SMALL MAMMAL ABUNDANCES IN ISOLATED AND NON-ISOLATED PRIMARY FOREST RESERVES NEAR MANAUS, BRAZIL.

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SUMMARY

Abundances of small, terrestrial mammals were estimated in 10 and 100-ha, isolated and non-isolated primary forest reserves near Manaus, Brazil between October 1983 and March 1984. The small mammal abundance pattern in a 10 ha reserve isolated for approximately three years differed significantly from that in other reserves, primarily due to higher capture rates of ***Marmosa cinerea, Rhipidomys mastacalis,*** *and* ***Oryzomys paricola*** *in the isolated reserve. Diet type and re-invasion potential may be important factors structuring small mammal communities in forest patches. Variation in the small mammal community among other reserves was primarily due to variation in the abundances of* ***Proechimys*** *and* ***O. capito****. At least part of this variation was attributable to temporal effects, but variation due to reserve effects also was suggested. Small mammals were much more abundant in the reserves during the present study than in 1982.*

INTRODUCTION

The mammalian fauna of the Amazon basin is poorly known. Given the exponential rate of cutting of Amazonian forests (Fearnside, 1982), and the general conclusion that sound conservation decisions can be made only when autoecological data is available (Zimmerman & Bierregaard, 1986), much basic ecological information must be collected to save even a fraction of the Amazon's immense wealth of mammals.

The "Minimum Critical Size of Ecosystems" (MCSE) project (Lovejoy **et al.**,1984; 1986) provides an **in situ** experiment on ecosystem decay within reserves of different sizes at a site in the Amazon basin near Manaus. Clearly, the most efficient way to learn about species-area relationships and causes of extinction in reserves is to make detailed biological studies of the reserves themselves. Such knowledge will facilitate realistic conservation decisions in other parts of the Amazon basin, and in other tropical forests. Research on nocturnal, terrestrial mammals in the MCSE reserves began in February 1982 (Emmons, 1984; Lovejoy **et al.**, 1984) and continued for 5.5 months. A second study, from which preliminary results are presented, began in October 1983. The research investigated

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three related questions: 1) did mammalian species abundance patterns differ between isolated and non-isolated forest reserves? 2) did species abundance patterns differ among reserves in undisturbed forest? and 3) did differences in habitat structure among reserves explain observed differences is small mammal abundance patterns?

In six months of study, I visited 10 forest reserves, and in each reserve censused terrestrial mammals using visual surveys at night and live-traps. Of the 10 reserves, four had been isolated from contiguous forest via clear-cutting of surrounding forest. Three were isolated two to seven months prior to study, and one was isolated more than three years previous to censusing. Data from this latter reserve are of special interest because this reserve was sampled previously for mammals. In 1982, approximately 1.5 years after the reserve was isolated, 13 of 20 mammal species trapped or observed in undisturbed forest were absent from this reserve, including **Proechimys**, the most common terrestrial small mammal of undisturbed forest (Lovejoy **et al**., 1984). Has further species loss occurred since 1982?

The remaining six reserves were non-isolated, i.e., they consisted of networks of trails at sites in continuous forest. Variance in species abundances among reserves in undisturbed forest has important implications for the study of the decay process subsequent to isolation. First, recognition of isolation effects requires proper controls. In the present experiment, the small mammal community in continuous forest was censused at a variety of sites and at a variety of times, hence it was possible to distinguish variation due to isolation from variation due to temporal and location effects. Second, the change in species abundance patterns after isolation may depend on species allotment at the time of isolation. A species initially rare in one reserve may soon became locally extinct, whereas it may persist in another reserve due to initially higher densities. Different species compositions among reserves may lead to different interactions, and eventually to different communities. Alternatively, mammalian faunas may decay to the same level regardless of initial allotment, as would be the case if species turnover was very high in the reserves.

In addition to the isolation history of a reserve, differences in habitat characteristics represent a possible cause of variation in mammalian abundances among reserves Mammalian diversity has been related to the complexity of tropical habitats (August, 1983) but the importance of within-habitat variation in determining distributions of tropical mammals is poorly known.

MATERIALS AND METHODS

Reserves are approximately 80 km North of Manaus (2°25'S, 59°50'W) in upland (terra firme) forest. Monthly rainfall in the Manaus area (70 year average) ranged from 42-162mm between June and November and from 211 - 300 mm between December and May. The yearly average was 2105 mm (Ribeiro & Adis, unpubl. data).

Trapping

Terrestrial traps were set in three 100 ha and three 10 ha reserves in undisturbed forest (reserves 1301, 2303, 1302, 1205, 1208 and 1204), in one 100 ha and two 10 ha reserves isolated in 1983 (reserves 3304, 3209, and 1207), and in one 10 ha reserve isolated in 1980 (reserve 1202) (Table 1). A brief description of each reserve is provided in Lovejoy **et al**. (1986). In each reserve, traplines were established along a network of parallel trails. In 10 ha reserves, three traplines 100 m apart each consisting of 15 trap stations spaced at 20m intervals were established and in 100-ha reserves four traplines 200 m apart of 30 stations each were established. In the last 100 ha reserve sampled (reserve 1302), I used eight traplines of 15 stations each, which allowed direct comparison with 15-station lines in 10 ha reserves. Since individuals were rarely captured on more than one trapline, traplines within each reserve could be considered independent samples, and hence mean number of individuals per trapline could be compared among reserves. Fuller (1977) used a similar method to compare abundances of **Clethrionomys gapperi** among years.

Each trap station consisted of a Tomahawk trap (14 by 14 by 40 cm) and a Sherman trap (8 by 8 by 23 cm) placed 2 to 4 m apart and 4 to 6 m perpendicular to the trail. Within a reserve, traps were placed off the same side of the trail. After November, Tomahawks were covered with a palm leaf (reserve 2303) or with a piece of clear plastic. Traps were baited with banana and peanut butter and were checked and rebaited each morning for nine trap nights. Captures were identified (Pine, 1973; Musser & Carleton, pers. comm. for **Oryzomys** spp.), toeclipped, weighed, and measured (total, tail, ear, and hindfoot length). **Proechimys** spp. were identified only to genus. Unfortunately, at the time of trapping we did not distinguish between **Marmosa cinerea** and **M. murina** or between **Oryzomys paricola** and **Rhipidomys mastacalis**. However, morphological analysis based on subsequent trapping allowed us to confidently place almost all of these individuals into one or the other species. Two individuals in the genus **Marmosa** could not be classified unambiguously, and hence were excluded from analyses. Sexual condition of males (testes scrotal or abdominal) and females (lactation and vaginal perforation) was noted for some individuals caught prior to mid-November, and for all individuals caught afterwards.

At least four sources of variation could contibute to differences in species abundances among reserves: 1) whether or not reserves were isolated, 2) the length of time reserves had been isolated, 3) temporal effects (whether seasonal or multiannual), and 4) reserve location effects. I tested for isolation effects by comparing species abundances in isolated reserves with the distribution of species abundances among the six non-isolated reserves. Since the study ran for less than one year, it was not possible to distinguish between seasonal and multiannual variation in species abundance. Also, since reserves were trapped only once, it was not possible to test for reserve (location) effects.

Habitat features

At each trap station, I stood equidistant between the two traps and within a circle of diameter 6 m counted the number of trees and vines with first branch above 1.25 m, the

the number of trees and vines higher than 0.5 m with first branch below 1.25m, the number of palms higher than 0.5 m, and the diameter (in 10 cm increments) at breast height (DBH) of the largest tree. Slope (in 5^o increments), percent (in 5 percent increments) fallen timber and openness of the canopy, and distance (in 2 m increments) to the nearest "fresh" treefall (defined as having free standing branches) and its DBH (in 10 cm increments) were estimated for each trap station. In addition, DBH of the largest stump, tree or log within 2 m of each trap was measured in 10 cm increments.

Preferred habitat of each species was determined by comparing habitat features at stations where a species was caught with habitat features at stations where the species was not caught. Individuals were assigned only one capture location, either their most frequent capture location, or for those individuals caught equally frequently at more than one capture location, their first capture location.

Night surveys

During night surveys, my assistant and I walked trails within reserves at a slow pace (1.9 km/h) and scanned both sides of the trail using headlamps. Routes were chosen that minimized trail overlap within and among nights, and hence the probability of viewing the same individual. Surveys commenced on average at 1935 h (range 1907 - 2005 h) and continued for 1.8 h (range 0.8 - 2.6 h). Data recorded for each sighting included genus, estimated detection distance when first encountered, perpendicular distance of the mammal to the trail, and height above ground.

RESULTS

Trapping

During 6750 station-nights, 149 **Proechimys**, 105 **Oryzomys capito**, 77 **O. macconnelli**, 2 **O. paricola**, 2 **O. bicolor**, 5 **Rhipidomys mastacalis**, 23 **Marmosa cinerea**, 1 **Marmosa murina**, 27 **Marmosa parvidens**, 23 **Metachirus nudicaudatus**, 34 **Didelphis marsupialis**, 18 **Monodelphis brevicaudata**, and one **Caluromys philander** were captured. Six species (**O. macconnelli**, **O. paricola**, **O. bicolor**, **R. mastacalis**, **M. murina**, and **C. philander**) had not been caught previously in the MCSE reserves.

Abundances among reserves differed significantly for **Proechimys**, **O. capito**, **O. paricola**, **M. cinerea** ($\underline{P} < 0.01$; one-way analysis of variance), and **R. mastacalis** ($\underline{P} < 0.05$) and multivariate analysis of variance indicated significant variation in species abundance patterns among reserves ($\underline{P} < 0.01$). I used canonical discriminant analysis to examine the variation in species abundance patterns among reserves. Canonical variables one and two were significant, accounting for 79 and 11 percent of the variance in the sample respectively. A plot of the two variables revealed two axes of variation (Fig. 1). The first axis, which was largely explained by canonical variable one, separated reserve 1202 from the other reserves, due to high capture rates of **M. cinerea**, **R. mastacalis**, and **O. paricola** in this reserve. I caught 15 **M. cinerea** in this reserve, whereas trapping in other reserves usually yielded only one individual of this species. Reserve 1202 was also unusual because it was the only reserve where **O. macconnelli** was not caught (Table 1). The second axis, which was largely explained by the second canonical variable, was correlated with abundances of **O. capito**, and to a lesser degree, with those of **Proechimys**.

Was the observed variation in species abundance patterns solely due to the isolation history of the reserves? I used pairwise F-ratios (Dixon, 1981) from the canonical discriminant analysis to answer this question (Table 2). Reserve 1202, which had been isolated longest (approximately 3.5 years), was significantly different from all other reserves ($P < 0.01$), and as noted above, accounted for the majority of the variation in the sample. Reserves isolated two to seven months before study (3304, 3209, and 1207) were not significantly different from each other, and in most cases they did not differ from non-isolated reserves. Also, heterogeneity of species abundances patterns was evident among non-isolated reserves, indicating variability not attributable to isolation. Therefore, aside from reserve 1202, little of the variation among reserves could be attributed to isolation.

As noted above, aside from reserve 1202, the major source of variation among reserves was variation in the abundances of **O. capito** and **Proechimys**. As evident from the pairwise F-tests, little of this variation was attributable to isolation. To determine if variation among reserves in abundances of these two species was correlated with time, I regressed mean abundances in the reserves against time of trapping using simple linear regression and second-degree polynomial regression. The second-degree polynomial regression was significant for **Proechimys** ($P < 0.01$; $F_{2,7} = 7.31$) and showed that abundances peaked in December and January. Abundances of **O. capito** also were highest in January, but neither regression was significant. Much of the variation in abundance of **O. capito** was obviously not temporal. Although reserves 2303 and 1302 were trapped in consecutive months, I caught 33 **O. capito** in reserve 2303 and none in reserve 1302. Also, although trapped simultaneously, I caught only three **O. capito** in reserve 1208, and 15 in the recently isolated reserve 1207.

Sample sizes for **Proechimys**, **O. capito**, and **O. macconnelli** were sufficient to compare some demographic parameters among reserves. The ratio of males to females captured did not differ among the reserves (X^2 test, $P > 0.05$ for each species). Approximately equal numbers of male and female **Proechimys** were captured (the ratio of males: females was 75:71), however for **O. capito** and **O. macconnelli**, males outnumbered females (respective ratios were 60:42 and 41:32). Recapture rates did not differ between the sexes for any of the three species, nor did they differ among reserves (sexes combined). For **Proechimys**, approximately 33 percent of individuals were recaptured (the ratio of individuals recaptured to individuals not recaptured was 49:92), whereas for **O. capito**, individuals were more frequently recaptured than not (63:37). Approximately equal numbers of **O. macconnelli** were recaptured and not recaptured (36:31).

Ratios of scrotal: abdominal males and perforate: imperforate females were significantly different among reserves for **Proechimys** and **O. capito** (X^2 test, $P < 0.05$), but not for **O. macconnelli** (Fig. 2a). In general, proportionately more scrotal males and perforate females were caught in reserves trapped after mid-January than in reserves trapped before mid-January. Twenty-eight male **Proechimys** caught before mid-January had abdominal testes, whereas of 21 males caught after mid-January, 7 had scrotal testes. Similarly, for **O. capito**, of 26 males caught before mid-January, 8 were scrotal, whereas 12 of 16 males caught after this date were scrotal. Five of 29 female **Proechimys** caught after mid-January were perforate, however 34 females caught between October and mid-January were imperforate. All of 15 female **O. capito** caught prior to December were imperforate, whereas 14 of 27 caught after December were perforate. **O. macconnelli** showed a similar trend; the proportion of perforate females was higher near the end of the study than at the beginning. Very few of the females captured were lactating. Only two **Proechimys**, one in 3304 and one in 1204, were lactating and only one **O. capito**, captured in 1207, and one **O. macconnelli**, captured in 1302, was lactating.

For each of the three species, I compared head plus body length and body weight among reserves and between sexes using two-way (reserve by sex) analysis of variance. Males were significantly heavier than females in all three species, and in general were longer, although significantly so only for **Proechimys** ($P < 0.05$). Mean body weights and head plus body lengths differed among reserves for all three species ($P < 0.05$). In general, mean size of individuals captured in the reserves increased through the study (Fig. 2c, d).

Average distance between successive captures (D) has been used as an index of home range size (Wolfe, 1968; Fleming, 1971) and for each of the three species was compared between sexes and among reserves using two-way (reserve by sex) analysis of variance. For **Proechimys** and **O. capito**, mean D differed significantly among reserves ($P < 0.01$), but not between sexes. For these two species, individuals caught in reserve 2303 tended to move further between successive captures than those caught in other reserves (Fig. 2b).

Habitat features

For each species except **O. paricola, O. bicolor, R. mastacalis, M. murina**, and **C. philander**, I used multivariate analysis of variance to test whether habitats at locations where individuals were captured differed, on average, from habitats at locations where individuals were not captured. In all cases, the test was not significant. Therefore, the fine-grain distribution of the measured habitat features could not explain the variability in species abundances among reserves.

Night censuses

Greatest survey effort was expended in reserves 3304 (14.2 h) and 1302 (8.1 h) (Table 3). Except for **Dasypus**, more individuals in each genus were observed per hour in 3304 than in 1302. Similar results were obtained if data from 3304 were compared with combined data from all non-isolated reserves (21.9 h of census). To test the significance of this result, I calculated the number of mammals seen per hour for each night of survey and compared these data between reserve 3304 (n = 8 nights) and combined data from non-isolated reserves (n = 12 nights). Means were not significantly different (Mann-Whitney test).

DISCUSSION

Observed differences in small mammal abundance patterns among non-isolated reserves were due primarily to variation in abundance of **O. capito**, and to a lesser extent, of **Proechimys**. At present, it is not possible to distinguish variation due to seasonal and multiannual effects, because the study ran for less than a year, or to separate reserve effects from residual error, because reserves were trapped only once. However, it seems likely that at least a part of the observed variation in abundance was due to reserve effects. Reserves 2303 and 1302 were trapped in consecutive months, yet abundances of **O. capito** in the two reserves differed radically. Little of this variation could be attributed to differences in the measured structural habitat features between the two reserves. In fact, structural features of the habitat, such as proximity to tree fall gaps, tree density, etc., appeared to be unimportant for all of the species frequently captured. It remains possible that demographic features (for example, generally high densities) masked habitat preferences of the various species. Also, several other possible factors may explain fine-grained differences in species abundance patterns. Phenology of fruiting is known to affect movements and distributions of animals in tropical forests (Charles-Dominique **et al**., 1981) and localized differences in rainfall frequency and intensity may lead to localized variations in insect-prey densities or fruiting phenology.

Population densities of **Proechimys** and **O. capito** have been observed to vary seasonally at locations in Central and South America, with maximum densities occurring in the wet season (Davis, 1945; Fleming, 1971; O'Connell, 1981; Guillotin, 1982a; Gliwicz, 1984). Generally, seasonal density fluctuations in the two species have been attributed to seasonal fluctuations in breeding intensity or mortality of offspring. When population levels are highest, the proportion of juveniles in the population is usually greatest(Fleming, 1971; Guillotin,1982b, O'Connell, 1981; Gliwicz, 1984). I also observed peak densities in the wet season; however, I found little evidence of an increased proportion of juveniles in the wet season. Increase in body length of **Proechimys** and **O. capito** (and **O. macconnelli**) through the study instead probably indicated an increase in mean age of the populations. In fact, I obtained very little evidence of breeding during the study. If breeding was starting toward the end of the present study, as sexual condition and possibly movements would seem to indicate, one would expect an increased proportion of juveniles in the population during the dry season (after April) (a curious result given that peak fruiting apparently occurs during the first half of the wet season in the MCSE reserves area (J. Rankin, pers. comm.)). Thus, whether the temporal variation in abundance observed in the present study was seasonal remains unresolved. Certainly, the changes in densities of **Proechimys** and **O. capito** observed in the present study cannot be explained by recruitment. Other possibilities include trapability, mortality and movements. Several years' data will probably be required to understand demographic events in one area, or to compare demographic events among areas. Important questions remain unanswered such as: is breeding seasonal in some years but not in others? does the timing of breeding vary from year to year? and what initiates breeding?

Emmons (1984) censused mammals in the MCSE reserves in 1982, and it is of interest to compare her data from non-isolated reserves with data obtained in the present experiment. It is difficult to compare trapping results directly, as Emmons (1984) used only Tomahawks, whereas in the present study both Tomahawks and Shermans were used and the two traps were close enough together that captures could not be considered independent. However, except for **O. capito**, capture rates are probably directly comparable between studies since all **M. nudicaudatus**, all but two **D. marsupialis**, and most **Proechimys** were caught in Tomahawks. Capture rates of these four genera over the 5.5 month period of Emmons' (1984) study were much lower than average capture rates in the present experiment (Table 4). Similarly, for all genera but **Potos** and **Mazama**, Emmons (1984) observed fewer individuals per hour of night survey (Table 4). Since both of us sampled in the reserves during February through April (in 1982 and 1984 respectively), these data seem to indicate a change in density between years. As was true at other sites (unpub. data cited by Fleming, 1971; Everard & Tikasingh, 1973; O'Connell, 1981; Guillotin, 1982b; Emmons, 1984), **O. capito** showed greater variance between years than did **Proechimys**. The reason for these changes in densities of mammals in the MCSE reserves between years is at present unknown. On Barro Colorado Island, heavy dry season rains in 1970 led to a crash in fruit production, and increased mortality and switching to non-preferred foods among mammal population (Foster, 1980). Rainfall data from July 1981 to June 1984 from Reserve Ducke (approximately 40 km distant from the MCSE reserves) indicated substantial variation in year to year rainfall patterns. The dry season of 1982 was long and pronounced; rainfall during the period July 1982 to February 1983 was only 632 mm whereas respective amounts for the preceeding and following dry seasons were 1187 and 1389 mm (Ribeiro, unpub.data). It is possible that the relatively wet dry-seasons lead to decreased fruit production, as was observed at Barro Colorado Island in 1970. High small mammal populations during the present study may have been the result of pronouced seasonality of rainfall the previous year. The importance of these long term fluctuations in mammal densities for conservation has been noted by Eisenberg & Thorington (1973). Only with an understanding of the long term dynamics of survival of mammal species in the tropics will it be possible to predict minimum population sizes and establish appropriate reserves for maintaining diversity.

Understanding regional variation in species abundance patterns will be equally important. Emmons (1984) made an important first step in comparing mammalian densities among rainforest sites in the Amazon basin. In general, she concluded that mammal densities were low in the MCSE reserves compared to Cocha Cashu and Rio Tambopata in Peru, possibly due to poorer soils. Certainly, the data presented here complicate matters somewhat. Abundances reported here are close to mean abundances from three years at Cocha Cashu, and are greater than those observed at Rio Tambopata. Also, species richness may vary with overall mammalian densities, due to sampling effects. For example, Emmons (1984) did not catch **O. macconnelli** in the MCSE reserves, but in the present study, it was the third most abundant mammal. More recent data from Cocha Cashu indicated an increase in mammal populations (Emmons, in litt.), whereas more recent data from the MCSE reserves indicate that mammal populations have decreased significantly. Thus, it may be that Cocha Cashu usually has greater mammalian densities. To fully test the hypothesis of regional variation in abundances, several years data from each site will be required.

Localized variation in abundance also has important conservation implications. Variation among reserves in undisturbed forest has the potential of producing quite different mammal communities in these reserves for some time after they are isolated. Does initial allotment influence events subsequent to isolation of a reserve?

A comparison of mammal populations in reserve 1202 between 1982 and 1984 suggests that, for some species at least, initial allotment may have a relatively minor effect on subsequent isolation events, because of high turnover in the reserve. When sampled by Emmons in 1982 (Lovejoy **et al.**, 1984), **Proechimys** were apparently absent from reserve 1202. When trapped in 1984, this reserve contained at least 16 individuals. Assuming a home range of approximately 0.6 ha (Guillotin, 1982a), and hence a trapline strip width of 87 m, a more realistic estimate would be 21 individuals. Even if a few individuals were missed in 1982, it is very unlikely that the population sampled in 1984 arose solely from reproduction within the reserve, since most animals captured were adults. Instead, it seems more likely that the high abundance of **Proechimys** in 1202 was largely a function of high population levels in surrounding forest and of ease of invasion from the surrounding forest. Similar reasoning would probably apply for **O. capito**. High population levels of these species in isolated reserves 1202 and 1207 may have resulted from invasion coupled with subsequent frustrated dispersal from within the reserves.

Measurement of variations in abundance of mammalian species in non-isolated reserves has potential use as a measure of expected persistence time in isolated reserves. Species with high coefficients of variation may go extinct relatively rapidly (Wright & Hubbel, 1983). However, Crowell (1973) observed that the presence of three rodent species on oceanic islands was positively related to their variances in abundance. ***Microtus pennsylvanicus*** was most widespread, which Crowell (1973) attributed to more frequent colonization, and also exhibited the greatest variation of abundance in mainland populations. If variation in abundance is positively related to re-invasion potential, and negatively correlated with persistence, then we might expect more variable species such as **O. capito** to exhibit higher rates of extinction and re-invasion than less variable species such as **Proechimys**.

In addition to re-invasion potential, diet type may be an important factor structuring small mammal populations in reserve 1202. High capture rates of **M. cinerea** on the ground in this reserve did not appear to be solely a function of greater abundances in the reserve, since arboreal trapping in 1202 and the non-isolated 1205 indicated approximately equal numbers of this species in the canopy (unpubl. data). Instead, high capture rates on the ground in 1202 suggested a behavioral shift; of the 16 individuals captured in the canopy in 1202, 12 were captured on the ground, whereas of the 13 individuals captured in 1205, only one was captured on the ground. Parallel results have been obtained for birds most abundant mammal. More recent data from Cocha Cashu indicated an increase in mammal populations (Emmons, in litt.), whereas more recent data from the MCSE reserves indicate that mammal populations have decreased significantly. Thus, it may be that Cocha Cashu usually has greater mammalian densities. To fully test the hypothesis of regional variation in abundances, several years data from each site will be required.

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In conclusion, although variability in abundances of tropical mammal populations is becoming increasingly apparent, we are a long way from understanding the causes of this variation. Until more is known about the biology of tropical species, and interactions among species, it seems likely that much of this variation will remain unexplained. In addition to their importance for conservation, studies of tropical forest fragmentation have potential for obtaining insight into the biology of tropical species, and factors structuring tropical mammal communities.

ACKNOWLEDGEMENTS

The sucess of this study was in large part due to the efforts of my assistant, Jairo M. Lopes. I would also like to thank R. Bierregaard, T. Lovejoy, P. Oyens, J. Rankin, and B. Zimmerman for their assistance at various times during the study. J. Eisenberg, K. Redford, D. Stotz, and two anonymous reviewers made helpful comments on the manuscript. Funding was provided by the World Wildlife Fund-US, the Instituto Nacional de Pesquisas da Amazônia (INPA), and the Instituto Brasileiro de Desenvolvimento Florestal (IBDF). This paper represents publication number 28 in the Minimum Critical Size of Ecosystems Project (Dinâmica Biológica de Fragmentos Florestais) Technical Series.

RESUMO

As abundâncias de pequenos mamíferos terrestres foram estimadas em reservas de floresta primária de 10 e 100 ha, isoladas e não-isoladas, perto de Manaus, AM, entre Outubro de 1983 e Março de 1984. O padrão de abundância de pequenos mamíferos numa reserva de 10 ha, isolada há três anos, foi significantemente diferente do padrão em outras reservas, principalmente devido às taxas de captura maiores de ***Marmosa cinerea, Rhipidomys***

mastacalis, *e* ***Oryzomys paricola*** *na reserva isolada. Diferenças dietéticos e de potencial de re-invasão são sugeridas como factores importantes na estruturação de comunidades de pequenos mamíferos em fragmentos florestais. A variação entre as outras reservas foi atribuída primariamente à variação nas abundâncias de* ***Proechimys*** *e* ***Oryzomys capito****. Pelo menos uma parte desta variação foi atribuída a efeitos temporais. No entanto, os dados também sugerem efeitos de localidade das reservas. Pequenos mamíferos foram muito mais abundantes no presente estudo que em 1982.*

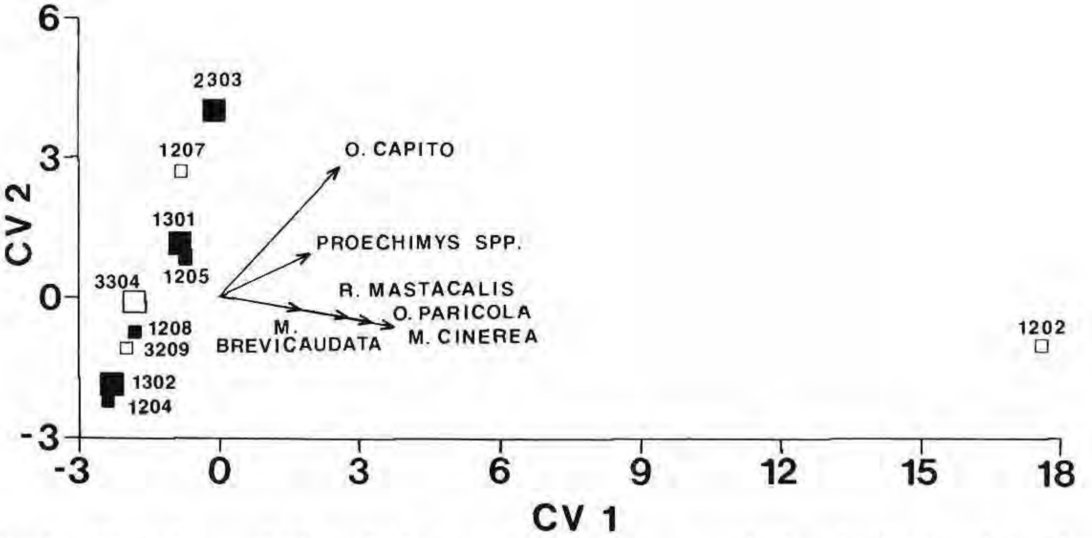

Fig. 1. Plot of canonical variables one and two from a canonical analysis discriminating among reserves. Points represent means from the three to eight traplines in each reserve. Symbol features represent reserve features (small square = 10ha, large square = 100ha, closed square = non-isolate, open square = isolate). Vectors represent correlations (multiplied by four) of the canonical variables with the original variables (species abundances per trapline) and are shown for species with a correlation greater than 0.4. The magnitude of the correlation between an axis of variation in discriminant space and the variation in abundance of a species is indicated by the length and orientation of the vector. Long vectors parallel to the axis represent high correlations.

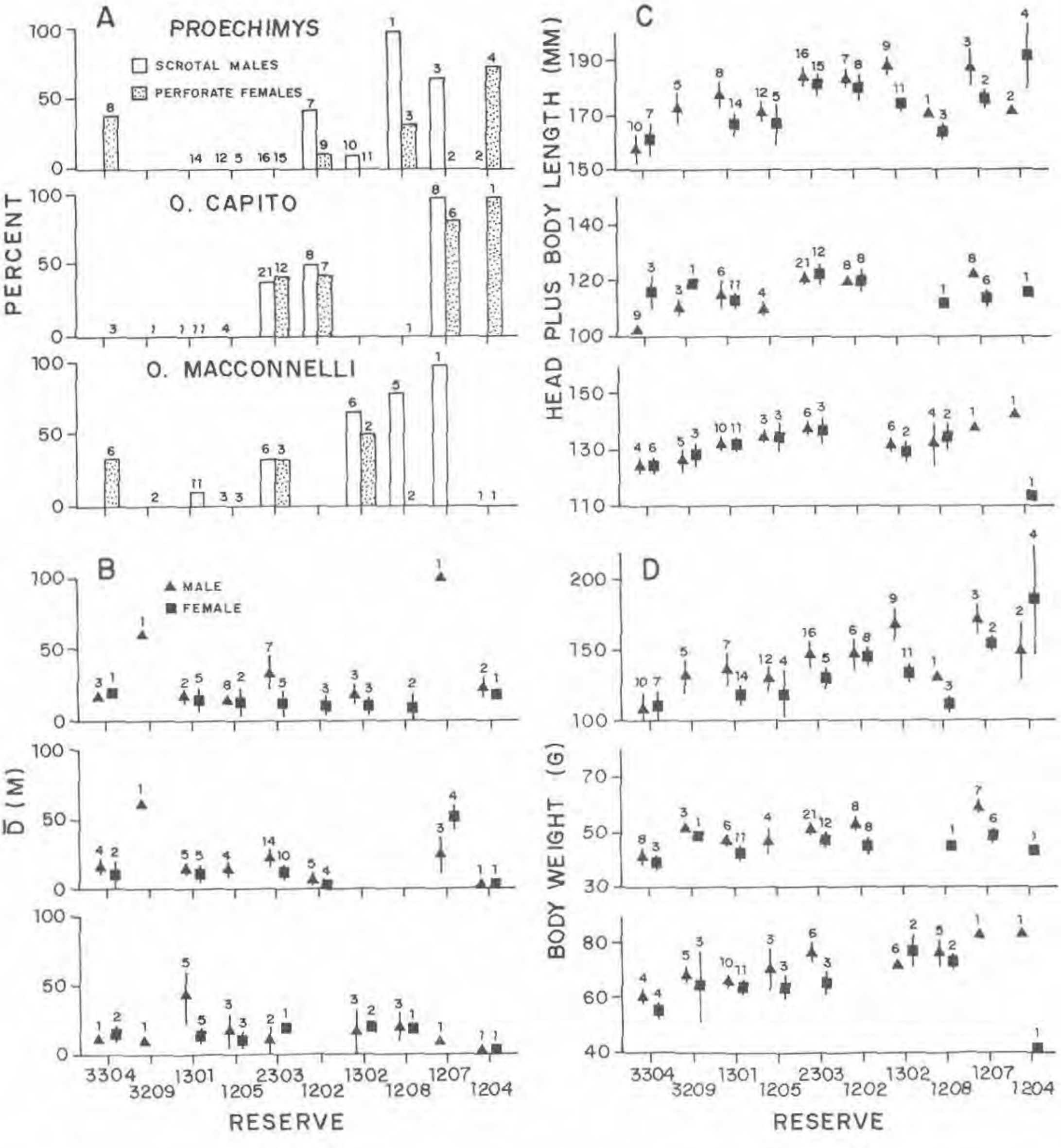

Fig. 2. Sexual condition (A), mean average distance between successive captures (B), and mean head plus body length (C) and body weight (D) of three rodent species captured in 10 primary forest reserves. Order of reserves on the horizontal axis is by date trapped. Verticle bars represent plus or minus one SEM. Numbers above standard error bars are sample sizes.

Table 1. Mean (± SEM) number of individuals per trapline (15 trap stations set for nine nights), number of traplines, number of hectares, date isolated, and date traps first set in 10 primary forest reserves near Manaus, Brazil.

	RESERVE									
	3304	3209	1301	1205	2303	1202	1302	1208	1207	1204
Proechimys spp.	2.25±0.52	1.67±1.20	2.88±0.43	5.67±0.33	4.13±0.94	5.33±0.67	2.63±0.26	1.67±0.88	1.67±1.20	2.00±0.00
Oryzomys capito	1.63±0.75	1.33±0.33	2.25±0.48	1.33±0.88	4.13±0.43	5.67±1.33		0.33±0.33	4.67±0.88	0.33±0.33
O. macconnelli	1.25±0.43	3.33±1.33	2.75±0.43	2.00±0.58	1.13±0.43		1.13±0.61	2.33±0.88	0.67±0.33	0.67±0.33
O. paricola						0.67±0.33				
O. bicolor						0.33±0.33	0.13±0.13			
Rhipidomys mastacalis						1.67±1.20				
Marmosa cinerea	0.25±0.14		0.13±0.13	0.33±0.33	0.25±0.14	4.67±0.88	0.13±0.13	0.33±0.33		0.33±0.33
M. murina								0.33±0.33		
M. parvidens		1.00±1.00	0.50±0.20		0.25±0.14	1.33±0.88	1.25±0.31	0.67±0.33	0.33±0.33	0.33±0.33
Metachirus nudicaudatus	0.25±0.14	0.67±0.33	0.25±0.14	1.00±0.58		1.33±1.33	0.75±0.31		0.67±0.67	0.67±0.33
Didelphis marsupialis	0.38±0.24	0.33±0.33	1.00±0.41	0.33±0.33	1.25±0.48	0.67±0.33	0.38±0.26	1.00±1.00	1.00±0.58	
Monodelphis brevicaudata	0.38±0.13		0.63±0.47		0.38±0.13	1.00±0.00	0.38±0.18			0.33±0.33
Caluromys philander					0.13±0.13					
Number of traplines	4[a]	3	4[a]	3	4[a]	3	8	3	3	3
Reserve size (ha)	100	10	100	10	100	10	100	10	10	10
Date isolated	Aug 1983	Aug 1983				Aug 1980			Aug 1983	
Date traps first set	7 Oct 1983	20 Oct	3 Nov	17 Nov	5 Jan 1984	18 Jan	23 Feb	11 Mar	11 Mar	25 Mar

[a] Traplines consisted of 30 trap stations set for nine nights, hence prior to calculating means, the number of individuals per trapline was halved.

Table 2. Pairwise F statistics (df = 13, 16) comparing reserves in discriminant space. See text for details.

Reserve	3304	3209	1301	1205	2303	1202	1302	1208	1207
3209	0.6								
1301	0.5	0.8							
1205	1.0	1.3	0.9						
2303	2.1	3.1^{a}	1.2	1.5					
1202	28.5^{b}	25.7^{b}	25.9^{b}	22.9^{b}	25.6^{b}				
1302	0.9	0.7	1.9	2.1	5.2^{b}	38.7^{b}			
1208	0.8	1.1	1.1	1.6	2.8^{a}	25.6^{b}	1.5		
1207	1.3	1.5	1.0	2.0	1.4	23.7^{b}	3.5^{a}	2.3	
1204	0.3	0.6	1.2	1.4	3.3^{a}	26.3^{b}	0.3	0.9	2.1

$^{a}P < 0.05$
$^{b}P < 0.01$

Table 3. Number of sightings per hour of night census and census effort in isolated and non-isolated reserves.

	Isolated reserves				Non-isolated reserves						All non isolated reserves
	3304	3209	1202	1401	1301	1302	1204	1105	2303	2206	
Oryzomys	0.14		0.73		0.45				0.59		0.09
Proechimys	0.35	0.37	2.17		1.82	0.12		1.23			0.32
Myoprocta	0.28		0.73			0.25	0.38				0.14
Agouti	0.21			0.56	0.45						0.14
Marmosa	0.14	0.37					0.38				0.05
Metachirus	0.07		0.73				0.38				0.05
Didelphis	0.14										
Potos	0.07										
Dasypus						0.49					0.18
Mazama	0.14										
Unidentified	0.21	0.37	1.45	0.28		0.25	0.38	0.62	0.59	0.45	0.27
Number of census nights	8	2	1	2	1	5	1	1	1	1	12
Total survey time (h)	14.2	2.7	1.4	3.6	2.2	8.1	2.6	1.6	1.7	2.2	21.9

Table 4. Comparison of percent trap success and sightings per hour of night census in the MCSE reserves between Emmons (1984) and the present study.

	Percent trap sucess		**Individuals per hour of night census**	
	Present study[a]	Emmons (1984)	Present study[a]	Emmons (1984)
Oryzomys	1.54[b]	0.06[b]	0.12	0.02
Proechimys	2.21	0.60	0.40	0.14
Myoprocta			0.20	n.c.[c]
Agouti			0.15	0.06
Marmosa			0.10	0.03
Metachirus	0.34	0.03	0.07	0.03
Didelphis	0.50	0.12	0.05	0.00
Potos			0.02	0.03
Dasypus			0.10	0.09
Mazama			0.05	0.05
Unidentified			0.30	0.03
Total	4.59	0.81	1.37	0.48
Sample effort	6750[d]	3434	40.3[c]	66

[a] All reserves combined.

[b] **Oryzomys capito** only.

[c] n.c. = not calculated.

[d] Station-nights (present study) or trap-nights (Emmons 1984).

[e] Hours of night census.

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(Aceito para publicação em 16.09.1988)