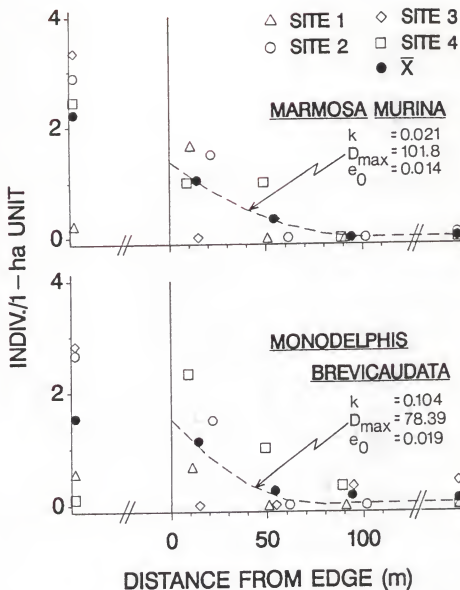


Figure 7-2. Mean number of individuals per 1-ha sub-sampling unit in primary forest at various distances from the matrix/forest edge, and in matrix (left-hand-most points) and continuous forest (right-hand-most points). The best fit of equation (1) (see text), and the corresponding parameter estimates, are shown for each species.

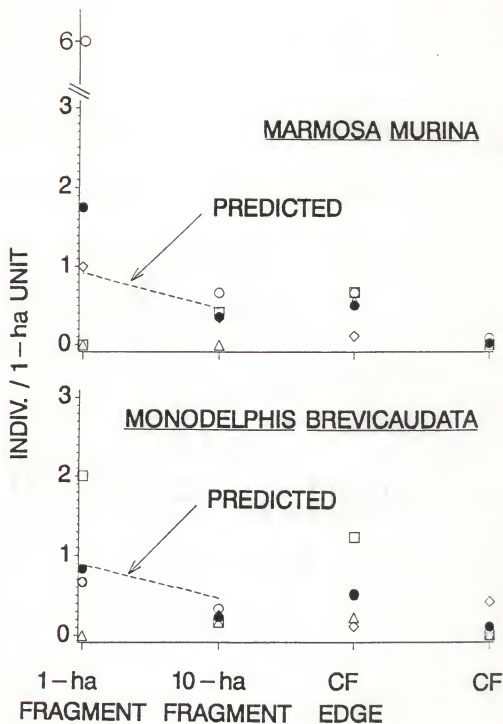


Figure 7-3. Parameter estimates from the best fit of equation (1) (Figure 2) were used to predict average abundances in 1- and 10-ha forest fragments. Symbols are as in figure 7-2. See text for a description of the model used to predict abundances.

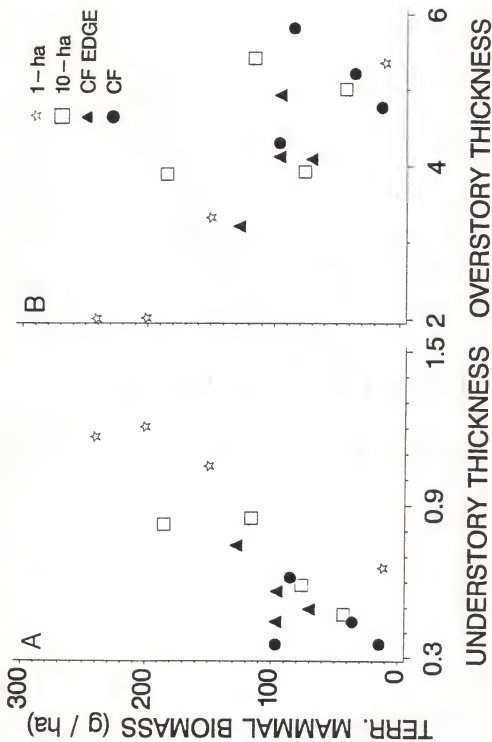


Figure 7-4. Terrestrial small mammal biomass against understory (Part A) or overstory (Part B) vegetation thickness. See text for calculations of biomass and vegetation thickness. Mean biomass, adjusted for the covariate, did not differ significantly between "isolated" (open symbols) and "non-isolated" (closed symbols) primary forest sites.

overstory thickness decreased, terrestrial mammal biomass increased), and did not appear to differ between isolated sites (10- and 1-ha fragments) and non-isolated sites (CF and CF edge).

In the analyses of canonical covariance, I included only the six taxa whose abundances varied significantly among treatments (Duncan's test). The canonical analyses of non-isolated (CF and CF edge) and isolated (10- and 1-ha) sites were remarkably similar (table 7-2). In both, the first canonical variable was positively correlated with the abundance of C. philander and understory and overstory thickness, and the second was positively correlated with M. murina and M. brevicaudata abundance and understory thickness, and negatively correlated with C. philander abundance and overstory thickness. In addition, the second canonical variable from the analysis of isolated sites was positively correlated with the abundance of Rhipidomys mastacalis. This second variable thus represented a community measure of correlation, and was used to predict community structure in the excluded treatment group. As predicted, isolated sites fell on the axis of correlation (canonical correlation) defined from the non-isolated sites, although variation among 1-ha reserves was high (figure 7-5A). Interestingly, although CF edge sites fell on the axis defined from isolated sites, CF sites did not (figure 7-5B). To identify the source of this discrepancy, I combined all sites, and calculated correlations between the canonical variables and mammalian abundances. Relative to the other sites in the space, CF sites were unique; abundances of C. philander and Didelphis marsupialis were high, and abundance of M. hispidus was low.

Table 7-2. Weighted correlations between mammalian species abundances and vegetation thicknesses in two treatment groupings, and between each set of variables and their canonical variables. Non-isolated sites included those in continuous forest and its edge; isolated sites included those in 10- and 1-ha forest fragments.

	Non-isolated ($n = 8$)				Isolated ($n = 8$)			
	Understory thickness	Overstory thickness	Mammal CV 1	Mammal CV 2	Understory thickness	Overstory thickness	Mammal CV 1	Mammal CV 2
<u>Marmosa murina</u>	0.56	-0.55	-0.13	0.73	0.57	-0.51	-0.02	0.62
<u>Hoedelphis brevicaudata</u>	0.86	-0.47	0.13	0.92	0.65	-0.64	-0.09	0.73
<u>Bidelphis marsupialis</u>	-0.17	0.15	0.02	-0.21	0.02	-0.20	-0.21	0.09
<u>Caluromys philander</u>	-0.09	0.62	0.48	-0.39	-0.30	0.76	0.60	-0.52
<u>Rhipidomys mastacalis</u>	-0.09	0.01	-0.05	-0.08	0.39	-0.42	-0.10	0.44
<u>Meromys hispidus</u>	-0.17	0.16	0.04	-0.21	0.12	0.20	0.35	0.01
Vegetation CV 1	0.51	0.78	1.00	-	0.32	0.58	1.00	-
Vegetation CV 2	0.86	-0.63	-	1.00	0.95	-0.81	0.99	-

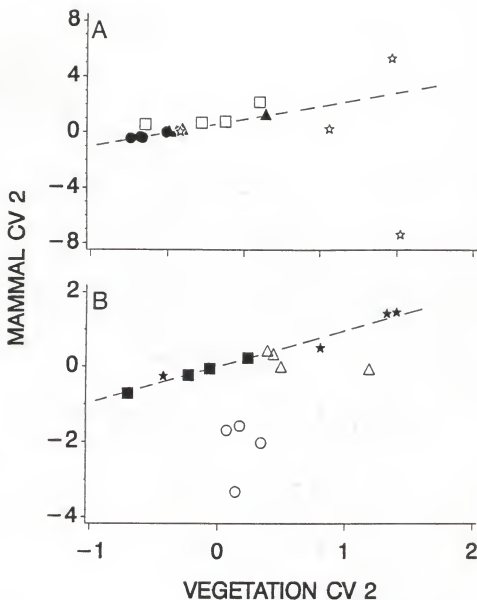


Figure 7-5. The second canonical axes of correlation from analyses of canonical correlation between the abundances of six small mammal species and understory and overstory vegetation thickness. In part A, "non-isolated" sites (closed symbols) were analyzed, and the resulting coefficients were used to plot "isolated sites" (open symbols) in the canonical plane. In part B, "isolated" sites (closed symbols) were analyzed, and the resulting coefficients were used to plot "non-isolated sites" (open symbols) in the canonical plane. Symbols are as in figure 7-4.

Experiment 2: Matrix Habitat

Of the 11 taxa captured in matrix habitat, two (Philander opossum and Neacomys guianae) were never captured in CF, whereas of the 14 taxa captured in CF, five were never captured in matrix (Metachirus nudicaudatus, Caluromys philander, Oryzomys macconnelli, Mesomys hispidus, and Isothrix pagurus). Three of the last five were captured only once in CF (table 7-3). To compare abundances between matrix habitat and CF, I separated matrix sites by matrix type (pasture or secondary forest [SF]), and used t-tests (species frequently captured in both habitats) and Median tests (species rarely captured in one habitat or the other) (table 7-3). Marmosa cinerea was significantly more abundant in SF than in CF, and Monodelphis brevicaudata nearly was ($P = 0.07$ [Median test]). Abundance of Marmosa murina was significantly greater in matrix habitat than in CF. Oryzomys capito was significantly more abundant in pasture than in CF, and there was some evidence that M. cinerea was less abundant in pasture than in CF ($P = 0.07$ [Median test]). C. philander was significantly less abundant in matrix than in CF. The total number of individuals captured was significantly greater in SF than in CF.

To investigate whether distance from CF influenced community structure in the matrix, I ranked the abundance of each species among units at a site, and looked for correspondence with distance rankings. Rankings corresponded at more than one site for only one species (M. brevicaudata); at three of four sites (two SF sites and one pasture site), this species was most abundant in the unit closest to CF and least abundant in the unit farthest from CF. Abundance in the unit

Table 7-3. Mean (\pm SD) number of individuals per 1-ha unit at four sites in matrix habitat and in continuous forest trapped during October 1987 - March 1989. Units in pasture consisted of 12 terrestrial trap stations, those in secondary forest consisted of 12 terrestrial and 12 understory (1.8-m height) trap-stations, and those in continuous forest consisted of 12 terrestrial and 12 arboreal (14-m height) trap-stations.

Taxon	Matrix habitat ($n = 4$ sites)				
	Pasture		Secondary forest		Continuous forest ($n = 4$ sites)
	Site 1 ($n = 3$ units)	Site 4 ($n = 3$ units)	Site 2 ($n = 3$ units)	Site 3 ($n = 2$ units)	
<i>Marmosa cinerea</i> ^a	0	0	3.111 \pm 2.219	3.833 \pm 1.179	0.500 \pm 0.180
<i>M. murina</i> ^b	0.222 \pm 0.192	2.556 \pm 0.839	2.889 \pm 1.072	3.333 \pm 0.943	0.021 \pm 0.042
<i>Monodelphis brevicaudata</i>	0.556 \pm 0.385	0.111 \pm 0.192	2.667 \pm 0.333	2.833 \pm 0.236	0.104 \pm 0.208
<i>Bidelphia marsupialis</i>	0.111 \pm 0.192	0.333 \pm 0.577	0.111 \pm 0.192	0.167 \pm 0.236	0.229 \pm 0.356
<i>Philander opossum</i>	0	0.111 \pm 0.192	0	0	0
<i>Metachirus nudicaudatus</i>	0	0	0	0	0.021 \pm 0.042
<i>Caluromys philander</i> ^b	0	0	0	0	0.950 \pm 0.210
<i>Oryzomys capito</i> ^c	0.889 \pm 1.018	1.444 \pm 1.018	0	0.167 \pm 0.236	0.146 \pm 0.080
<i>O. macconnelli</i>	0	0	0	0	0.104 \pm 0.158
<i>Oecomys paricola</i>	0	0	1.222 \pm 0.839	0	0.042 \pm 0.048
<i>O. bicolor</i>	0	0.111 \pm 0.192	0.111 \pm 0.192	0	0.021 \pm 0.042
<i>Neacomys guianae</i>	0	0.778 \pm 0.385	0.333 \pm 0.577	0	0
<i>Rhipidomys mastacalis</i>	0	0.444 \pm 0.385	0	0	0.354 \pm 0.443
<i>Proechimys</i> spp.	0.111 \pm 0.192	0	0.444 \pm 0.509	0.333 \pm 0.471	0.313 \pm 0.185
<i>Hesomys hispidus</i>	0	0	0	0	0.021 \pm 0.042
<i>Isotrich pagurus</i>	0	0	0	0	0.021 \pm 0.042
Total number of individuals ^a	1.9 \pm 1.6	5.9 \pm 1.0	10.9 \pm 0.5	10.7 \pm 2.4	2.9 \pm 0.8

^a A t-test comparing mean abundance between secondary and continuous forest sites was significant at $P < 0.01$.

^b A median test comparing abundance between matrix and continuous forest sites was significant at $P < 0.05$.

^c A t-test comparing mean abundance between pasture and continuous forest sites was significant at $P < 0.01$.

farthest from CF was still greater at SF sites than at CF sites. At two sites, total abundance was greatest in the unit closest to CF and least in the farthest unit, but the converse was true at another site. Thus, the contrasts between matrix and CF discussed above appeared to be true regardless of distance from CF; little evidence suggested a distance effect within the matrix habitat.

In contrast, small mammal community structure varied strongly with vegetation thickness. In the plot of principal components one and two, two axes of variation were indicated (figure 7-6). One was due to relatively high species richness in a single unit at site 4; the other separated pasture and SF sites. Abundances of five taxa loaded highly and positively on this second axis, and the abundance of one (Oryzomys capito) loaded highly and negatively. Total vegetation thickness also was highly correlated with this axis. Not surprisingly given this pattern, total small mammal abundance appeared to correlate highly with vegetation thickness (figure 7-7). All units in SF had greater small mammal abundance (and greater vegetation thickness) than units in pasture. Distance from CF correlated highly with neither of the axes (figure 7-6).

Thus, small mammal community structure in the matrix varied with vegetation structure in the matrix. To test whether this variation influenced abundances in primary forest edge, I regressed total abundance per census in fragments and CF edge against total abundance per census in the surrounding matrix, and used Spearman's correlation (note that the test was temporally pseudo-replicated). As predicted, abundance in matrix most closely approximated abundance in habitats with

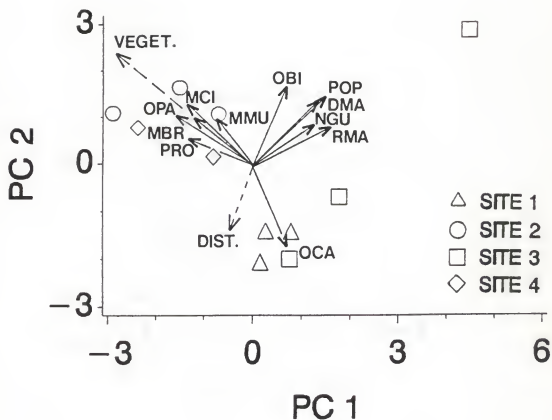


Figure 7-6. Principle components 1 and 2 from an analysis of mean number of individuals per 1-ha unit in matrix habitat (censuses combined). Eigenvectors (times four) are shown for each small mammal taxon captured; three letter codes identify taxa (PRO = *Proechimys* spp.; otherwise, the first letter of the genus and the first two letters of the species). Correlations (times four) between mean vegetation thickness in a unit and the principal component scores, and between the distance from a unit to continuous forest and the principal component scores, are also shown.

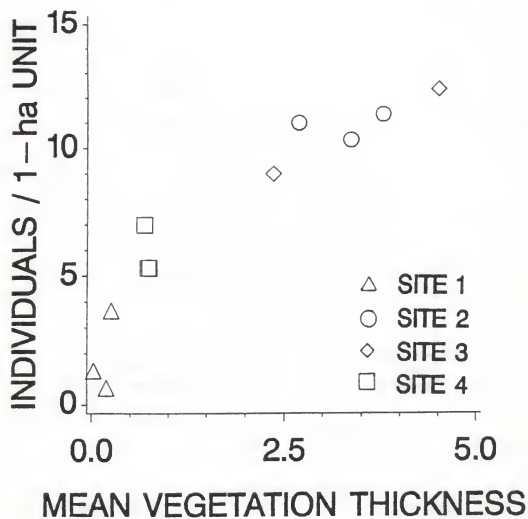


Figure 7-7. Mean total number of individuals per 1-ha unit in matrix habitat (censuses combined) against mean vegetation thickness in the unit.

proportionally more edge-modified habitat; correlation between abundance in 1-ha fragments and in matrix was significant ($P = 0.02$), and abundances were on average approximately equal; correlation between 10-ha fragments and matrix was only close to significant ($P = 0.11$), and abundance in matrix was usually greater than in the fragments; and correlation between CF edge and matrix was not significant ($P = 0.86$), and abundance in matrix was almost always greater than abundance in CF edge (figure 7-8). Not surprisingly, of the eight taxa that on average were more abundant in matrix than in CF, seven were more abundant in 1-ha fragments than in CF (the exception was Oecomys bicolor). Likewise, of the eight that on average were less abundant in matrix than in CF, five were less abundant in 1-ha fragments than in CF (exceptions were Metachirus nudicaudatus, Rhipidomys mastacalis, and Proechimys spp.).

Experiment 3: Immigration

The defaunation of fragment 1112 failed as an experiment to estimate recolonization rates. Only two species (Oecomys paricola and Rhipidomys mastacalis) were less abundant in censuses 2 and 3 than in the first census (none was more abundant in censuses 2 and 3 than in census 1). Moreover, both were less abundant in secondary forest in censuses 2 and 3 than in census 1, hence the decline in the fragment may have been unrelated to defaunation per se (figure 7-9). Because the fragment appeared to be close to completely defaunated during census 1 (the last three nights of trapping yielded only one individual), it seems safe to infer that the 6 - 7 mo between censuses was sufficient for the original community to completely reestablish itself.

Figure 7-8. Mean total number of individuals per unit per census in continuous forest edge (Part A), 10-ha fragments (Part B), and 1-ha fragments (Part C) against mean total number of individuals per unit per census in matrix habitat at the same site. Symbols are as in figure 7-7.

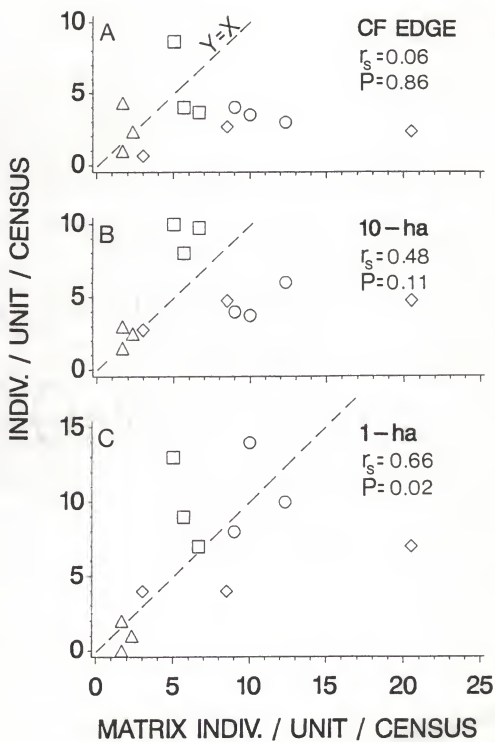
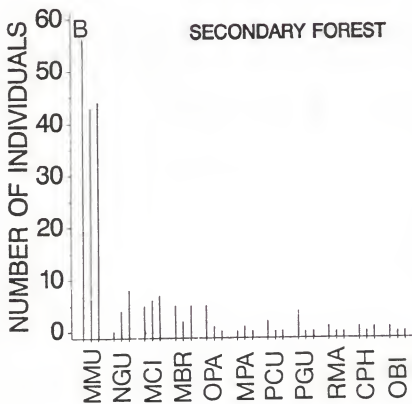
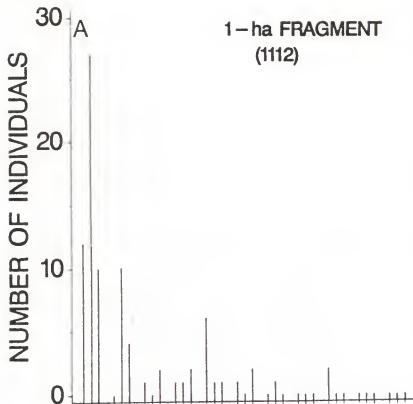


Figure 7-9. Number of individuals of 11 small mammal species captured during three defaunations of a 1-ha fragment (Part A) and during three censuses of the matrix habitat surrounding the fragment (Part B). Left-hand-most bars represent individuals captured during the first defaunation or census; right-hand-most bars represent individuals captured during the third defaunation or census. Three letter codes identify taxa (the first letter of the genus and the first two letters of the species). Ordinates are scaled so that 1 cm equals the same percentage of total captures in both parts.



Interestingly, the community of the fragment was virtually indistinguishable from that of the surrounding secondary forest; both communities were characterized by a super-abundance of Marmosa murina, and relatively high abundances of Neacomys guianae, Marmosa cinerea, M. brevicaudata, and Oecomys paricola (figure 7-9).

In total, 21 individuals were radio-collared (six M. cinerea, twelve C. philander, and one each of O. macconnelli, P. guyannensis, and Isothrix pagurus) and translocated either to the opposite side of the strip of pasture or to a site on the same side of the strip. Six individuals (three M. cinerea and three C. philander) were translocated twice, hence 27 translocations were performed in total. Of the nine translocations of M. cinerea and 15 of C. philander, five and nine, respectively, were to the other side of the strip and four and six were to the same side of the strip. Homing of C. philander was markedly reduced by the strip of pasture. Of the 11 individuals whose location was known at 70 h post-translocation, four individuals released on the same side of the strip had all returned to near their capture location, whereas of seven individuals translocated to the other side of the strip, only one had returned ($P = 0.02$, Fisher's test). Tabulation of whether or not an individual had returned to its capture site at its last known location (regardless of the number of hours post-translocation) displayed a similar trend. In this case, of six C. philander released on the same side of the strip, five returned, and of nine released on the other side of the strip, only three returned ($P = 0.12$, Fisher's test). Four of the five individuals that homed through continuous forest did so in less than 12 h (the fifth individual's

transmitter was not functioning when it was re-trapped near its capture location at approximately 108 h post-translocation), whereas the three individuals that traversed the pasture did so at 24 - 48, 108 - 132, and 132 - 156 h post-translocation. In contrast, homing of M. cinerea seemed little affected by the nature of the intervening habitat, and there was some indication that individuals released in contiguous forest were less likely than C. philander to return to their capture location. At 70 h post-translocation, one of two individuals released on the same side of the strip of pasture had returned, and one of two released on the other side had returned. Considering last known locations, two of four returned from release sites on the same side, and two of five returned from the other side. The translocated O. macconnelli was found in the middle of the pasture 6 h after translocation to the other side, but was never located again. The individual of I. pagurus still had not returned from the other side of the strip at its last known location at 54 h post-translocation. The P. guyannensis was never located after its release on the same side of the strip.

Discussion

Three lines of evidence presented here suggest that insularization per se was not important in structuring the small mammal communities of these small forest fragments. Instead, changes in the communities of fragments after isolation appeared to result from changes in resource/habitat levels in the fragments (apparently driven by edge effects), coupled with invasions from superabundant populations in the matrix habitat surrounding fragments.

First, as predicted from the proportion of edge-modified forest in a habitat, when significant variation in abundance was indicated among habitat types, habitat-specific abundances could be ranked in the sequence: CF, CF edge, 10-ha fragment, 1-ha fragment. The abundance of only one species (*Mesomys hispidus*) could not be ranked in this sequence (abundance was significantly greater in 10-ha fragments than in 1-ha fragments or CF edge); however, its abundance did not vary significantly among habitats in phase 1 (and abundance was greatest in CF) (Chapter 4). In Chapter 4, I used a larger data set to compare only three habitat types (CF, 10-ha fragments, and 1-ha fragments), and similarly found that abundances could almost always be ranked in the sequence: CF, 10-ha fragment, 1-ha fragment. This latter sequence is predicted by a number of area-related processes (see Chapter 4), and does not favor one over the other; however, the difference in abundances between CF and CF edge is not predicted by processes based on insularization per se. Note that failure to reject the predicted sequence did not exclude isolation-dependent processes; for example, a species might be less abundant in edge-modified habitat due to a changed resource base, and even less abundant in fragments due to increased area-related extinction probabilities.

A second line of evidence, the "null" models, provided a more powerful test. According to the most restrictive (and powerful) model, habitat/resource changes are entirely determined by proximity to the clearcut/forest edge ("edge effects"). The model I tested here is more realistic than other edge models, and can theoretically be used to predict edge effects in fragments of any size or shape. Unfortunately,

data for small mammal abundances were insufficient to provide a strong test of this model. For the two species that provided at least some data, the model performed relatively well; predicted abundances in 10- and 1-ha fragments were within the range of observed values, and relatively close to the observed mean. This model provided the most elegant expression of purely edge-driven community changes, and deserves further testing.

Changes in habitat/resource distributions within fragments result in part from edge-effects, and in part from chance events unique to an individual fragment (error variance in the above model). Resource/habitat levels also might be determined in part by processes dependent on insularization, although I found no evidence to suggest that insularization was needed to explain changes in vegetation structure or insect biomass within fragments (Chapters 5 and 6). Thus, a more complete "null" model relies on actual measurements of resource/habitat levels in fragments, and predicts that variation in small mammal community structure among fragments, and between fragment and continuous forest sites, is attributable to variation in resource/habitat levels. I was unable to reject this hypothesis; given equal "habitat/resource" levels, isolated (1- and 10-ha fragments) and non-isolated (CF edge and CF) sites appeared to have the same small mammal community.

To measure "habitat/resource" levels, I used understory and overstory vegetation thickness, since these variables, or ones similar to them, have proved important in partitioning habitat-related variation among Neotropical small mammal communities (August 1983, Nitikman and

Mares 1987, Fonseca 1988, Stallings 1988). In addition, they appear to correlate with a host of other habitat and resource variables that may be important to small mammal species, including changes in the quantity of fallen timber (unpublished data) and insect biomass (Chapter 6). I found little evidence to suggest that within-habitat correlations among habitat/resource variables varied between isolated and non-isolated habitats, so I assumed that these variables provided a measurement of overall "habitat/resource" levels. If covariation among habitat/resource variables important to small mammals differs between non-isolated and isolated sites, however, the "null" hypothesis of habitat/resource-driven changes in community structure becomes difficult to test, and could even provide spurious results. A possible example comes from the second canonical analysis (figure 7-5B); sites in CF did not fall on the axis of correlation defined from isolated sites, but sites in CF edge did. One possible explanation is that habitat/resource variables in CF never covary in a way similar to that in forest close to edges. An attempt to utilize the correlation structure in CF to predict events along the edge would therefore be doomed to failure, and experimentation would be the only recourse. Thus, as a methodological caveat, it seems wise to use only CF edge as a control of habitat/resource changes, and not CF. An improvement in the use of CF edge as a control is also possible. In general, the more closely the range of variation in habitat/resource levels in CF edge matches that in fragments, the less extrapolation is required, and the more exact is the test of equal community structure given equal resources. Small peninsulas of forest are exposed to edge on more than one side, and

although not censused in the present study, they may prove useful as controls for the extensive habitat changes in small fragments.

A third line of evidence suggested that the effect of proximity to clearcut varied with the kind of habitat present in the matrix; in effect, small mammals "overflowed" from the matrix into the forest. As a result, increases in the proportion of forest in a habitat that was close to the edge resulted in increased similarity between the habitat's and the matrix's communities. This effect of the matrix on fragment communities was dramatically demonstrated in 1-ha fragments. Censuses in fragment 1112, a fragment surrounded by secondary forest, yielded 31 individuals of eight species, whereas those in fragment 1104, surrounded by pasture and the remains of a recently cut and burned secondary forest, yielded only three individuals of two species (see figure 4-6). This interaction between matrix and primary forest has two important implications: i) parameter estimates in edge models, such as the one tested here and in Chapter 5, will be specific to certain matrix types, and ii) models based solely on measurements of habitat/resource levels may fail, because they do not consider the source of the animals that utilize the resources. It seems likely that the small mammal community close to an edge will be determined in part by the habitats/resources available to them close to the edge, and in part by productivity in the adjoining matrix.

In the present study, the species that were less abundant in fragments than in CF may have been able to maintain population densities in fragments equal to those expected based on habitat/resource levels because of the proximity of the fragments to continuous forest.

Presumably, the rate of immigration was sufficient (or more than sufficient) to offset population extinctions. If fragments had been farther from continuous forest, abundances of these species might have been below those expected based on habitat/resource levels. Matrix habitat in particular seemed to present a strong barrier to movements of Caluromys philander. Individuals released in continuous forest some 300 m from their capture site usually returned to their capture site within 12 hours, whereas most individuals released on the other side of a strip of pasture did not return, and those that did, only returned after several days.

Although sample sizes were small, roughly one-half of the Marmosa cinerea returned, regardless of their release site. This latter species is evidently a habitat generalist, a conclusion also reached by Fonseca (1988) and Stallings (1988). It is interesting to speculate on the difference in homing of C. philander and M. cinerea through continuous forest. Compared to M. cinerea, C. philander is more frugivorous, longer lived, has smaller litter sizes, and a relatively larger brain (Charles-Dominique et al. 1981, Eisenberg and Wilson 1981, Atramentowicz 1982, Charles-Dominique 1983, Atramentowicz 1986). Eisenberg and Wilson (1981) suggest that in species that locate and exploit energy-rich but widely dispersed food patches (such as frugivores), selection has resulted in larger brains with enhanced information storage and retrieval. One possible explanation of the difference in homing in the two species is that C. philander requires information about the distribution and phenology of fruit resources in its range, and hence returns to its capture locality, whereas M. cinerea forages on

rapidly-replenishing insect prey, and makes more fine-grained foraging decisions.

As noted in Chapter 4, the effect of fragmentation was to increase the abundance of almost all small mammal species within the forest fragments. This result is surprising in light of other studies of faunal responses to fragmentation. Bierregaard and Lovejoy (1989) found that fragmentation led to a decrease in avian richness and abundance. Similarly, fragmentation decreased primate richness (Schwarzkopf and Rylands 1989) and the abundance and richness of coprophagous beetles (Klein 1989). Given the results presented here, it seems likely that the different responses of these groups to fragmentation relate to their different responses to secondary forest. Charles-Dominique (1983) argued that marsupials are essentially r -strategists and are ideally suited to respond to the increased primary production, and resulting increased secondary consumer productivity, in young secondary forests. Their high reproductive rate, rapid growth, and lack of territoriality permit them to attain high densities around abundant food sources (Charles-Dominique 1983). Based on Charles-Dominique's (1983) results, Fonseca (1988) and Stallings (1988) also suggested that the super-abundance of marsupials in their respective studies was due to a preponderance of secondary forest in their research areas. However, although increased abundance in fragments in the present study was especially true of marsupials, it was not restricted to this phylogenetic group. Of nine marsupial taxa, seven were more abundant in both trapping periods in fragments than in CF, and of nine rodent taxa, five were more abundant in fragments than in CF (Chapter 4).

The question: Why are so many Neotropical small mammals able to exploit secondary forest so successfully? can be reworded: Why are there so few primary forest specialists among them? It has been proposed that relative to other groups, small mammals are, in general, adapted for earlier successional forests, or ecosystems with relatively higher disturbance regimes (Stallings 1988). This, in turn, implies that speciation has proceeded differently in small mammals than in other taxa, and replaces one problem with another. Alternately, specialization for utilization of primary forest may essentially preadapt small mammals for utilization of secondary forests.

A possible reason for the different responses of faunal groups to fragmentation lies in the way that they perceive and select habitats. Unfortunately, the importance of habitat segregation in permitting coexistence of the small mammal fauna of Neotropical forests is poorly known. Studies that used terrestrial trapping have generally found weak correlations between species' abundances within a macrohabitat and environmental features of the habitat (Fonseca 1988, Malcolm 1988, Stallings 1988). Stallings (1988) suggested that habitat segregation per se was unimportant, and, following Charles-Dominique et al. (1981), suggested that segregation instead occurred spatially (foraging height) and with respect to the type of resources utilized (which in turn was partly a function of size of the animal). The lack of correlations between habitat features within a macrohabitat and species' abundances in a stratum, however, may in part be attributable to the crude measurements that traps provide on microhabitat utilization. Spool-and-line devices (Miles et al. 1981) indicate that microhabitat

utilization can differ markedly between species. For example, based on a preliminary analysis of information collected using this technique, I found that M. brevicaudata is usually underneath fallen logs, whereas Proechimys spp. is more often on top of them. This differential use of microhabitats may be equally true of arboreal species, which appear to differ in their use of supporting branches, as reflected by average diameter and orientation of the support (Charles-Dominique et al. 1981). Likewise, Dickman (1988) suggested that ecological separation of insectivores is likely to be achieved by differential exploitation of foraging microhabitats as opposed to specializations for feeding on different sized prey. His arguments may well apply to many of the small mammals of primary forests, and especially secondary forests, where common fruit species such as Cecropia spp. do not appear to be extensively utilized by small mammal species (Charles-Dominique 1986). Thus, it may be that in comparison to other faunal groups, small mammals select habitat on tactile cues related to the structure of foraging microhabitats. When viewed from this perspective, primary and secondary forest may differ only in degree. In contrast, gross visual cues, presumably of more importance to diurnal animals such as birds and primates than to nocturnal small mammals, identify primary and secondary forests as radically different environments.

In summary, it appears that the majority of the "fragmentation effect" in the small mammal community can be attributed to changes in the resource/habitat base that accompanies fragmentation, and to events in the surrounding matrix. While the experiments here do not exclude processes that depend on insularization, they do suggest that the great

majority of the "fragmentation effect" has little to do with insularization per se. Attempts to measure, or in some way control, habitat variation among island and mainland sites are rare, but it is clear that unless such efforts are made, variation due to island effects will remain confounded with that due to resource changes. The use of the edge of the mainland as a control for habitat variation provides a powerful "natural" experiment, one that, to my knowledge, has not been used previously.

Intriguingly, the increased abundance of small mammals in response to secondary forests and fragmentation appears to differ from the responses of other faunal groups. Knowledge about the way in which communities respond to fragmentation will have important implications for attempts to conserve primary forest ecosystems, a subject to which I will turn in the final chapter.

CHAPTER 8
SYNTHESIS AND IMPLICATIONS FOR CONSERVATION

Proximity to the forest/clearcut edge led to pervasive changes in the forest environment, including changes in the physical environment (Kapos 1989), the density of understory and overstory vegetation (Chapter 5), the vertical distribution of insect biomass (Chapter 6), and the structure of small mammal communities (Chapter 7). This dramatic change in the abiotic and biotic environment close to the forest edge can be expected to have important effects on many other as yet unexamined ecosystem characteristics. Because the world's rainforests appear convergent in many aspects of ecosystem structure (Walter 1971), we can reasonably expect similar patterns of edge-driven ecosystem change in other tropical forests.

Animal communities of the forest remnants at this Amazonian site differed markedly from those of continuous forest (Bierregaard and Lovejoy 1988, Klein 1989, Schwarzkopf and Rylands 1989, Chapter 4), and at least for small mammals, it appears that much of the difference can be attributed solely to edge effects. Insularization in itself seemed to be unimportant; given equivalent proximity to the edge, and the same habitat and resource base, I found little evidence to suggest that communities at sites close to the edge of continuous forest differed from those at sites in fragments.

These results have a number of important implications for conservation. First, edges reduce the amount of habitat available to many interior forest species. As a result, sets of species interactions characteristic of forest interior may also be lost. This loss of habitat, and resultant changes in ecosystem function, will depend both on fragment size and shape. For example, if edge effects were to extend some 100 m into the forest, then a square 100-ha fragment would preserve 64 ha of interior habitat. Ten square 10-ha fragments would preserve in total only 13 ha of interior habitat (a size effect) and a rectangular 100-ha fragment 200 by 5000 m would preserve no interior habitat (a shape effect). Thus, two commonly cited design considerations (Simberloff 1988) find support in the present study: larger fragments and more circular fragments preserve proportionally more interior habitat (since they minimize the perimeter to area ratio). Obviously, if edge effects extend far into the forest, then relatively large fragments will be required to maintain interior forest conditions. In the present study, edge effects extended approximately 100 m into the forest. Janzen (1983) has argued that more subtle edge-induced changes can extend much farther into the forest.

A second implication involves the nature of the habitat bordering the edge. Edge effects are of course ultimately dependent on changes that occur outside the forest, hence different habitats abutting an edge will lead to different edge effects. In the present study, the importance of these external influences in determining edge effects was dramatically illustrated in the 1-ha fragments. Those surrounded by secondary forest had superabundant small mammal populations, whereas

those surrounded by pasture had few small mammals (Chapters 4 and 7). Different matrix habitats will lead to different edge effects, differences that will "ripple" through fragment communities. For example, several bird and bat species forage extensively for fruit in secondary forest, but utilize primary forest for roosts and perches (Charles-Dominique 1986). Seeds transported from secondary forest to primary forest can be expected to alter the primary forest seed bank, and ultimately, the nature of succession within primary forest. In contrast, rodents may act primarily as seed predators, and one result of increased rodent densities in secondary forest may be high rates of seed mortality in primary forest close to the forest edge. Putz et al. (1990) suggested that differential seed predation led to changes in the flora of small islands of Lake Gatún in Panama. They found that the flora of small islands, in contrast to the mainland, were dominated by just a few tree species that tended to have large seeds. They argued that the absence of small seed-eating mammals on the islands gave trees with large seeds an advantage over those with small seeds. Since a goal of conservation is to conserve functioning primary forest ecosystems, future research must explore the role of these small mammals in intact primary ecosystems. As seed predators and dispersers, small mammals probably influence the nature of succession within intact forest, and changes in their abundance in the habitat around forest fragments can be expected to have important consequences for succession within fragments.

Only two species in the present study were convincingly more abundant in primary forest than in young secondary forests or fragments: Caluromys philander and Oryzomys macconnelli. The first is apparently

among the most frugivorous of the small mammals captured (Charles-Dominique et al. 1981). Unfortunately, the biology of the second is unknown. Apparently, the presence of these species in small primary forest fragments was the result of relatively infrequent dispersal from continuous forest. Thus, as deforestation proceeds, and the average distance between fragments increases, one could reasonably expect the loss of these two species. Other rarely captured species (such as Echimys chrysurus) might also be in danger. However, most of the small mammal species captured were able to utilize secondary forests, and there is no reason to believe that primary forest is, in itself, necessary for their existence. With a decrease in the average age of successional forests in the matrix, some of these species can be expected to disappear from the matrix, and as a result, from small fragments.

Among small mammals at the Biological Dynamics of Forest Fragments site, species characteristic of Amazonian savannahs (such as Bolomys spp.) are apparently not yet present, but will most likely appear as human-created "savannahs" inter-connect naturally occurring ones. Certainly, as agricultural activities in the matrix intensify, the mammal communities in the small forest remnants will probably diverge even more from the intact communities of continuous forest. This may have already occurred in the Atlantic rainforest, an ecosystem that has been decimated by human activities (see Fonseca 1988). A predominance of marsupials, even in large primary forest tracts, may be indicative of these changes on a landscape level (Fonseca 1988).

Hence, my results and those of Fonseca (1988) and Stallings (1988), suggest that a mixture of primary forest and different-aged secondary forest stands will ensure the preservation of many of the small mammals of intact Neotropical forest. However, because fragmentation in the tropics often leads to the creation of exactly this type of environment, small mammals do not appear to be in imminent danger. In fact, to focus on their plight may detract from the task at hand: the preservation of intact tropical ecosystems and the numerous species that are adversely affected by fragmentation. Instead, the presence of a superabundant and speciose small mammal fauna may be a good indicator of an ecosystem gone awry.

In summary, edge effects lead to marked changes in the plant and animal communities of tropical forest fragments. A possible management tool to maximize the conservation value of fragments will be to control human activities in the surrounding matrix, and hence to control these edge-induced habitat changes.

APPENDIX
BODY WEIGHTS, MAXIMUM DISTANCES BETWEEN RECAPTURES,
AND RADII OF TRAPABILITY OF
CENTRAL AMAZONIAN SMALL MAMMALS

Table A-1. Mean body weight (\pm SD (\bar{n})), maximum distance between recaptures (MDR) (\pm SD (number of individuals recaptured)), and radii (\bar{r}) of trappability of small mammal captures.

Taxon	Terrestrial trapping						Arboreal Trapping					
	Phase 1 ¹		Phase 2 ²		Phase 1 ³		Phase 2 ²		Phase 1 ³		Phase 2 ²	
	Body weight ⁴ (g)	MDR ⁵ (m)	\bar{r}	MDR (m)	\bar{r}	MDR (m)	\bar{r}	MDR (m)	\bar{r}	MDR (m)	\bar{r}	MDR (m)
<i>Marmosa cinerea</i>	92 \pm 31 (376)	34.2 \pm 33.7 (56)	39	22.9 \pm 10.7 (14)	27	37	54.8 \pm 51.5 (42)	47	49.5 \pm 28.4 (32)	63	54	
<i>M. parvidens</i>	17 \pm 6 (93)	30.0 \pm 10.7 (8)	30	20.0 \pm 0.0 (1)	24	29	0	-6	0	-	-	
<i>H. murina</i>	41 \pm 15 (341)	28.0 \pm 17.9 (5)	23	35.4 \pm 22.8 (7)	37	31	0	0	0	0	-	
<i>Monodelphis brevicaudata</i>	58 \pm 25 (198)	44.0 \pm 56.7 (15)	26	20.0 \pm 20.0 (3)	30	27	0	0	0	0	-	
<i>Pithecheilus murguipalilis</i>	793 \pm 527 (167)	63.0 \pm 66.8 (61)	126	63.6 \pm 32.3 (4)	92	124	190.0 \pm 99.0 (2)	76	0	0	124	
<i>Phylander opossum</i>	355 \pm 379 (12)	0	-	0.0 \pm 0.0 (2)	<10	124	0	0	0	0	-	
<i>Metachirus nudicaudatus</i>	245 \pm 100 (116)	32.9 \pm 32.9 (16)	23	53.8 \pm 0.0 (1)	70	26	0	0	0	0	-	
<i>Calomys phillander</i>	169 \pm 53 (168)	40.0 \pm 40.0 (3)	53	0	-	37 ⁷	68.7 \pm 47.9 (32)	65	58.6 \pm 29.2 (21)	72	68	
<i>C. lanatus</i>	278 \pm 71 (11)	0	-	0	-	37 ⁷	0	-	53.8 \pm 0.0 (1)	70	68 ⁷	
<i>Oryzomys capito</i>	48 \pm 16 (292)	27.6 \pm 28.5 (98)	27	30.0 \pm 24.5 (5)	40	28	0	0	0	0	-	
<i>O. macconnelli</i>	68 \pm 16 (167)	30.6 \pm 29.6 (62)	27	40.0 \pm 0.0 (1)	33	27	0	0	0	0	-	
<i>Oecomys paricola</i>	37 \pm 11 (84)	20.0 \pm 28.3 (4)	17	33.5 \pm 23.2 (4)	33	25	50.0 \pm 42.4 (2)	54	56.9 \pm 4.3 (2)	67	61	
<i>O. bicolor</i>	23 \pm 7 (44)	0.0 \pm 0.0 (1)	<10	0	-	25 ⁷	0	0	0	0	61 ⁷	
<i>Mesocorys guianae</i>	16 \pm 2 (45)	0	-	0	-	25 ⁷	0	0	0	0	-	
<i>Thioldomys mustacalis</i>	51 \pm 19 (166)	40.0 \pm 28.3 (2)	43	0.0 \pm 0.0 (1)	<10	25 ⁷	35.0 \pm 29.7 (16)	37	37.1 \pm 24.9 (38)	37	37	
<i>Proechimys</i> spp.	156 \pm 68 (532)	26.7 \pm 26.8 (114)	25	47.3 \pm 26.7 (6)	56	27	0	0	0	0	-	
<i>Mesocorys himpidus</i>	111 \pm 28 (31)	0	-	0	-	25 ⁷	0.0 \pm 0.0 (1)	<10	60.0 \pm 0.0 (1)	43	61 ⁷	
<i>Ischiria parvula</i>	202 \pm 65 (8)	0	-	0	-	25 ⁷	0	0	20.0 \pm 0.0 (1)	27	37 ⁸	

¹ Within trapline recaptures during May 1985 to July 1987 in continuous forest, 10-ha fragments, and a 100-ha fragment.

² Within hectare recaptures during October 1987 - March 1989 in continuous forest, 10-ha fragments, and 1-ha fragments.

³ Within trapline recaptures during January 1984 to September 1986 in continuous forest and 10-ha fragments. Radii used in biomass calculations (see text).

⁴ All individuals captured, regardless of capture date or location.

⁵ Radii of trappability used in biomass calculations.

⁶ - = not calculated.

⁷ Estimated from *M. cinerea*, *O. paricola*, or *G. phillander*.

⁸ Estimated from *E. mustacalis*.

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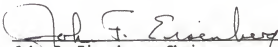
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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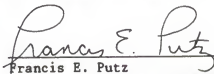
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements of the degree of Doctor of Philosophy.

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