BIOLOGY AND NATURAL HISTORY OF BRAZILIAN ATLANTIC FOREST SMALL MAMMALS

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ABSTRACT

During a 17-month study, 20 small mammal species were recorded in the forests of the western slopes of the Brazilian Atlantic coastal region in the state of Minas Gerais. A trapping effort of 57,120 trap nights resulted in 1366 captures of 692 individuals belonging to 8 marsupial and 12 rodent species. Both terrestrial and arboreal traps were used.

The common opossum *Didelphis marsupialis* was the most frequently trapped small mammal, followed by *Marmosa incana*. The spiny rat *Proechimys setosus* was the third most common small mammal and the most abundant rodent species. One marsupial and five rodent species were considered rare in this study, being represented in the sample by two or fewer individuals. Population turnover at the traplines was high for all species, with most individuals only appearing once in the total study sample.

Average body weight for the largest species, *Didelphis marsupialis*, was close to 1000 g, while for the smallest species, *Oryzomys nigripes*, it was approximately 20 g. Sexual dimorphism was common among marsupial species, but rare in rodents. Male marsupials, on average, tended to be larger than females. Male *Oryzomys trinitatis*, on the other hand, were slightly smaller than females.

Most marsupials are seasonal breeders, while rodents tend to reproduce throughout the year. The western slopes of the Atlantic forest are characterized by a pronounced dry season, and reproduction is concentrated in late dry and the early and midwet season. Seasonality of marsupial reproduction was recognized not only by the presence of breeding males and females, but also by juvenile recruitment into the population in subsequent months.

The vast majority of small mammal species have demonstrated a high degree of overlap in substrate use. A large number of small mammals have some level of scansorial ability, even the ones which are more frequently caught at the forest floor. It is also suspected that most species have mixed diets. Therefore, potential competition for resources is a definite possibility.

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RESUMO

Durante um período de 17 meses consecutivos de levantamento, vinte espécies de pequenos mamíferos foram registradas nas florestas da região ocidental da Mata Atlântica Brasileira, no estado de Minas Gerais. Um esforço de captura de 57.120 armadilhas-noite resultou em um total de 1.366 capturas de 692 indivíduos de oito espécies de marsupiais e doze de roedores. Fez-se uso tanto de armadilhas ferrestres quanto de arbóreas.

O gambá comum *Didelphis marsupialis* foi o pequeno mamífero mais frequentemente capturado durante o estudo, seguido por *Marmosa incana*. O rato-de-espinho *Proechimys setosus* foi a espécie mais comum de roedor capturada neste estudo. Uma espécie de marsupial e cinco de roedores foram consideradas raras, sendo representadas na amostra por, no máximo, dois indivíduos. A rotatividade de indivíduos nas linhas de captura foi bastante alta para quase todas as espécies, sendo que a maioria dos indivíduos foram registrados uma só vez no total da amostra deste estudo.

A média de peso corporal para a maior das espécies, *Didelphis marsupialis*, foi de aproximadamente 1.000 gramas, sendo que para a menor espécie, *Oryzomys nigripes*, a media de peso esteve próxima de 20 gramas. A maioria das espécies de marsupiais mostrou dimorfismo sexual, uma característica rara entre roedores. Os machos das espécies de marsupiais tendem a ser, em média, mais pesados e maiores do que as fêmeas. Por outro lado, os machos de *Oryzomys trinitatis* são um pouco menores do que as fêmeas.

As atividades reprodutivas da maioria dos marsupiais são sazonais, enquanto que os roedores se reproduzem ao longo de todo o ano. As encostas ocidentais da Mata Atlântica são caracterizadas por uma estação seca pronunciada, e a reprodução de pequenos mamíferos está concentrada no final da estação seca e no início e meio da estação chuvosa. A ocorrência de reprodução sazonal em marsupiais foi determinada pela observação de machos e fêmeas em condição reprodutiva e pelo recrutamento de jovens na população em meses subsequentes.

A grande maioria das espécies de pequenos mamíferos mostrou superposição no uso de substratos para locomoção, utilizando-se tanto de substratos arbóreos quanto do solo das matas. Um grande numero de espécies demonstra habilidade escansorial, mesmo aquelas que locomovem-se mais frequentemente no solo. Suspeita-se também que a maioria dos pequenos mamíferos possuem dietas mixtas, ocorrendo superposição de vários itens alimenticios. Existe a possibilidade, portanto, de ocorrência de competição por recursos entre estas espécies de pequenos mamíferos.

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INTRODUCTION

The neotropical region encompasses some of the most threatened ecosystems in the world, and yet the mammalian fauna of this area still remains very poorly known (Mares and Genoways 1982). In South America, the Brazilian Atlantic forest has been the vegetation formation subjected to the highest rate of destruction, with less than 5% of the region retaining some form of forest cover (Fonseca 1985a), and probably less than 1% in undisturbed state (Mittermeier et al. 1982). Nonetheless, the few natural history studies conducted on its fauna have indicated that species diversity is quite high, with many faunal elements being unique to the region (Mello-Leitao 1946; Muller 1973; Fonseca, unpublished data). The pioneer works of Moojen (1952), Vieira (1955), and Cabrera (1957; 1961) provide a general data base indicating that there are at least 129 species of non-volant mammals in the Atlantic forest region, about 40% of which are endemic. Were the taxonomy of most of the groups better understood, other species would probably be described. There are at least 23 marsupial and 57 rodent species described for the Atlantic forest, of which 39% and 53 %, respectively, are endemic to the region.

Because of past and present habitat destruction, the fauna is increasingly isolated into small patches, and many members of this unique ecosystem are now endangered. This situation has been documented for the most conspicuous elements of the mammalian fauna, the primates (Coimbra-Filho and Mittermeier 1977; Mittermeier et al. 1982; Fonseca 1985b). Nonetheless, the rich and highly endemic small mammal fauna of the Brazilian Atlantic forest region has been the subject of very few long-term studies, especially when compared to the Amazon region (e.g. Pine 1973; Lovejoy et al. 1984; 1986; Terborgh et al. 1984; Malcolm 1987) or the Cerrado (Alho 1981; Alho et al. 1986; Fonseca and Redford 1984; Lacher et al., in press; Nitikman and Mares 1987). The only detailed study of Atlantic forest small mammals is now over 40-years-old (Davis 1946).

Historically, the Brazilian Atlantic forest extended from the coast to the eastern and portions of the western slopes of the coastal mountains (Hueck 1972; Alonso 1977). This vegetation formation was originally distributed over an area of approximately 700,000 square km. Where rainfall permits the presence of tall, evergreens, this type of forest extends into the western slopes of the coastal formation. Due to a rain shadow, the vegetation of the western slopes, where this study was conducted, possesses a number of deciduous tree species, which lose their leaves during the approximately 6 months of the dry season. During the wet season, however, the forests of both the eastern and western regions are physiognomically undistinguishable. In addition, the faunal elements are mostly the same, generally belonging to the same biogeographical region (Muller 1973).

The objective of this study was to investigate several aspects of the biology and natural history of eastern Brazilian non-volant small mammals. During a 17-months period, data on the general aspects of population dynamics, breeding, substrate use and movement patterns of small mammals (marsupials and rodents) were collected in six forest plots, at three main sites in the state of Minas Gerais, Brazil. Morphometric data were also collected. The present study was part of a larger research project on small mammal community structure, in which it has been shown that primary forests are comparably poorer in species richness and diversity when compared to secondary vegetation in mid-stages of succession. In addition, it was also suggested that predation may exert a high degree of influence on the patterns of community composition and structure in the forest fragments of the Atlantic coastal region of Brazil. Patterns of species composition, relative abundances, habitat preferences, predation pressure and other community structure param are presented in Fonseca (1988).

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MATERIALS AND METHODS

Study Sites

Small mammal communities of six forest plots, two at each of three sites in the state of Minas Gerais, were the subject of this study (Fig. 1). At each site, a primary and a secondary forest plot was selected. The objective was to cover the widest possible spectrum of habitats. A set of three parallel transect trapping lines was established in each. The primary forest plots showed vertical stratification, with an average canopy height of 19 m. Tall buttressed emergents were a common occurrence (Fig. 2a). The herbaceous stratum was somewhat sparse, while the midstory was generally well developed. The secondary forests, on the other hand, were mostly in their mid-stages of succession (Fig. 2b). Average canopy height was approximately 12 m; herbaceous cover was frequently extensive, with masses of tangled vines being a common occurrence. Epiphytes and emergents were conspicuously absent from the secondary forests.

The first site was Fazenda Esmeralda, located in the county of Rio Casca (Fig. 1). The farm is under extensive agricultural use, with very little remaining under forest cover. Located

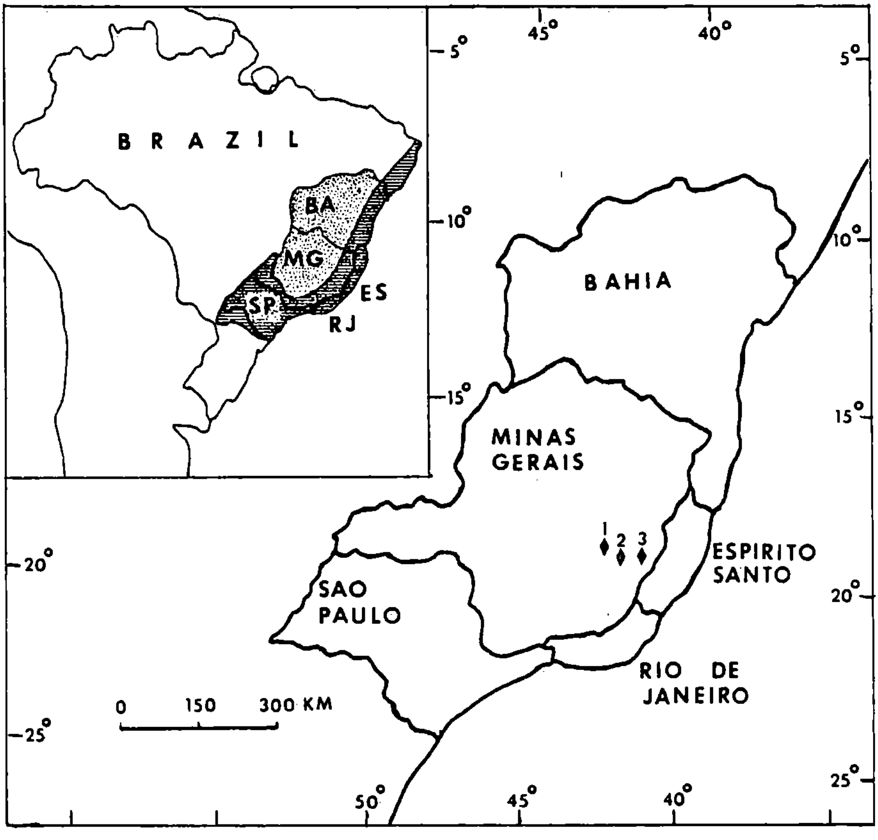

Figure 1. Locations of study sites in the state of Minas Gerais' Brazilian Atlantic forest (1 = Fazenda Esmeralda; 2 = Rio Doce State Park; 3 = Fazenda Montes Claros).

along the plains of the Rio Doce River, the farm was covered almost completely by pristine forest as recently as 1964. Wood extracting rights were then sold to the largest steel industry of the state of Minas Gerais and by 1970 most of the farm was deforested. Forest patches located on the top of two hills were selected for the study, one with a 60 ha second growth, and the other with 80 ha of primary forest, known locally as "Lagoa Fria."

The second site was the Rio Doce State Park (also treated in detail by Stallings 1988), which has portions of its area within the county of Marlieria (Fig. 1). The park, with its 35,973 ha, constitutes the largest continuous area under tropical forest in the state of Minas Gerais. It was created in 1944 and has been under the jurisdiction of the Government of the state of Minas Gerais since that time. Since the creation of the State of Minas Gerais Forest Institute (IEF) in the late 1960s, the park has been under its administration. It has recently become one of the best maintained and protected areas under the Brazilian State Parks system. Because of several extensive fires in the 1960s, a considerable area of the park is second growth. One of these, "Mata do Hotel," was selected as a study area. A pristine primary forest, known locally as "Campolina," constituted the second patch selected for study within the Rio Doce Park.

Fazenda Montes Claros was selected as the third site for this study. It is a coffee and cattle farm located within the counties of Ipanema and Caratinga (Fig. 1). The total area of the farm is about 1200 ha, 860 ha of which remain under forest cover. A research station under the administration of the Brazilian Foundation for Conservation of Nature (FBCN) and the Federal University of Minas Gerais (UFMG) was established on the farm in 1983. A second growth forest patch at Fazenda Montes Claros, known as "Jao," was selected, and another under primary forest, "Matao," was also used.

Figure 2. (a) Secondary forest of Fazenda Esmeralda, one of the study sites. (b - on facing page) Buttressed tree characteristic of the primary forests that were surveyed in this study (photo by Kent H. Redford); Jody Stallings is in the foreground.

Climate

Climatological data were collected at all three sites, but because of the extreme similarity in temperature and rainfall regimes among study sites, only information collected at Fazenda Montes Claros are presented here.

Hueck (1972) states that rainfall for the western slopes of the Atlantic forest region is always below 1600 mm annually. In some areas, it can achieve a little over 1000 mm. A climatogram of Walter (1971), constructed with data collected at this study, can be found in Figure 3. During the study period, the region experienced an unusually dry period; total rainfall for the first 12 months of trapping was 850 mm, while for the last 12 months rainfall totaled 931 mm. Rainfall is highly seasonal, being concentrated between the months of September and February (Fig. 3). Average monthly precipitation for the rainy season was 128 mm, while dry season rainfall averaged only 30 mm monthly.

Mean minimum annual temperature during the study period was about 18° C, close to the average for the region (Hueck 1972). Average daily differences between minimum and maximum temperatures are quite constant throughout the year. Rainfall maxima coincide with the warmest months of the year, while winters are usually very dry. For the purpose of this analysis, the dry season is considered to occur between the months of March and August, and the wet season between September and February.

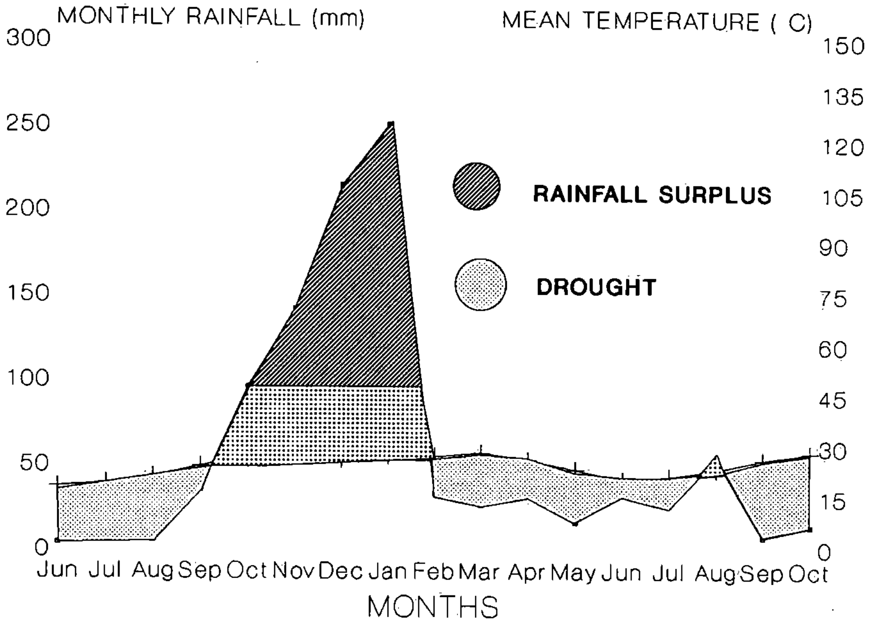

Figure 3. Climate diagram of Walter (1971), constructed using climatological data collected at Fazenda Montes Claros between June 1985 and October 1986. The diagram indicates periods of drought and water surplus. The dry season can be defined between the months of March and August. Temperatures are given in °C, and rainfall in mm.

Trapping

Three transect lines 300 m long were established in each plot at each of the three sites. These transects were as parallel to each other as possible and separated by 100 m. Each transect line possessed 16 trapping stations 20 m apart. Traps were placed in suitable locations within a 3.5 meter radius measured around center of station. A squirrel-size Tomahawk live trap (one-door folding trap, size 203, Tomahawk Live Trap Co., Tomahawk, WI) was placed on the ground at each station. At every other station, a second Tomahawk trap of the same size was wired either to a branch or vine at heights from 1 m to 4 m high. In addition to these traps, every other station possessed a mouse-sized collapsible Sherman trap (H. B. Sherman Traps, Inc., Tallahassee, FL), with alternation of ground and tree traps. Moreover, the two outermost transect lines had, at every other station, a large 80 x 30 x 30 cm wire home-crafted live trap. Therefore, each outer line possessed 16 ground Tomahawk traps, 8 tree-bound Tomahawk traps, 4 ground and 4 tree-bound Sherman traps, and 8 ground large wire traps. The total for each outer line was 40 traps. The mid-line did not have large traps, but a total of 24 Tomahawk and 8 Sherman traps. In summary, each forest plot had 48 trap stations disposed into 3 transects of 16 stations each, and a total of 112 permanent based traps. With the exception of Sherman traps, all traps were closed at the end of each five-night trapping session and left in place. Sherman traps were removed, washed, and replaced each month.

Trapping took place between June 1985 and October 1986, i.e. for 17 consecutive months. Each forest plot was trapped for five consecutive nights every month. During the course of the study, a total of 9520 trap nights was accumulated for each plot. Therefore, trapping effort for all six forest plots together totaled 57,120 trap nights.

Fresh pineapples, oatmeal, and a cotton ball soaked with a commercial codfish oil solution were used as baits. Traps were checked every morning for captures and for adequacy of bait, which was replaced as needed.

For each individual, the following information was recorded:

1. Species. If not readily identifiable, the individual was preserved for later taxonomic identification. The only individuals that were consistently prepared as skins and skulls were representatives of *Oryzomys trinitatis* and *Oryzomys nigripes*. Specimens of the former species show a high degree of variability in skin color and pattern and were considered, during field work, as belonging to more than one species. Whenever possible, animals that died in the traps were also preserved. Moreover, live trapping and snap-trapping were conducted on other locations within the same forest type for preparation of voucher specimens and determination of stomach contents. Taxonomic identification of voucher specimens was provided through the kindness of the following specialists: Drs. M. Carleton, K. Creighton, L. Emmons, G. Musser, P. Myers, and J. Patton.
2. Location in grid.
3. Individual identification. If already tagged with metal fish tags (fish and small animal tag, size 1, National Band and Tag Co., Newport, KY), the animal was promptly released; otherwise the animal was tagged. Individuals with positive taxonomic identification were released at the same station where captured.
4. Sex.
5. Weight.
6. Body length.
7. Tail length.
8. Ear length.
9. Hind foot length.
10. Reproductive condition. Female rodents were checked for perforated vaginas. I also noticed whether individuals were pregnant (in late stages) or lactating. Male rodents were considered in breeding condition if testes were descended. Female marsupials were considered in breeding condition if neonates were found in either pouch or attached to nipples, or if the nipple area showed signs of recent nursing by previous litter. Male marsupials with testes of reduced size were considered pre-pubertal, while

for some species (*Metachirus nudicaudatus*, *Marmosa incana*, *Marmosa cinerea*, *Marmosa agilis*, and *Philander opossum*) abdominal or sternal scent gland activity indicated breeding condition. We also recorded any pouch young old enough to be sexed.

11. Behavior upon release.

Analysis of variance (Procedure GLM: PC-SAS, SAS Institute, Cary, NC) was used to test the null hypothesis of absence of sexual dimorphism, using the following morphological characters: weight, body length, tail length, hind foot length, and ear length. Kruskal-Wallis tests were performed to test for differences in persistence times in traplines among sexes.

Since the number of arboreal traps in each set of three traplines (N=36; 32 %) was different from that of terrestrial ones (N=76; 68 %), analysis of differential trapping success of arboreal versus terrestrial traps was conducted with corrections to account for the differential probability of trapping in the different strata. Where sample size permitted, chi-square tests were performed to test the null hypothesis of lack of difference in substrate use among sexes. For this analysis, all proportions were arc-sin transformed (Sohkal and Rohlf 1981).

RESULTS AND SPECIES ACCOUNTS

During the course of this study, a total of 692 individuals of 8 marsupial and 11 rodent species were caught 1366 times in all six forest plots (Table 1).

Table 1. Trapping results for all six forest plots together during 17 months of trapping.

Species	Number of First Captures	Total Number of Captures
Caluromys philander	6	7
Didelphis marsupialis	144	404
Marmosa agilis	7	11
Marmosa cinerea	43	120
Marmosa incana	127	220
Marmosa microtarsus	1	1
Metachirus nudicaudatus	105	156
Philander opossum	14	29
Abrawayomys ruschi	1	1
Akodon cursor	29	53
Nectomys squamipes	10	14
Oryzomys capito	1	2
Oryzomys nigripes	5	5
Oryzomys subflavus	1	1
Oryzomys trinitatis	84	99
Oxymycterus roberti	2	2
Rhipidomys mastacalis	1	1
Echimys sp.	1	1
Proechimys setosus	110	239
TOTAL	692	1366

One individual of the species *Monodelphis americana* was trapped on one of the auxiliary lines at the primary forest of Fazenda Montes Claros. Mean trapping success, averaged over 17 months of trapping at all sites, was 2.4 %. For most species, trapping success was much higher during the cold, dry months, dropping sharply around October with the onset of rains.

Caluromys philander. Woolly opossums (Fig. 4) were only registered for the Rio Doce State Park. Although occasionally trapped on the ground, this species is mostly arboreal (Davis 1947; Nowak and Paradiso 1983). In this study, only one individual was captured on the ground. Upon release, all individuals climbed into canopies, disappearing from sight at heights of about 10 m. Both the small number of arboreal traps (32%) relative to terrestrial ones, and the absence of traps in higher strata of the forest may have accounted for the low trapping success for this species. Only three males and three females were captured during the course of the study. One female was recaptured once. Morphometric data on these individuals are presented in Appendix 1A.

Didelphis marsupialis. Opossums occurred at all sites and represented the most common small mammal species captured in the majority of forest plots. This is a generalist species, found in all habitat types (Hunsaker 1977; Miles et al. 1981; Alho et al. 1986). Adult males were significantly heavier than females (Appendix 1B). Hind feet were also sexually dimorphic. Other biometric param did not vary between sexes.

Opossums have been previously described as being mainly terrestrial, although they are able to climb opportunely while foraging (Miles et al. 1981). These generalizations were confirmed here. Overall, 73% of *D. marsupialis* captures were from terrestrial traps, while 93% of individuals released also remained on the ground. However, young opossums tend to use aerial substrate more often than adults. Approximately 23% of the individuals released (11 out of 37) climbed into trees and/or onto vines. The same result was obtained by Davis (1947). There were no significant differences in substrate use between adult males and females.

A total of 79 males and 64 females was captured 196 and 204 times, respectively, with sex ratios of both number of individuals and total captures deviating very little from 1:1. Based upon recaptures, males did not persist for long periods on averaging 1.74 months. Females stayed within the traplines an average of 2.6 months, but this difference is not significant ($p = 0.14$). Record persistence times were achieved by one female and one male, which were recorded for a total of 12 months. Fleming (1972) found similar low persistence times for *Didelphis marsupialis* in Panama. If the conclusions of Sunquist et al. (1987) with *D. marsupialis* from Venezuela are extrapolated to

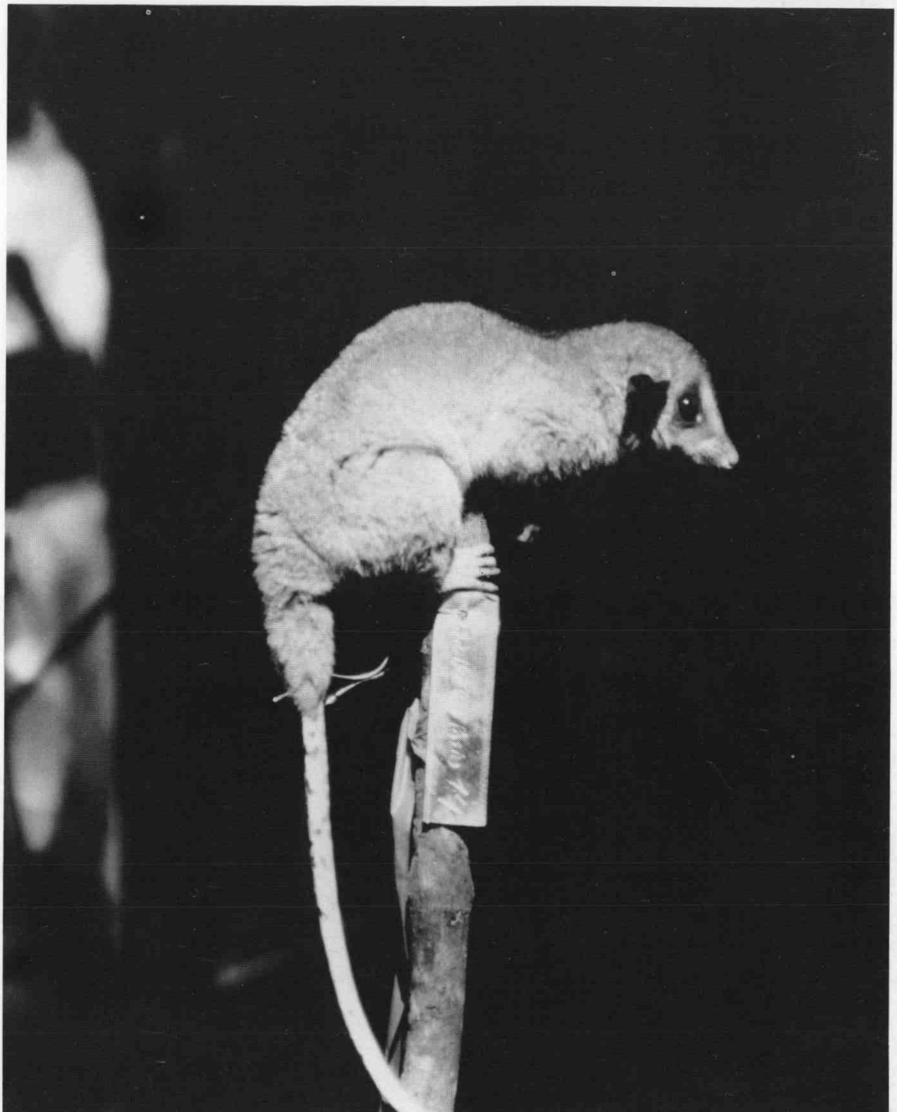

Figure 4. Adult *Caluromys philander* captured at the Rio Doce State Park.

the present study, the low persistence times can probably be attributed to high mortality rates rather than to dispersal.

The distance traveled between successive captures were not significantly different between males and females. The overall mean was 143.4 m (maximum = 400 m), slightly higher than the figure given by Fleming (1972). However, similar to grid trapping methods, traplines underestimate actual distances traveled in a night, which Sunquist et al. (1987) found, using radio transmitters, to average one kilometer.

Even though trapping success during the first three months of study was very high, population levels, as reflected by the number of captures, did not appear to vary between dry and rainy seasons (Appendix 1B). Reproductive activity, on the other hand, was highly seasonal, with most females breeding just prior and well into the rainy season. The number of juveniles recorded also followed this same pattern (Appendix 1B). Two females were recorded as having two consecutive litters, the first in August, and the second in October. The same has been observed in Brazil by Collins (1973 *in* Nowak and Paradiso 1983). The occurrence of two consecutive litters has also been reported elsewhere for *D. marsupialis* in Colombia (Tyndale-Biscoe and Mackenzie 1976) and southeastern Brazil (Davis 1946).

An interesting result was the decrease in opossum abundances during the second year's late dry season, especially in the small forest plots. Smaller plots are where *D. marsupialis* was found to be most abundant during the first year of trapping, and capture success was much lower than for the previous year (Appendix 1B). The reason for this apparent population crash is not yet clear, but may be due to a reduction in food resources that occurred as a result of a severe dry season. Although the reduction in abundance was observed across all plots, smaller forests experienced the highest decrease, lending support to this hypothesis, since populations inhabiting smaller plots should be more susceptible to a decrease in food resources.

Average litter size of pouch young was 8.6, with a M:F sex ratio of 1.7:1.0, highly skewed towards males (Appendix 1B). Overall, two-thirds of females produced male-biased litters. This average litter size is much higher than those obtained in Colombia by Tyndale-Biscoe and Mackenzie (1976) or by Fleming (1973) in Panama. Both studies reported averages of approximately 6.5 young. In addition, these studies found that sex ratios of pouch young did not differ from a 1:1 ratio. Austad and Sunquist (1986) were able to experimentally induce male-biased sex ratios in *D. marsupialis* by providing dietary supplementation. Therefore, relative to the sites studied by Fleming (1973) and Tyndale-Biscoe and Mackenzie (1976), the forests sampled in the present research may be more productive for common opossums, which may have resulted in the observed skewed sex ratios.

Marmosa agilis. This small arboreal marsupial (Fig. 5) can be fairly common in gallery forests of the Cerrado region (Nitikman and Mares 1987), but was infrequently caught in this study. The first individual of the species was recorded only after 12 months of trapping. In total, three males and four females were caught 11 times in two forest plots. Of the 11 captures, 10 (91 %) were in traps placed on trees or vines, which is a capture rate on arboreal traps similar to that obtained by Nitikman and Mares (1987). Alho et al. (1986) also found *M. agilis* to be preferentially arboreal in gallery forest habitat.

Except for two males and one female, which were recorded in traplines for two months, no other animal was recaptured in subsequent trapping sessions. The only individual for which data on movement between trapping stations were obtained traveled 40 m in consecutive nights, a figure very close to that determined by Nitikman and Mares (1987). Biometric data on *M. agilis* are presented in Appendix 1C.

Marmosa cinerea. This species (Fig. 6) is one of the largest within the genus (Nowak and Paradiso 1983) and was fairly common at the Rio Doce Park, but was conspicuously absent from both Fazenda Montes Claros and Fazenda Esmeralda. Most individuals were captured during the cold, dry months (Appendix 1D), with trapping success during the rainy season being fairly low. Lactating females, on the other hand, were only trapped during the rainy season, indicating that the high trapping success of the following months reflected the addition of recently born young into the population.

A total of 8 males and 35 females was caught 120 times (Table 1), making it the species with the highest recapture rate in this study (31% for males and 37% for females). While sex ratio for first captures was 1.6:1.0, total captures approximated a 1.0:1.0 ratio. This might indicate that females are captured more frequently than males, which may be due to the fact that males are more transient than females (chi-square=5.17; df=1, $p<0.02$) and averaged only about 1.8 months in traplines. Females, on the other hand, persisted in the areas for an average of 3.8 months. The longest tenancy in traplines was also by a female that was recorded present for 14 months. In addition, males also traveled farther between successive captures than females (males=142 m, maximum:380 m; females=80 m, maximum:180 m), which also supports the contention that transient males are a frequent occurrence.

On average, adult males were found to be slightly heavier than females. However, the species did not show sexual dimorphism for any biometric parameter measured (Appendix 1D). Although trapped frequently on the ground, *M. cinerea* appeared to be primarily arboreal, especially the females (Appendix 1D). The behavior upon release also revealed that, while 56% of the males remained on the ground, only 27% of the females displayed a similar

Figure 5. *Marmosa agilis*, recorded in Fazenda Esmeralda and Fazenda Montes Claros (Photo by Kent H. Redford).

behavior. Terborgh et al. (1984) list *M. cinerea* as being able to exploit several forest strata, from understory to canopy. Miles et al. (1981) determined *M. cinerea* to be mostly arboreal, with all nests also located above ground.

Marmosa incana. This was the second most frequently caught species in this study (Fig. 7). It was present in all six forest plots sampled. We captured 80 males and 44 females a total of 220 times. Three individuals escaped before their sex could be determined. Sex ratio for first captures was 1.8:1.0, and 2.9:1.0 for all captures. Males also persisted on the traplines more than females (chi-square=8.1, df=1, $p<0.005$), on average 1.9 and 1.2 months, respectively. Therefore, in contrast with *M. cinerea*, *M. incana* males appear to be more sedentary than females. *M. incana* males traveled an average of 64.7 m between successive captures (maximum=200 m), while the only female recaptured in the same trapping session traveled 40 m.

Figure 6. *Marmosa cinerea*, recorded only at the Rio Doce State Park.

Marmosa incana adult males were sexually dimorphic for all morphometric characters measured, with males being, on average, 20% heavier than adult females (Appendix 1E). Body length of males was also 14% larger than of females. Adult females also lack the sternal gland, which is functional in males during the breeding season.

As with *M. cinerea*, trapping success increased markedly with the end of the rainy season (Appendix 1E). This population growth is accounted for by the increase in the number of juveniles trapped (Appendix 1E). The hypothesis that increased trapping success is due to juvenile recruitment is further supported by the observation that the occurrence of breeding males and especially breeding females is tied tightly to mid to late rainy season (Appendix 1E).

Marmosa incana can be characterized as a scansorial species, as its use of arboreal and terrestrial traps was approximately evenly split (Appendix 1E).

Figure 7. *Marmosa incana*, trapped at all study sites.

The same result was obtained by using behavior upon release as a measure of differential substrate use. Approximately 53% of individuals released climbed trees or vines, while 47% remained on the ground. There were no statistical differences in substrate use between males and females (chi- square= 3.19; $p > 0.05$).

Marmosa incana appears highly insectivorous. Three stomachs analyzed in this study contained only insects, mostly belonging to the orders Coleoptera and Orthoptera. Nowak and Paradiso (1983) reported that most members of the genus *Marmosa* are insect and fruit eaters, although vertebrates are also occasionally consumed.

Marmosa microtarsus. During the last month of the survey, October 1986, an adult male of this species was caught in an arboreal trap in the secondary forest of the Rio Doce Park. The species was previously described as being quite abundant in both secondary and primary forests of the Atlantic forest region (Davis 1947). *Marmosa microtarsus* is similar in morphology to *Marmosa agilis*, and it is usually difficult to distinguish them. Morphometric data from this individual are as follows: weight=31 g; body length=106 mm; tail length=148 mm; ear length=14 mm; hind foot=17 mm.

Metachirus nudicaudatus. This relatively large-bodied terrestrial didelphid (Fig. 8) was the third most common marsupial species trapped in this study (Table 1). The brown four-eyed opossum was present in all six forest plots surveyed. A total of 60 males and 45 females were caught 88 and 68 times, respectively. The sex ratio for first captures was equal to that of recaptures (1.3:1.0). Adult males were, on average, larger than females, with most biometric param measured proving sexually dimorphic (Appendix 1F). Males were, on average, 25% heavier than adult females.

Even though the species was relatively common throughout the year, a trapping success peak was observed following the rainy season (Appendix 1F). This peak probably coincides with the onset of breeding in mid rainy season and the beginning of the dry months. Both lactating females and males with functional abdominal glands were frequently caught at this time (Appendix 1F). *Metachirus nudicaudatus* may also be able to produce a second litter in the same year. One female had a litter in March and the second in October. The number of pouch young ranged from 5 to 9, with an average of 7.2 young (Appendix 1F). For the two females in which young were old enough to be sexed, there was a biased sex ratio towards females.

Nowak and Paradiso (1983) regard brown four-eyed opossums as being arboreal, but the species caught in an arboreal trap was only once in 156 captures. Furthermore, only once was an individual observed to use aerial substrate upon being released. In fact, the large and non-graspable hind feet and clumsy behavior on above ground support do suggest a complete terrestrial life for the species. Using a spool-line device, Miles et al. (1981) also found *Metachirus nudicaudatus* to be completely terrestrial. Terborgh et al. (1984) also regard gray four-eyed opossums as a species confined to the ground.

Male and female brown four-eyed opossums did not differ in persistence times in traplines, with both sex classes averaging 1.7 months. Two males and two females were also recorded in traplines over a nine-month period. Distances traveled between successive trapping were among the lowest for marsupials, averaging 36.7 m (maximum = 120 m; N = 6) for males and 40 m (maximum = 80 m; N = 7) for females.

Monodelphis americana. Short-tailed opossums have a fairly wide distribution in Brazil (Streilein 1982). Only one female was caught in an auxiliary line established in the primary forest at Fazenda Montes Claros, for

Figure 8. *Metachirus nudicaudatus*, trapped at all study sites.

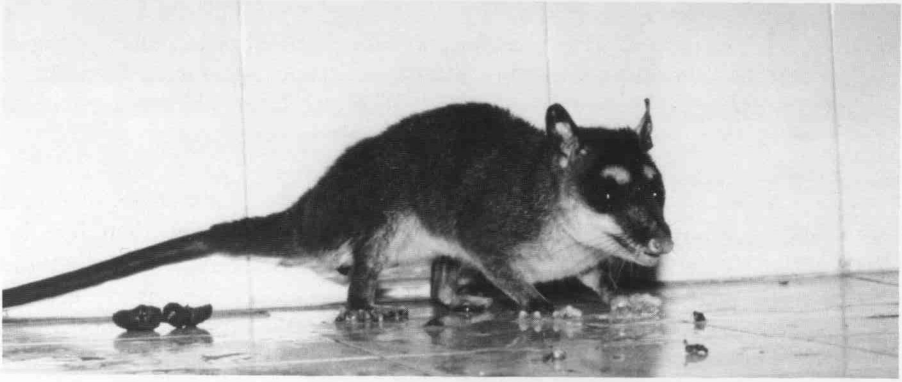

Figure 9. *Philander opossum*, captured at all sites, except at the Rio Doce State Park.

the purpose of collecting voucher specimens. The capture site did not differ physiognomically from the regular traplines, and therefore the species might also occur consistently at this site. However, it is felt that trapping methods were not proper to adequately represent the species. Its small body size and foraging habits on the forest litter may have accounted for its low representation in the sample (Davis 1947). The biometric data on this individual are as follows: weight = 19 g; body length = 92 mm; tail length = 46 mm; hindfoot = 16 mm; ear length = 13 mm. Comparisons with data provided by Nowak and Paradiso (1983) indicate that this individual was probably a juvenile.

Philander opossum. Gray four-eyed opossums (Fig. 9) were trapped in all forest plots, except at the Rio Doce Park. Fourteen individuals were caught during the course of this study. The occurrence of this large didelphid marsupial is apparently tied to the presence of standing or running water (Davis 1947; Handley 1976; Nowak and Paradiso 1983; Alho et al. 1986). As only a few transects occurred close to streams, this may explain the low trapping success for this species. As with other species, trapping success was much higher during the dry season (Appendix 1G).

While only three individual females were recorded, these had a much higher recapture rate; 11 males were caught 17 times, while 3 females were captured in 12 different occasions. The longest persistence times on the traplines were 4 and 5 months, achieved by two adult females.

All females caught were lactating, and two still had pouch young. Nowak and Paradiso (1983), based on several studies, concluded that *P. opossum* breeds aseasonally. However, the small sample size of the present study does not allow any conclusions as to seasonality of reproduction. One female had pouch young in February, while the remaining were caught lactating in August and September. Each had 5 young attached to the nipples. The figure given by

Davis (1947) in the Atlantic forest was an average number of pouch young of 4.5, with a maximum of seven, while litter sizes in Nicaragua were found to be slightly larger (Phillips and Jones 1965). For one litter which sex could be determined, there were four female and one male young.

Even though the small sample size precluded statistical analysis of sexual dimorphism, adult males were on average over 30% heavier than females (Appendix 1G). As noticed by Nowak and Paradiso (1983), in this study the species also proved to be primarily terrestrial with only 17% of captures in arboreal traps, and 7% of individuals climbing trees after being released. Based on field observations, however, it is felt that gray four-eyed opossums are able, if needed, to efficiently use arboreal substrate. The same was suggested by Miles et al. (1981) and Crespo (1982).

Abrawayomys ruschi. This rare monotypic murid rodent, endemic to the Atlantic forest of eastern Brazil, is only known through its type specimen, collected in the state of Espirito Santo (Nowak and Paradiso 1983). A single adult male, with descended testes, was collected at the secondary forest of the Rio Doce State Park in January 1986, for which measurements are as follows: weight=63 g; body=128 mm; tail length=146 mm; hind foot=31 mm; ear length=20 mm.

Akodon cursor. The genus *Akodon* comprises over 40 species, and *A. cursor* is among the largest. Sexual dimorphism is lacking in *A. cursor* (Appendix 1H), although males weighed more than females in another study (Nitikman and Mares 1987). This species occurred frequently in the Rio Doce Park secondary forest, but also was caught occasionally at other sites, especially in some auxiliary lines that were located in humid grasslands. Within the traplines, a total of 29 individuals was caught 53 times (Table 1), 27 of which were trapped at the Rio Doce Park. Sex ratios for first captures and all captures were, respectively, 2.3:1.0 and 3.4:1.0.

Akodon cursor was previously described as being completely terrestrial (Crespo 1982; Alho et al. 1986; Nitikman and Mares 1987). However, the species demonstrated scansorial ability in this study, with approximately one-third of trapping success being obtained at arboreal traps.

A distinct peak in population density was found between May and July. Very few individuals were recorded during the rainy season (Appendix 1H). This was attributed to recruitment of young into the population just at the end of the wet and in the dry season. This conclusion is supported by the observation that the number of males with descended testes closely follows that of trapping success, and coincides with mid dry season (Appendix 1H). Gestation and subsequent weaning are close to five weeks (Nowak and

Paradiso 1983), and the influence of reproduction activity on population density was readily noticeable in terms of increased trapping success.

Akodon cursor appears to be primarily insectivorous. Individuals trapped in both grasslands and forests had high amounts of insects in their stomachs, which possibly indicates that insects are a part of their diets in all habitats. The species also makes use of seeds, fruits, and vegetative parts, especially those of the Graminae (Appendix 1H).

Akodon cursor turnover rates appear very high, with 78% of individuals only being recorded during one trapping session. Maximum persistence was achieved by two individuals, but for only three and four months. The two individuals for which data on travel distances were available, moved 20 and 40 m between successive captures.

Nectomys squamipes. This semi-aquatic rat occasionally was trapped in the vicinities of small streams or flooded areas within forests. Alho et al. (1986) obtained 93% of all the captures of *N. squamipes* in the Cerrado region on flooded areas. A few individuals in the present study were found over 500 m from any source of water, suggesting that the species occasionally may exploit non-aquatic habitats. The three stomachs analyzed contained only vegetative material, two exclusively fruit pulp.

Nectomys squamipes is a fairly large-bodied rodent, with males attaining over 250 g (Appendix 1I). A total of eight males and one female was recorded in tree plots, one at each of the study sites. Another individual escaped before sex could be determined. All but one individual was caught during the mid dry season, i.e. between May and August.

Although adapted for semi-aquatic life, *N. squamipes* were trapped 38% of the times in arboreal traps. Two males persisted in the areas for three and four months, respectively.

Oryzomys capito. A widespread habitat generalist, this rodent is extensively distributed in South America (Handley 1976). It is possibly mostly terrestrial, and in the Cerrado region was found more commonly at dense forests (Alho et al. 1986; Nitikman and Mares 1987). However, it was a rare species in the forests sampled in this study and was represented by only one male and one female at the Rio Doce Park, both caught in September 1986. All captures were on ground traps. The measurements of these individuals are, respectively: weight=60 and 63 g; body length=122 and 132 mm; tail length=115 and 129 mm; hind foot= 32 and 34 mm; ear length=22 and 21 mm.

Oryzomys nigripes. This small cricetid rodent commonly occurred at auxiliary traplines located in grasslands, and it has wide distribution among Cerrado habitats (Alho et al. 1986; Nitikman and Mares 1987). It was, however, relatively uncommon in forests. Only five individuals, two males and three females, were caught in forest traplines. All trappings were done in mid to late rainy season, i.e. between January and April. Two of these captures were on arboreal traps, although it is felt that the species is certainly more terrestrial and/or scansorial, as it was also observed by Crespo (1982). Alho and Pereira (1985) in Cerrado gallery forests and Veiga-Borgeaud (1982) in the Atlantic forest region determined that *Oryzomys nigripes* (=*eliurus*) makes extensive use of low shrubs, with nests located about 1 meter from ground.

Stomach contents revealed high frequency of insects, complemented by fruit, seeds and leafy material (Appendix 1J). Barlow (1969 *in* Dalby 1975), and Crespo (1982) also found insects as part of *O. nigripes*' diet, even though in lower proportions. Biometric data are presented in Appendix 1J.

Reproduction occurs throughout the year, albeit it may increase in frequency at some periods. Two females, one caught in February and the other in August, both had four fetuses, coinciding with two major reproductive peaks observed by Veiga-Borgeaud (1982). A third female, trapped in April, had five implanted fetuses.

Oryzomys subflavus. Only one female of this otherwise fairly common Cerrado species (Melo 1977; Alho and Pereira 1985; Alho et al. 1986) was caught in an arboreal trap in the forest traplines. The measurements of this individual are as follows: weight=92 g; body length=165 mm; tail length=173 mm; hind foot=34 mm; ear length=25 mm.

Oryzomys trinitatis (=*concolor*). This cricetid (Fig. 10) was the most frequent rodent found in the forests sampled, being present at all sites. It is widely distributed, from Costa Rica to Paraguay (Nowak and Paradiso 1983), and found mostly in forested habitats (Alho and Pereira 1985; Nitikman and Mares 1987). A total of 84 individuals was captured 99 times (Table 1). Due to coat color variation, most individuals were prepared as skins. Therefore, recapture figures underestimate true recapture rates. Sex ratios at first captures were 1.35:1.00. In contrast to other small mammal species observed in this study, females were slightly heavier and longer than males. Other biometric param were found not to be significantly dimorphic (Appendix 1K).

The species appears to be mostly arboreal. Approximately 74% of males and 62% of females were captured in arboreal traps (Appendix 1K). This figure is very close to that observed by Nitikman and Mares (1987) in a gallery forest of Central Brazil. Males and females did not differ in degree of arboreality (chi-square=2.40; df=1; $p>0.05$). Since most individuals were prepared as voucher specimens, sample size was too small to evaluate the

Figure 10. *Oryzomys trinitatis*, captured at all study sites.

differential use of substrate by analyzing behavior upon release. However, the few individuals that were released demonstrated climbing ability. Even though relatively uncommon in the forests of Manu National Park in Peru, *Oryzomys trinitatis* (=*concolor*) was listed by Terborgh et al. (1984) as being able to use most all forest strata, from the understory to canopy.

Although there were variations in trapping success on a monthly basis, there does not seem to exist any season characterized by high population, in contrast to most other species (Appendix 1K). This might be a consequence of the absence of seasonal breeding. Reproduction seems to take place throughout the year, as breeding males and females were captured in 14 out of 17 months of study (Appendix 1K).

The two stomachs available for analysis indicated a high degree of insectivory. The stomach contents of an individual were 100% insects, while a second had 48% unidentified insects and coleoptera larvae, and 52% fruit pulp.

Oxymycterus roberti. This genus includes semi-fossorial cricetids. The genus is represented in these forests by only one juvenile male and one adult female of the species *roberti* (Table 1). Members of this genus are mostly insectivorous (Borchert and Hansen 1983; Redford 1984); two stomachs analyzed in the present study yielded 100% insects, especially Coleoptera larvae and ants. Species of the genus *Oxymycterus* are more commonly found in grasslands and inundated savannas (Borchert and Hansen 1983; Fonseca and Redford 1984; Redford 1984), a habit which can account for the rarity of the species in the forests of this study. Biometric data for the male and female are, respectively: weight=57 and 85 g; body length=124 and 245 mm; tail length= 111 and 112 mm; hind foot=27 and 30 mm.

Rhipidomys mastacalis. This arboreal rat (Fig. 11) was only caught once in this study, in the month of September. It is found mostly in moist, forested habitats (Davis 1947; Dietz 1983; Fonseca and Redford 1984; Alho et al. 1986), even though it can also invade households (Nowak and Paradiso 1983; J. Stallings, pers. comm.). The adult male measurements are as follows: weight=72 g; body length=137 mm; tail length=161 mm; hind foot=27 mm; ear length=18 mm.

Echimys sp. Members of this genus are entirely arboreal (Hershkovitz 1969). This may explain the low success in recording this species in the forests sampled. It is possible that it preferentially occupies higher canopy strata. Davis (1947) never trapped *Echimys* below 5 m, while Miles et al. (1981) found nests of *Echimys chrysurus* in tree cavities located at the canopy level.

Only one adult male was caught on the primary forest of Fazenda Montes Claros in July 1986, in an arboreal trap. The voucher specimen could not yet be identified beyond genus, but may possibly either be *Echimys brasiliensis*

Figure 11. *Rhipidomys mastacalis*, a rare species in the forests trapped in this study.

(*sensu* Moojen 1952) or a species which has not been described (L. Emmons, pers. comm.). This specimen had the following measurements: weight=225 g; body length=215 mm; tail length=205 mm; hind foot=38 mm; ear length=14 mm.

Proechimys setosus. Spiny rats were the third most abundant small mammal in this study (Table 1). Only opossums surpassed *P. setosus* in number of recaptures. Even though species of the genus *Proechimys* were also found to be quite common in other studies in the Atlantic forest (Davis 1947; Carvalho 1965; Avila-Pires and Gouvea 1977; Botelho and Linardi 1980; Miles et al. 1981; Fonseca et al. 1987), in the Cerrado (Fonseca and Redford 1984; Alho et al. 1986) and in the Amazon region (Bishop 1974; Emmons 1982; 1984; Terborgh et al. 1984; Malcolm 1987), spiny rats were surprisingly absent from the Rio Doce Park traplines. This can possibly be attributed to higher predation rates by mammalian carnivores, owls and other predators at the Rio Doce Park (see Fonseca 1988). The park has a larger and richer carnivore fauna which exert a larger impact upon *P. setosus* populations than the comparatively depauperated predator community of the smaller forest plots.

Sex ratios of first captures deviated little from a 1:1 sex ratio, with 56 male and 49 female individuals being trapped. Five individuals escaped before their sex could be determined. Females were recaptured at a slightly higher rate than males, yielding a sex ratio for all captures of 0.83:1.00.

Although spiny rats were caught in all 17 months of the study, a distinct mid to late dry season peak in trapping success was notable (Appendix 1L). This may result from the increase in the recruitment rate of juveniles into the population at this time (Appendix 1L). However, reproduction does not seem to be strictly seasonal, as it was also observed by Bishop (1974) in Mato Grosso, Brazil. Pregnant and lactating females were present in all trapping sessions, although an increase in the frequency of breeding individuals could be observed both in mid rainy season and in mid dry season (Appendix 1L). A few females had two litters in the same year, coinciding with the abovementioned breeding peaks.

There is no sexual dimorphism in this species of spiny rat, as none of the morphological characters measured significantly differ between sexes (Appendix 1L). *Proechimys setosus* is entirely terrestrial, lacking any scansorial ability. All 239 spiny rat captures were conducted in terrestrial traps. Analysis of stomach contents indicate that spiny rats are primarily frugivorous, but also make opportune use of insects and seeds (Appendix 1L). Emmons (1982) found *Proechimys* to be highly frugivorous, with insects being frequent in stomach samples.

Although, on average, females persisted in traplines more than males (respectively, 2.7 and 2.0 months), there were no significant differences between sexes (chi-square = 0.58, df = 1, $p > 0.05$). The records for persistence times were obtained by two females who stayed, respectively, 10 and 12 months within traplines. Males and females also did not differ in mean traveled distances between successive captures with, respectively, 98.7 (maximum = 220 m) and 87.5 m (maximum = 240 m).

DISCUSSION

Seasonality and Resource Use

One of the most striking phenomena common to several small mammals of the western slopes of the Atlantic forest is the occurrence of seasonal reproduction. With the exception of the two most abundant rodents (*Oryzomys trinitatis* and *Proechimys setosus*), all four species with sufficient sample size to allow analysis proved to concentrate breeding in the late dry season and into the early to mid wet season. These were all marsupials. The evidence for these patterns derive from both the increase in trapping success starting in late wet season, represented mostly by the addition of juveniles, as well as the observation of adults in breeding condition just previous to that period. Furthermore, the number of first-time captures of all small mammals is significantly and negatively correlated with average monthly precipitation ($r=0.55$; $p<0.02$), which indicates that recently weaned juveniles are recruited into the population at the end of the rains. *Akodon cursor* is also a seasonal breeder, but unlike marsupials its reproduction is concentrated in the dry season.

Davis (1946) and Laemmert et al. (1946) observed a pattern of cyclic reproduction among several Brazilian Atlantic forest small mammal species. Breeding was concentrated in the late dry winter and in the wet summer months, albeit less marked than in the present study. The possible reason for this may be that both these studies were in the eastern side of the Brazilian coastal mountains, where the dry season is shorter and less severe (Hueck 1972). These two studies have also revealed the lack of seasonality for some rodent species, especially ones from the genus *Proechimys*, which probably breed year-round throughout its range.

A large number of African rodents seem also to closely tie the onset of reproductive activities to just before the end of the wet season (Delany 1986). Cerrado species appear to be equally divided between seasonal and year-round breeders (Dietz 1983; Alho 1982; Alho and Pereira 1985). In Panama, over 50% of mammals are seasonal breeders (Fleming 1973), although reproduction is concentrated in the three months of the dry season, which results in most young being weaned at the beginning of the rains.

Other things being equal, reproductive output and juvenile survival of small mammals would be maximized if reproduction occurred when the environment is best in terms of resource availability (Fleming 1975). In fluctuating environments the energetic costs of pregnancy and lactation, coupled with the needs of adequate resources for newly weaned young, should pose constraints on the timing of reproduction. Lee and Cockburn (1985) state that all tropical didelphids are seasonal breeders, and the timing of reproduction is linked with availability of food. Marsupial food resources, in turn, are tied to the fluctuation in rainfall regimes of seasonal environments (Charles-Dominique 1983). Information on small mammal diets in this study are not sufficient to provide an accurate and longitudinal picture of diet composition. However, it is important to notice that all but the semi-aquatic *Nectomys squamipes* were observed to consume insects in variable quantities. All didelphid marsupials appear to be predominantly insectivorous (Nowak and Paradiso 1983), and even large-bodied species, such as *Didelphis marsupialis* and *Philander opossum*, depend heavily on insect prey (Charles-Dominque 1983). *Metachirus nudicaudatus*, *Marmosa* spp., and *Caluromys philander* have also been listed as being consumers of ants and termites (Redford 1987), although the latter species may rely more heavily on fruits (Atramentowicz 1982).

Results of studies on insect population fluctuations in the neotropics vary (see Elton 1975; Bigger 1976; Janzen and Schoener 1968; Janzen 1973; Wolda 1978), but most authors agree that samples obtained in wet season months are larger than comparable ones collected during the dry months (Davis 1946; Wolda 1978; Smythe 1982; Charles-Dominique 1983). Therefore, the trends of this study certainly support the notion that small mammal reproduction, especially that of marsupials, is influenced by availability of insect prey. However, until the variation in the cycles of prey populations across the year are described, explaining timing of reproduction of small mammals as a consequence of abundance of insect prey in the late wet to early rainy season will remain speculative.

Fruits and seeds were the other frequent items present in the stomachs of small mammals in this study, although it is felt that rodents may depend more heavily on these resources than the more insectivorous marsupials. If the number of trees with fruits can serve as a measure of food resource availability for small mammals, the timing of reproduction of most small mammal species seems to track that of resources. In the Brazilian Atlantic forest asynchronously fruiting trees may be found at every month of the year (Davis 1946). Nonetheless, fruit production of several plant species of seasonal neotropical environments has been shown to be influenced by precipitation, usually peaking just prior to the start of the rainy season (Foster 1982; Smythe et al. 1982; Charles-Dominique 1983). A second peak in fruit productivity can also be present at the end of the rainy season (Davis 1946). A preliminary study conducted in the Rio Doce Park (CETEC 1981) also indicated that there are tree species flowering and fruiting throughout the year, and also that there is a slight peak in the number of fruiting species in September and October, i.e. in early rainy season.

I expected marsupials, which use invertebrates to a larger extent than rodents, to display a higher degree of seasonality due the more fluctuating nature of their food resources. This was observed in the present study. Rodents, on the other hand, can probably rely on resources which are more seasonably stable in the Atlantic forest, such as fruits, seeds, and leaf tissue, and thus can reproduce throughout the year. The two most common rodents, *Proechimys setosus* and *Oryzomys trinitatis*, do not show seasonality in their reproductive patterns. Since they also have been shown to use and during some periods heavily rely on insects, the consequent larger resource spectrum should place lower limits on the reproduction of rodent species.

While some small mammals may exploit resources on the forest floor, most of the tropical forest productivity is located above ground (Eisenberg and Thorington 1973). Therefore, even for primarily terrestrial species, some level of scansorial ability should prove advantageous. There was a high degree of overlap in substrate use among small mammal species in this study. Twelve species are shown to use both aerial and ground substrate regularly, even though their relative degrees of arboreality varied. Among marsupials, only *Metachirus nudicaudatus* was confined to the ground level of the forest. Only 4 of 11 rodent species can be safely classified as terrestrial, while the remaining are at least marginally arboreal. This is consistent with descriptions of other neotropical small mammal fauna, where the majority of species show some level of climbing ability (see August 1984; Fonseca et al. 1987; Nitikman and Mares 1987).

It should be stressed that these findings do not imply that arboreality is the dominant mode of life among Atlantic forest small mammals. Of the species caught in the present study, only *Caluromys philander, Marmosa cinerea, Marmosa agilis, Oryzomys trinitatis, Rhipidomys mastacalis*, and *Echimys* sp. can be regarded as predominantly arboreal. It does, however, indicate the widespread ability of a greater fraction of the community in exploring a tri-dimensional environment. This may be especially important during certain periods of the year. Charles-Dominique (1983) provided data indicating that the insect faunas of the canopy and of the undergrowth can fluctuate asynchronously with each other. Therefore, if a particular food resource is undergoing a period of seasonal shortage, those species with versatile habits would be at an advantage. It has been demonstrated before that in the highly seasonal savanna region of central Brazil gallery forests play an important role in maintaining overall mammalian species diversity (Fonseca and Redford 1984) and become crucial during periods of stress. Part of the reason for this may be linked to the higher productivity of the tri-dimensional gallery forest environment, when compared, during periods of moisture deficit, to that of the cerrado savannas.

Life History Patterns

While the occurrence of pouch litters with skewed sex ratios in neotropical marsupial species has not often been reported, it was interesting to find *Didelphis marsupialis* with litters having a predominance of males. Skewed sex ratios have only been achieved experimentally under a regime of diet supplementation, a procedure which does not always produce the predicted male bias outcome (Austad and Sunquist 1986). Therefore, it is important that future investigations address this question. The female-biased sex ratio obtained for *Metachirus nudicaudatus* pouch young is not based on a large enough sample size and therefore remains inconclusive.

Three out of four marsupial species, for which sample size was large enough to allow statistical inference, proved sexually dimorphic. Male *Didelphis marsupialis* also has been found to be larger than females elsewhere in South America (O'Connell 1979). Other *Marmosa* species also have larger and heavier males (Nowak and Paradiso 1983), the same being true for *Philander opossum*. No references have been found to indicate size differences for *Metachirus nudicaudatus*, except for the present study. While larger males usually have been associated with polygynous species in which males strongly compete for females (Ralls 1976), there was no evidence of territorial defense by any of the marsupials studied here. However, this does not necessarily preclude males from actively competing for females at overlapping ranges. Fierce fighting for estrous females has been observed elsewhere in *Didelphis marsupialis* (Austad and Sunquist 1986). Since marsupial breeding in this study was usually confined to a certain season, the potential for male-male competition for estrous females is likely.

Rodents, on the other hand, are seldom dimorphic (see Eisenberg 1981), especially the smaller species. In only one species, *Oryzomys trinitatis*, could a size difference be found in this study. In this instance, however, females proved to be larger on average than males. This could be attributed to extra energetic demand placed on pregnant and lactating females, a cost non-existent for males who do not provide parental care (see Ralls 1976). Moreover, since rodent young do not undergo, unlike marsupials, a teat attachment phase, female placental mammals may increase litter size above that of the teats. The increase in rodent litter sizes may be achieved if the female is larger and better nourished. Marsupial litter sizes, on the other hand, due to the obligatory teat attachment phase, are constrained by the number of teats. Furthermore, marsupials can spontaneously terminate lactation, or more often in smaller species reduce litter size if energetically stressed (Lee and Cockburn 1985). Young are also born after a very short gestation period, making the reproductive investment minimal. For these reasons no added security would be achieved by genetically fixed propensity for larger marsupial females.

Population Turnover

Although the area sampled by traplines was not enough to represent the home range of several species, especially the larger ones, the reduced persistence time of the average small mammal individual was nonetheless striking. Average persistence times ranged from 1.2 months for male *Marmosa* *incana* to a maximum of 3.8 months for *Marmosa cinerea* females, with most species remaining in traplines within the range of 1.7 to 2.7 months. While it is reasonable to assume that some of the disappearances can be attributed to home range shifts (see Nitikman and Mares 1987) and/or juvenile migration and dispersal (Lidicker 1975), predation might also play an important role in increasing turnover rates among tropical small mammals. Monthly turnover rate for the small cricetid rodent *Akodon cursor* approached 80% in this study. Several authors have suggested that predators might cause variations in local abundances (August 1983), and sometimes they do take a large percentage of small mammal standing biomass (Hershkovitz 1969; Pearson 1985; Emmons 1987; Sunquist et al. 1987). Predation in traps was observed in this study on several occasions and it is felt that it may play a major role in the structure of these communities (Fonseca 1988).

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APPENDIX I -- A-L.

A. *CALUROMYS PHILANDER*

Biometric data for three males and three females of *Caluromys philander*. Weight is given in gms, and other body measurements in mm.

	MALE		FEMALE	
	Mean	St.Dev.	Mean	St.Dev.
Weight	171.3	57.6	180.5	40.5
Body length	210.7	30.0	206.8	11.4
Tail length	301.0	25.9	298.8	20.7
Hind Foot	36.3	2.5	36.3	2.6
Ear length	33.3	1.5	30.5	1.9

B. *DIDELPHIS MARSUPIALIS*

Biometric data for adult male and female *Didelphis marsupialis*. Weight is given in gms, and other body measurements in mm. N=number of individuals, St. Dev.=Standard Deviation. P refers to p-value associated with analysis of variance for sexual dimorphism (n.s.=$p>0.05$; *=$p<0.05$; **=$p<0.01$; ***=$p<0.001$).

	MALE			FEMALE			
	Mean	St.Dev.	N	Mean	St.Dev.	N	P
Weight	1,024.0	361.4	63	946.0	157.0	34	**
Body length	354.0	40.4	63	354.0	29.7	34	n.s.
Tail length	348.5	30.9	62	349.6	27.4	31	n.s.
Hind Foot	58.1	3.9	62	56.1	4.3	34	**
Ear length	51.2	4.2	62	50.0	3.6	34	n.s.

Litter sizes and sex ratios of *Didelphis marsupialis* pouch young.

ID Number	Number of Female Young	Number of Male Young	Total Young	Sex Ratio M:F
0076	-	-	9	-
0088	-	-	9	-
0055	-	-	7	-
0072	-	-	9	-
0087	-	-	9	-
0126*	-	-	3	-
0156	-	-	7	-
0162*	-	-	4	-
0067	-	-	7	-
0192	-	-	7	-
0193	-	-	10	-
0209	3	6	9	2.0:1.0
0072**	-	-	9	-
0081	-	-	11	-
0220	-	-	8	-
0251	-	-	8	-
0257	-	-	8	-
0258	-	-	8	-
0274	3	5	8	1.7:1.0
0209**	2	7	9	3.5:1.0
0278	-	-	5	-
0281	3	4	7	1.3:1.0
0227	5	5	10	1.0:1.0
0480	5	5	10	1.0:1.0
14/10	2	7	9	3.5:1.0
42P	2	5	7	2.5:1.0
11/12	4	4	8	1.0:1.0
Means			8.6	1.7:1.0

*Females were in poor condition, with multiple injuries. Therefore, their litter sizes were not used in calculating means.
**Second consecutive litter.

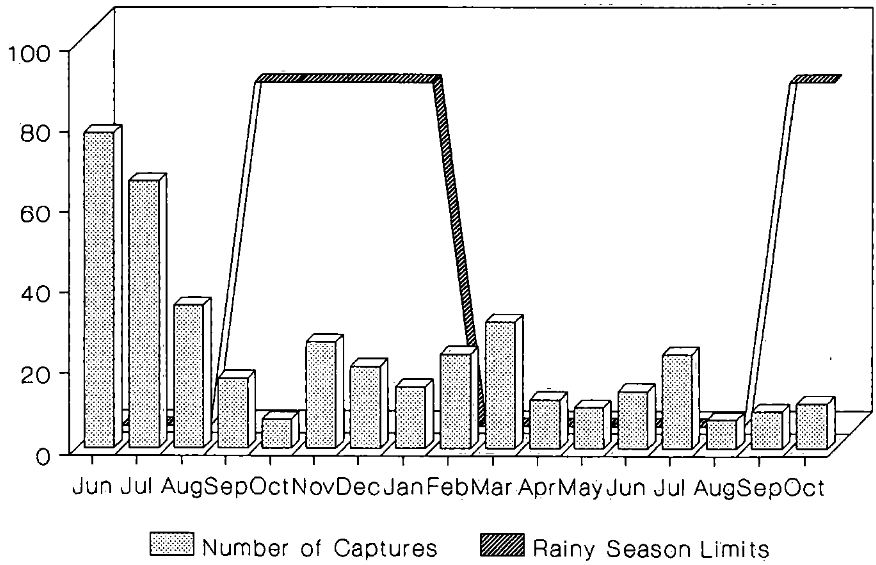

Figure 12. Number of captures of *Didelphis marsupialis* according to monthly trapping period. Straight lines enclose boundaries of rainy season (September to February).

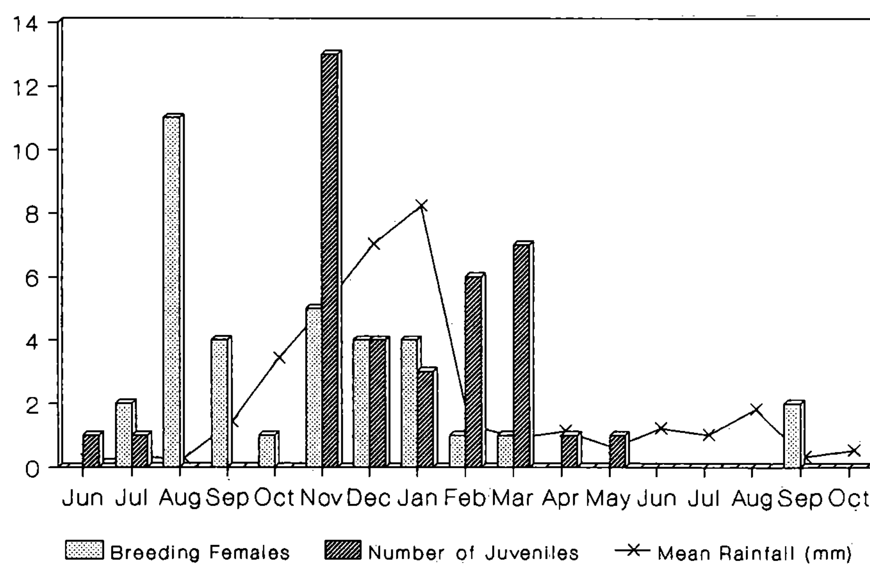

Figure 13. Number of breeding females and juveniles of *Didelphis marsupialis*, according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

C. *MARMOSA AGILIS*

Biometric data for four males and one female *Marmosa agilis*. Weight is given in gms, and other body measurements in mm.

	MALE			FEMALE		
	Mean	St. Dev.	N	Mean	St. Dev.	N
Weight	29.5	11.3	4	25.0	-	1
Body length	109.3	13.2	4	99.0	-	1
Tail length	155.3	7.1	4	151.0	-	1
Hind Foot	18.3	1.5	4	17.0	-	1
Ear length	20.5	0.6	4	21.0	-	1

D. *MARMOSA CINEREA*

Biometric data for adult male and female *Marmosa cinerea*. Weight is given in gms, and other body measurements in mm. P refers to p-value associated with analysis of variance for sexual dimorphism (n.s. = $p>0.05$; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$).

	MALE			FEMALE			
	Mean	St. Dev.	N	Mean	St. Dev.	N	P
Weight	117.3	29.4	24	99.7	16.7	11	n.s.
Body length	176.1	20.0	24	177.1	20.5	11	n.s.
Tail length	258.9	26.0	24	261.7	17.9	11	n.s.
Hind Foot	28.9	3.9	24	28.0	3.1	11	n.s.
Ear length	30.4	2.8	24	29.7	2.1	11	n.s.

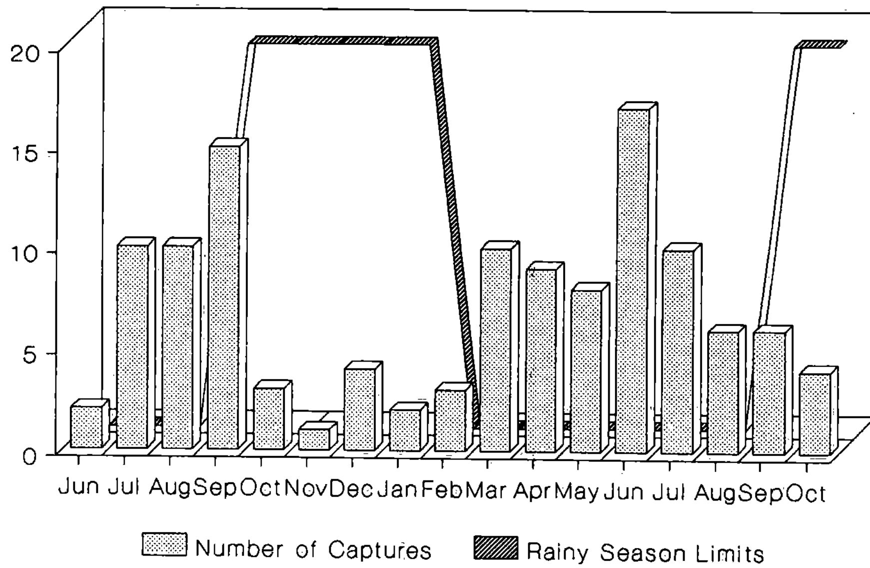

Figure 14. Number of captures of *Marmosa cinerea* according to monthly trapping period. Straight lines enclose boundaries of rainy season (September to February).

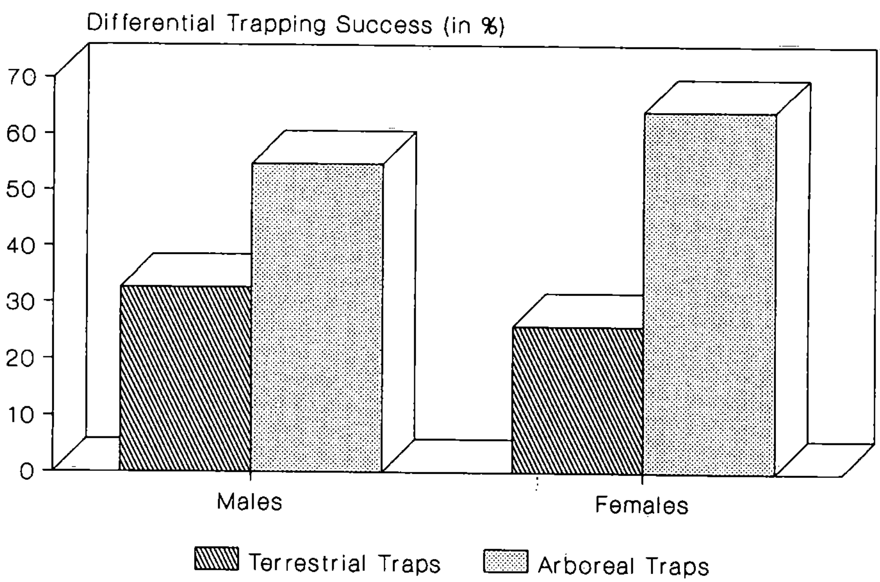

Figure 15. Differential trapping success (in percentages) of *Marmosa cinerea* in arboreal and terrestrial traps.

E. *MARMOSA INCANA*

Biometric data for adult male and female *Marmosa incana*. Weight is given in gms, and other body measurements in mm. P refers to *p*-value associated with analysis of variance for sexual dimorphism (n.s. $=p>0.05$; * $=p<0.05$; ** $=p<0.01$; *** $=p<0.001$).

	MALE			FEMALE			
	Mean	St. Dev.	N	Mean	St. Dev.	N	P
Weight	82.3	23.6	62	68.4	23.1	23	**
Body length	150.5	18.0	62	141.0	15.5	23	***
Tail length	203.9	18.2	62	191.2	18.2	23	***
Hind Foot	23.4	2.0	61	21.5	3.9	23	**
Ear length	28.1	2.4	61	26.5	3.0	23	***

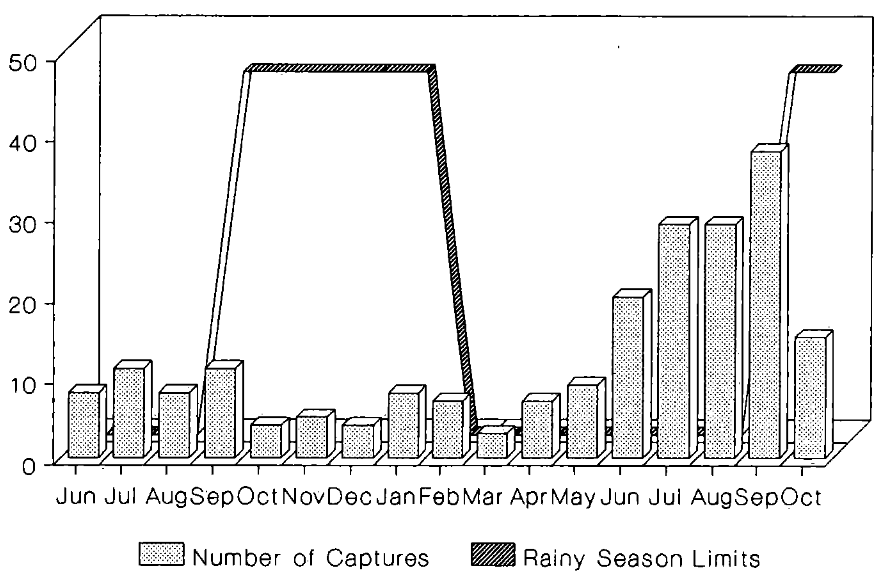

Figure 16. Number of captures of *Marmosa incana* according to monthly trapping period. Straight lines enclose boundaries of rainy season (September to February).

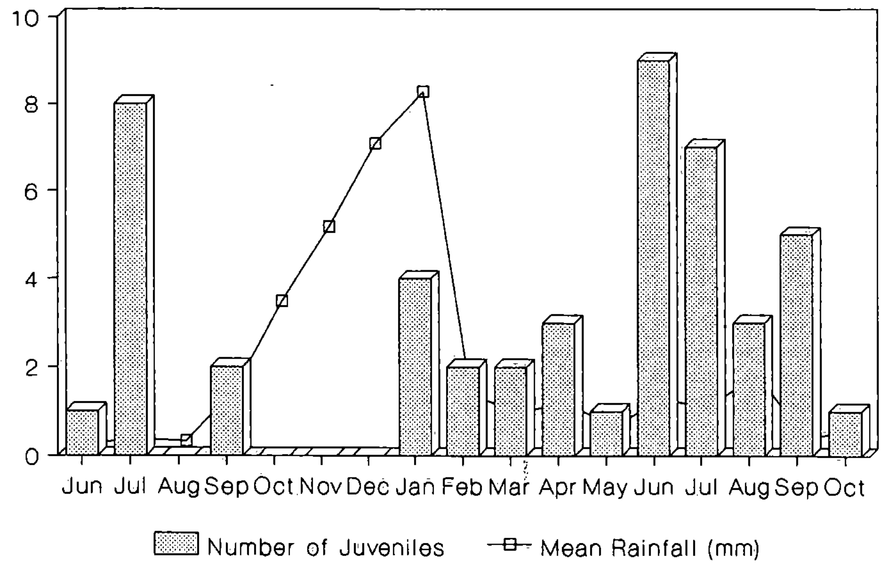

Figure 17. Number of juveniles of *Marmosa incana* according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

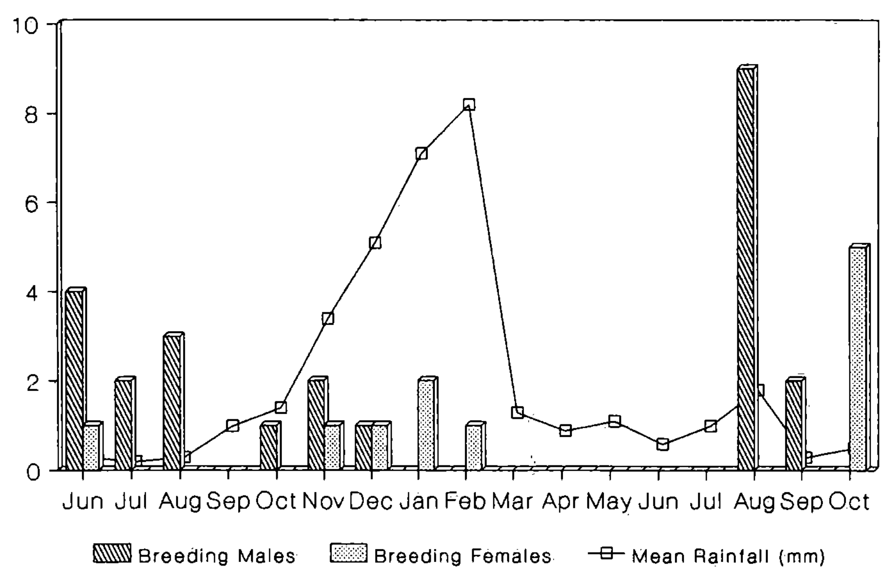

Figure 18. Number of breeding males and females of *Marmosa incana* according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

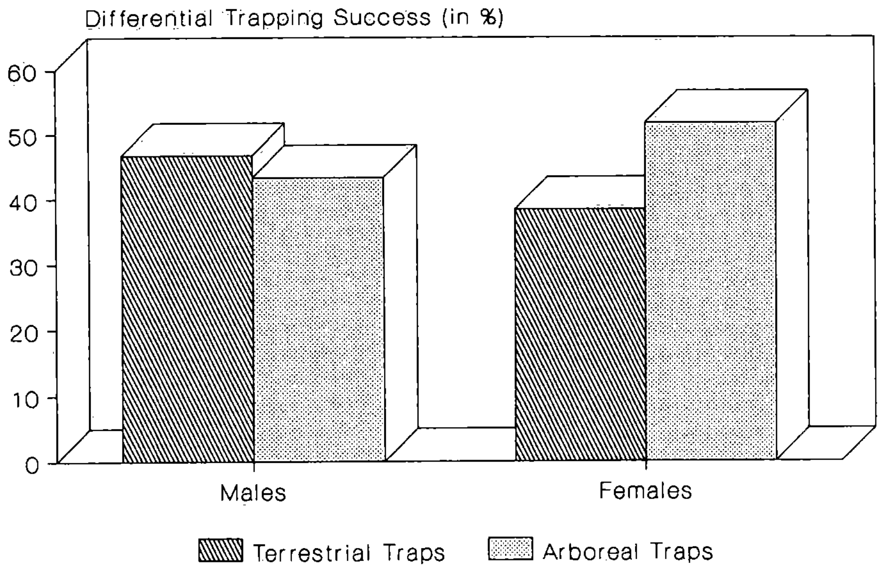

Figure 19. Differential trapping success (in percentages) of *Marmosa incana* in arboreal and terrestrial traps.

F. *METACHIRUS NUDICAUDATUS*

Biometric data for adult male and female *Metachirus nudicaudatus*. Weight is given in gms, and other body measurements in mm. P refers to p-value associated with analysis of variance for sexual dimorphism (n.s. $=p>0.05$; * $=p<0.05$; ** $=p<0.01$; *** $=p<0.001$).

	MALE			FEMALE			
	Mean	St. Dev.	N	Mean	St. Dev.	N	P
Weight	352.7	94.0	51	280.8	57.1	33	***
Body length	252.0	28.7	51	232.1	25.4	32	**
Tail length	324.1	30.5	51	315.9	34.0	31	n.s.
Hind Foot	44.9	3.1	51	42.3	3.3	32	*
Ear length	37.4	3.9	50	36.5	2.9	32	n.s.

Litter sizes and sex ratios of *Metachirus nudicaudatus* pouch young.

ID Number	Number of Female Young	Number of Male Young	Total Young	Sex Ratio M:F
271	-	-	9	-
322	-	-	5	-
338	-	-	8	-
346	3	2	5	0.7:1.0
338*	6	3	9	0.5:1.0
Means			7.2	0.6:1.0

* Second consecutive litter.

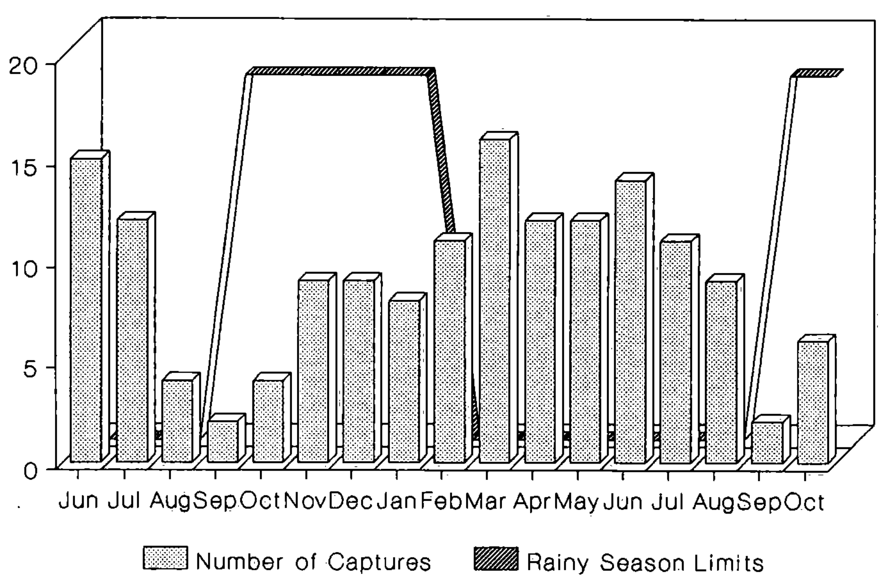

Figure 20. Number of captures of *Metachirus nudicaudatus* according to monthly trapping period. Straight lines enclose boundaries of rainy season (September to February).

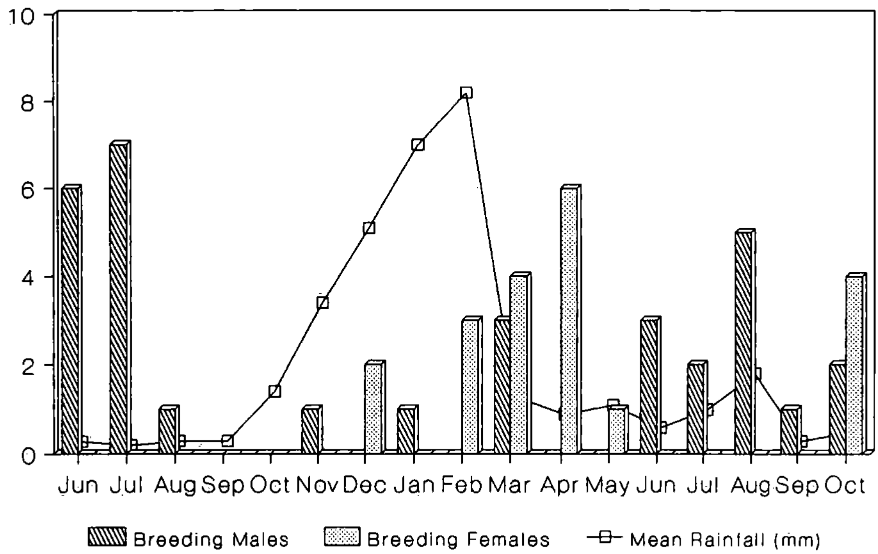

Figure 21. Number of breeding males and females of *Metachirus nudicaudatus* according to trapping period. Data points in line represent mean daily rainfall (in mm).

G. *PHILANDER OPOSSUM*

Biometric data for seven males and three females of gray four-eyed opossum, *Philander opossum*. Weight is given in gms, and other body measurements in mm.

	MALE		FEMALE	
	Mean	St. Dev.	Mean	St. Dev.
Weight	394.9	98.7	295.0	39.7
Body length	282.0	51.3	285.0	48.2
Tail length	325.5	21.6	295.0	18.0
Hind Foot	45.3	2.6	40.3	4.0
Ear length	32.7	3.0	29.3	3.1

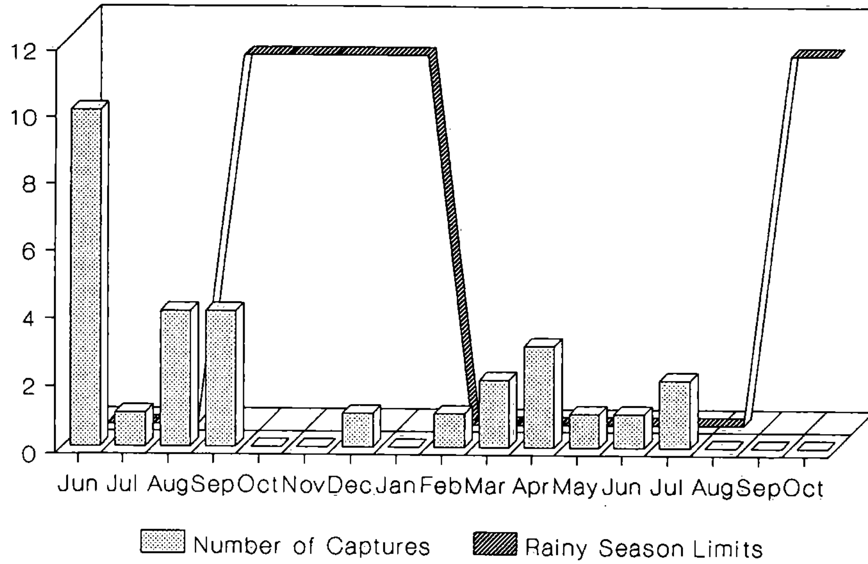

Figure 22. Number of captures of *Philander opossum* according to monthly trapping period. Straight line encloses boundaries of rainy season (September to February).

H. *AKODON CURSOR*

Biometric data for adult *Akodon cursor*. Weight is given in gms, and other body measurements in mm. P refers to p-value associated with analysis of variance for sexual dimorphism (n.s. $=p>0.05$; * $=p<0.05$; ** $=p<0.01$; *** $=p<0.001$).

	MALE			FEMALE			
	Mean	St. Dev.	N	Mean	St. Dev.	N	P
Weight	48.1	8.1	14	45.5	6.8	8	n.s.
Body length	107.8	10.1	13	103.0	14.3	8	n.s.
Tail length	98.8	9.9	12	94.9	10.4	8	n.s.
Hind Foot	26.9	1.3	13	25.9	1.3	8	n.s.
Ear length	18.1	1.6	14	18.8	0.9	8	n.s.

Stomach contents of four *Akodon cursor*.

	PERCENTAGE OF			
ID Number	Insects	Leafy Material	Seeds	Fruits
CEM1/10*	33	33	0	33
47P**	100	0	0	0
101P*	100***	0	0	0
106P*	96***	0	4	0

* Forest traplines.
** Grasslands.
*** Coleoptera and ants.

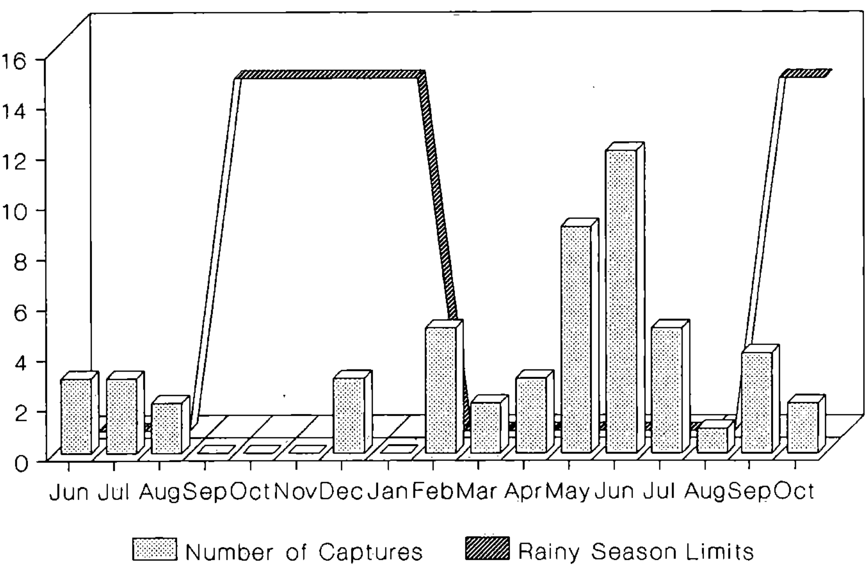

Figure 23. Number of captures of *Akodon cursor* according to monthly trapping period. Straight line encloses boundaries of rainy season (September to February).

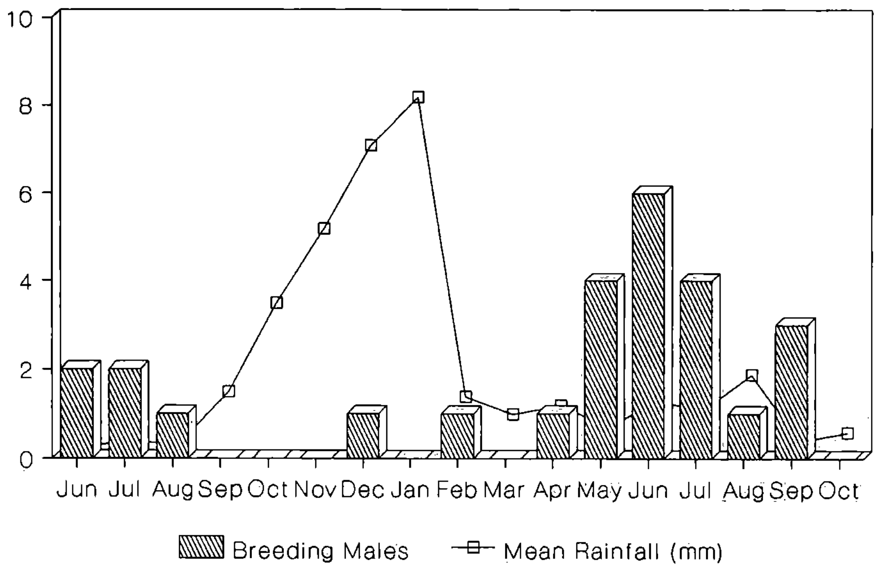

Figure 24. Number of males of *Akodon cursor* with descended testes according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

I. *NECTOMYS SQUAMIPES*

Biometric data for five males and one female *Nectomys squamipes*. Weight is given in gms, and other body measurements in mm.

	MALE			FEMALE		
	Mean	St. Dev.	N	Mean	St. Dev.	N
Weight	197.0	67.0	5	165	-	1
Body length	188.4	19.9	5	190	-	1
Tail length	207.8	24.9	5	210	-	1
Hind Foot	50.0	2.8	5	50	-	1
Ear length	22.0	2.2	5	22	-	1

J. *ORYZOMYS NIGRIPES*

Stomach contents of *Oryzomys nigripes*.

	PERCENTAGE OF			
ID Number	Insects	Fruit	Leafy Material	Seeds
105P	100	0	0	0
56P	20	0	0	80
CEM3	6	90	4	0
CEM2	30	12	58	0

Biometric data for two males and three females of *Oryzomys nigripes*. Weight is given in gms, and other body measurements in mm.

	MALE			FEMALE		
	Mean	St. Dev.	N	Mean	St. Dev.	N
Weight	19.5	0.7	2	18.3	2.9	3
Body length	87.5	0.7	2	83.0	5.3	3
Tail length	126.0	4.2	2	116.8	6.1	3
Hind Foot	23.5	0.7	2	24.0	1.0	3
Ear length	16.0	0.0	2	17.3	0.6	3

K. *ORYZOMYS TRINITATUS*

Biometric data for adult male and female *Oryzomys trinitatis*. Weight is given in gms, and other body measurements in mm. P refers to p-value associated with analysis of variance for sexual dimorphism (n.s.=$p>0.05$; *=$p<0.05$; **=$p<0.01$; ***=$p<0.001$).

	MALE			FEMALE			
	Mean	St. Dev.	N	Mean	St. Dev.	N	P
Weight	63.2	8.2	35	70.0	10.9	28	**
Body length	129.1	8.8	35	136.4	8.1	28	***
Tail length	152.3	10.2	35	159.4	18.2	27	n.s.
Hind Foot	30.4	4.1	35	29.1	2.0	28	n.s.
Ear length	18.6	3.0	35	19.0	1.8	28	n.s.

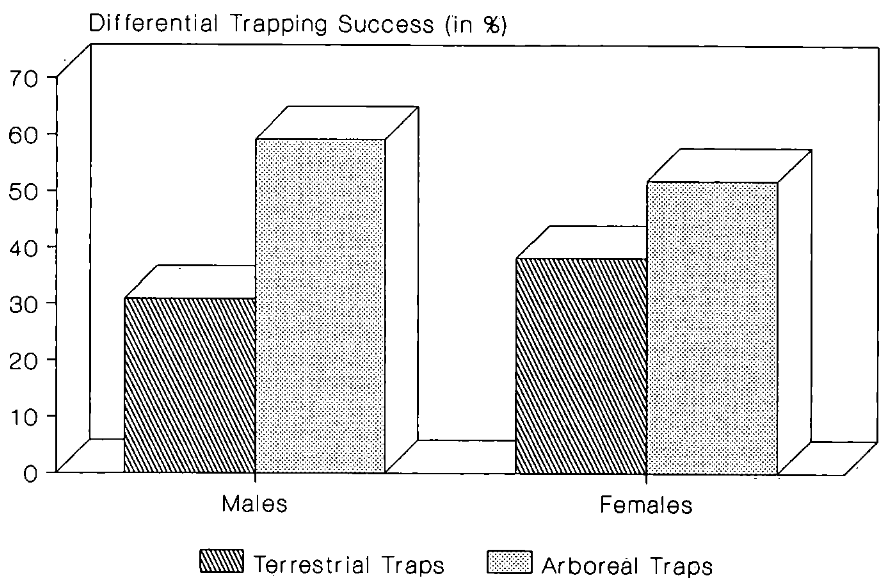

Figure 25. Differential trapping success of male and female *Oryzomys trinitatis* in arboreal and terrestrial traps.

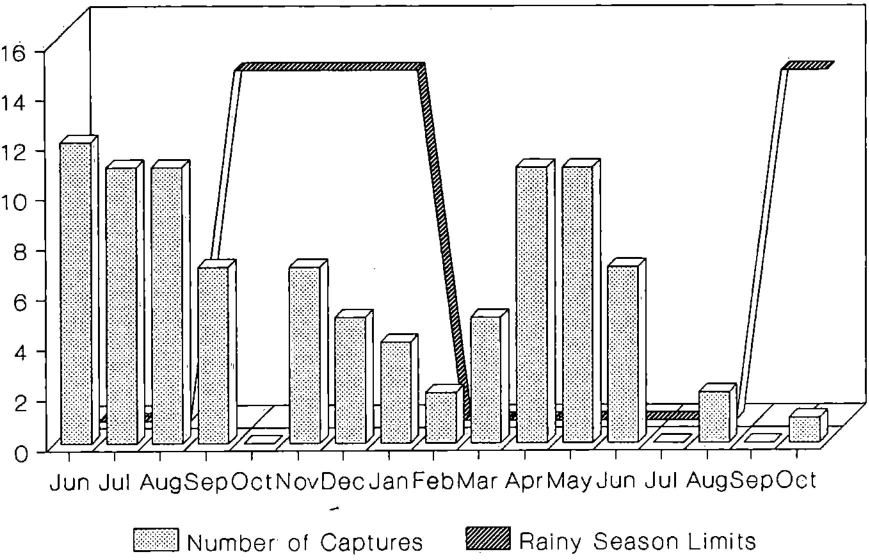

Figure 26. Number of captures of *Oryzomys trinitatis* according to monthly trapping period. Straight line encloses boundaries of rainy season (September to February).

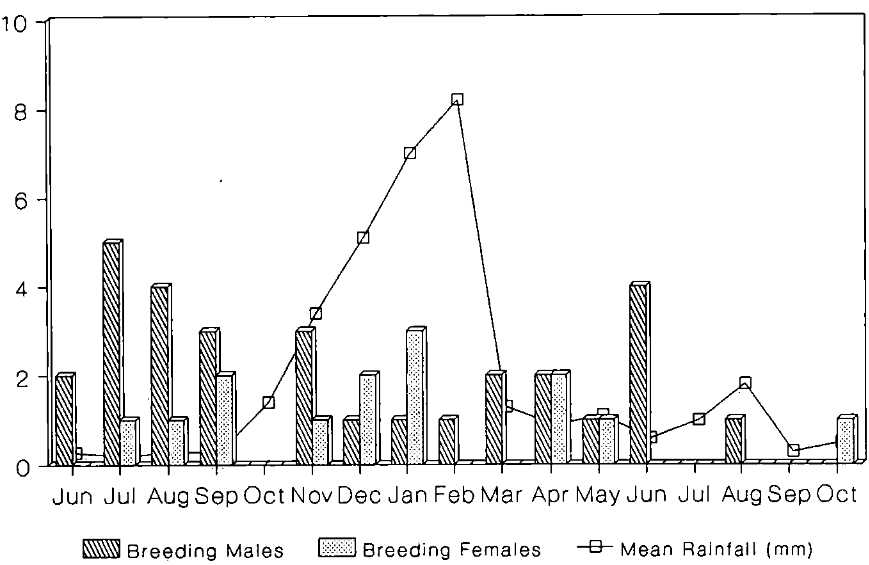

Figure 27. Number of breeding male and female *Oryzomys trinitatis* according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

L. *PROECHIMYS SETOSUS*

Biometric data for adult male and female *Proechimys setosus*. Weight is given in gms, and other body measurements in mm. P refers to p-value associated with analysis of variance for sexual dimorphism (n.s. $=p>0.05$; * $=p<0.05$; ** $=p<0.01$; *** $=p<0.001$).

	MALE			FEMALE			
	Mean	St. Dev.	N	Mean	St. Dev.	N	P
Weight	270.7	36.2	43	259.6	43.4	41	n.s.
Body length	200.2	14.2	42	196.5	18.9	40	n.s.
Tail length	212.3	13.9	39	208.3	15.4	39	n.s.
Hind Foot	51.2	2.1	43	50.7	4.6	40	n.s.
Ear length	29.2	2.1	43	30.6	2.8	40	n.s.

Analysis of seven stomachs of *Proechimys setosus*.

	PERCENTAGE OF		
ID Number	Fruit	Insects	Seeds
39P	81	0	19
93P	64	36	0
95P	100	0	0
90P	0	100*	0
91P	100	0	0
92P	100	0	0
79P	47	0	53

* Termites and Coleoptera larvae.

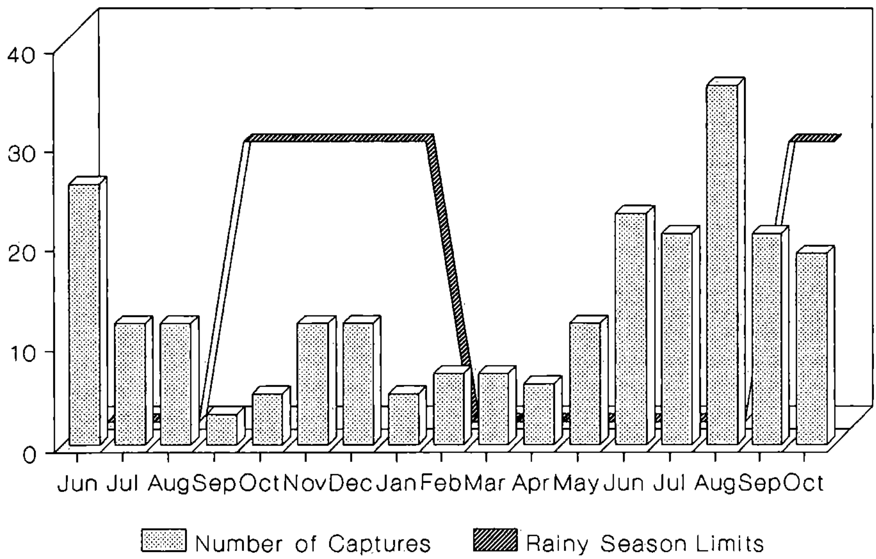

Figure 28. Number of captures of *Proechimys setosus* according to monthly trapping period. Straight line encloses boundaries of rainy season (September to February).

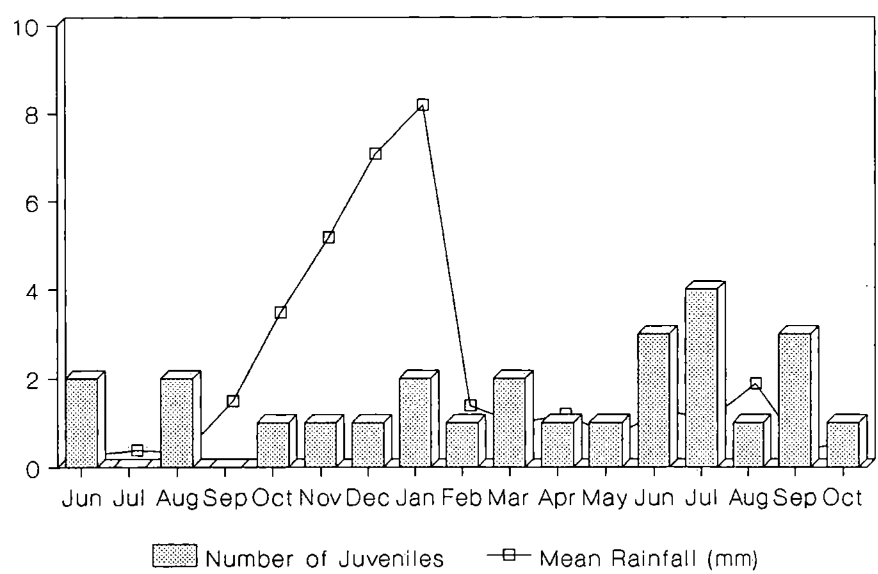

Figure 29. Number of *Proechimys setosus* juveniles according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

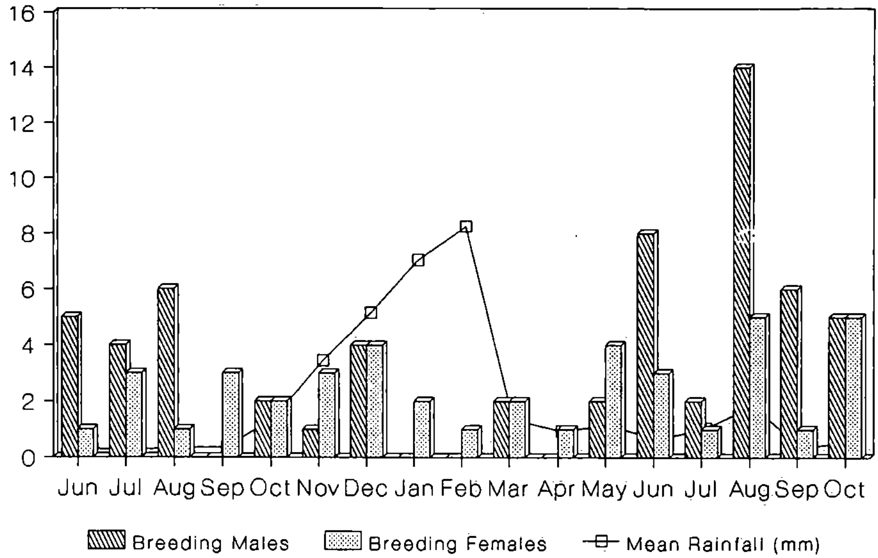

Figure 30. Number of breeding male and female *Proechimys setosus* according to monthly trapping period. Data points in line represent mean daily rainfall (in mm).

SMALL MAMMAL INVENTORIES IN AN EASTERN BRAZILIAN PARK

Jody R. Stallings

Plate 1 A. Didelphid marsupials *(Didelphis marsupialis* [top] and *Metachirus nudicaudatus* [bottom]*)* captured in Rio Doce State Forestry Park, Minas Gerais, Brazil (photographs by author).

SMALL MAMMAL INVENTORIES IN AN EASTERN BRAZILIAN PARK

Jody R. Stallings

Plate 1 B. Didelphid marsupials *(Marmosa cinerea* [top] and *Caluromys philander* [bottom]*)* captured in Rio Doce State Forestry Park, Minas Gerais, Brasil (photographs by author).

Plate 2 A. Cricetid rodents *(Oryzomys subflavus* [top] and *Abrawayaomys ruschii* [bottom]*)* captured in Rio Doce State Forestry Park, Minas Gerais, Brazil (photographs by author).