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# Small mammal community structure and composition in the Cerrado Province of central Brazil

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**ABSTRACT.** Community structure, macrohabitat selection, and patterns of species co-occurrence were examined during a 14-month study of small mammals in the Cerrado Province of central Brazil. Data were collected from mark-recapture grids in brejo and gallery forest, and from live-trapping and specimen collection in all habitat types within cerrado (campo limpo, campo sujo, cerrado [s.s.], cerradão, brejo, valley-side wet campo, and gallery forest). Gallery forest supported the highest species richness, most complex vertical distribution of species, highest level of trophic diversity, and highest macroniche diversity. Degree of habitat selection varied widely. All habitat types supported both rodents and marsupials, although marsupials tended to be much less common in the grasslands (campos) than in woodlands (cerrado) and forests (cerradão, gallery forest). Some species, such as *Didelphis albiventris*, occurred in all habitat types, while others were much more restricted. *Oryzomys bicolor*, for example, occurred only in gallery forest. No habitat type had a completely distinct fauna: overlap in species composition always occurred with at least one other habitat type. Because of the great variability of habitats, and the fact that subsets of the mammal fauna were frequently habitat specific, the overall species richness of any portion of mixed cerrado vegetation is remarkably high.

**KEY WORDS:** Brazil, community structure, gallery forest, habitat selection, marsupials, neotropics, rodents, tropical savanna.

## INTRODUCTION

South America supports many habitats, but two major phytogeographic provinces, both tropical, predominate. The Amazon rain forest, a mosaic of forest communities, encompasses about 5-6 million km<sup>2</sup>, while the cerrado, a complex of savanna grasslands and forested areas, extends over 1.5 million km<sup>2</sup> (e.g. Eiten 1974, Fearnside 1982). Together, these areas comprise 42% of the South American continent. The flora of both areas has been examined cursorily, while their faunas remain largely unknown (e.g. Alho 1982a, Mares 1982, 1986). The taxonomy of the mammals in these habitats is poorly known, and little ecological research has been conducted on this group (Mares 1982, Pine 1982). Both the Amazon Basin and cerrado are experiencing rapid development (Goodland & Irwin 1977, Myers 1980) and their faunas are considered

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threatened. In this paper, we examine habitat selection by small mammals, especially rodents, in the Cerrado Province of central Brazil. Most of our data were gathered in one of the Cerrado's most unusual habitats, the gallery forest.

Most descriptions of tropical forest in South America consider the lowland Amazon forest, the montane tropical forest rimming the Amazon Basin, or the montane rain forest of the east coast of Brazil. However, there is an extensive evergreen tropical forest that occurs along many thousands of kilometers of the cerrado watercourses and extends throughout the region in a serpentine fashion. Ultimately, this gallery forest joins the Amazon or Atlantic coastal forest (Eiten 1972, 1974), and so it is not surprising that many floral and faunal elements are shared among these sylvan habitats (Alho 1982b, Cerqueira 1982). Little ecological work has been done on the mammals of the gallery forest (Paula 1983), although some cerrado mammals have been examined ecologically (Alho 1981a, 1981b, 1981c, Dietz 1983, Souza & Alho 1980).

The habitat selection of tropical mammals, forest or otherwise is largely unknown, but it has been suggested that habitat specificity in tropical regions is more pronounced than in temperate areas (MacArthur *et al.* 1966). This has been especially true for research done on birds (MacArthur *et al.* 1972). Here we present preliminary data on habitat selection, species richness and macro-niche composition of the small mammal fauna of four habitats of the cerrado of Brazil. We compare these data to other studies conducted in the cerrado and point out the importance of having detailed information on species coexistence before generalizations on diversity patterns can be made. Our results apply to both ecological and biogeographic studies of this region.

#### STUDY AREA

Cerrado (*sensu lato*) is a major phytogeographic province located in the central plateau region of Brazil (Figure 1; Cabrera & Willink 1973). The climate is tropical, with distinct wet (October–April) and dry (May–September) seasons. Annual precipitation ranges from 750–2000 mm (Eiten 1974). Cerrado (*s. l.*), the dominant flora of the province, is a mosaic of xeromorphic upland vegetation types ranging from open grasslands to closed woodlands. Trees and shrubs with contorted trunks, thick bark, twisted limbs, and broad, thick leaves give a characteristic appearance to these upland formations. Edaphic factors, such as soil depth, drainage, and nutrient quality, influence the structure of the flora, and often produce physiognomic gradients (Eiten 1972). The upland flora is commonly divided into five physiognomic types (Eiten 1972, Goodland 1971): (1) *cerradão*, a forest of large and moderately tall trees, usually with a closed canopy and few shrubs; (2) *cerrado (sensu stricto)*, a shorter tree/shrub woodland with an open canopy and sparse grass understory; (3) *campo cerrado*, an open tree/shrub woodland with a ground cover of grasses; (4) *campo sujo*, a grassland with scattered trees and shrubs; (5) *campo limpo*, an open grassland with fairly low grasses.

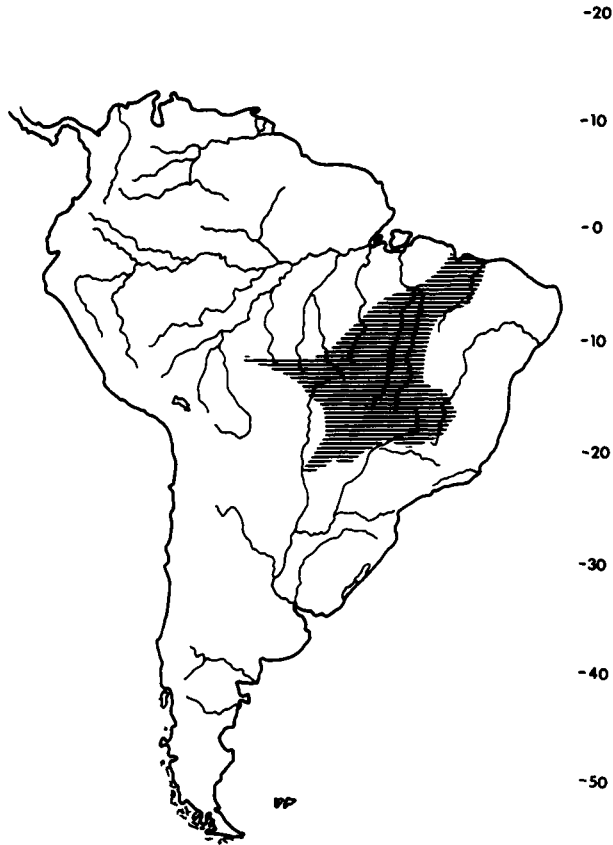


Figure 1. Map showing the limits of the Cerrado phytogeographic Province in South America.

The flora changes drastically along the drainage lowlands, where the water table is close to the surface. The dominant cerrado vegetation is replaced by mesophytic evergreen forest, which forms corridors along streams and rivers. These gallery forests often ascend the slopes of the valley and are usually 50-200 m wide (Eiten 1974). Two types of lowland marshes are frequently found along the edge of gallery forest: brejo, a sedge-dominated, permanently-inundated marsh; and valley-side wet campo, a grass-dominated, seasonally-inundated marsh that grades into upland cerrado vegetation.

In this paper, we group the vegetational types of the Cerrado Province into four habitats (Figure 2) for purposes of statistical analysis. We will consider cerradão, cerrado, and campo cerrado as a single habitat, *cerrado*. Further, we combine campo limpo, campo sujo, and valley-side wet campo into the single habitat, *campo*. Members of these habitat sets grade imperceptibly into one another, and our collecting effort was not sufficiently fine-grained to distinguish between the related habitat pairs. Brejo and gallery forest are considered separate habitats.

Data presented here were collected near Brasilia, Distrito Federal (15° 56' S,

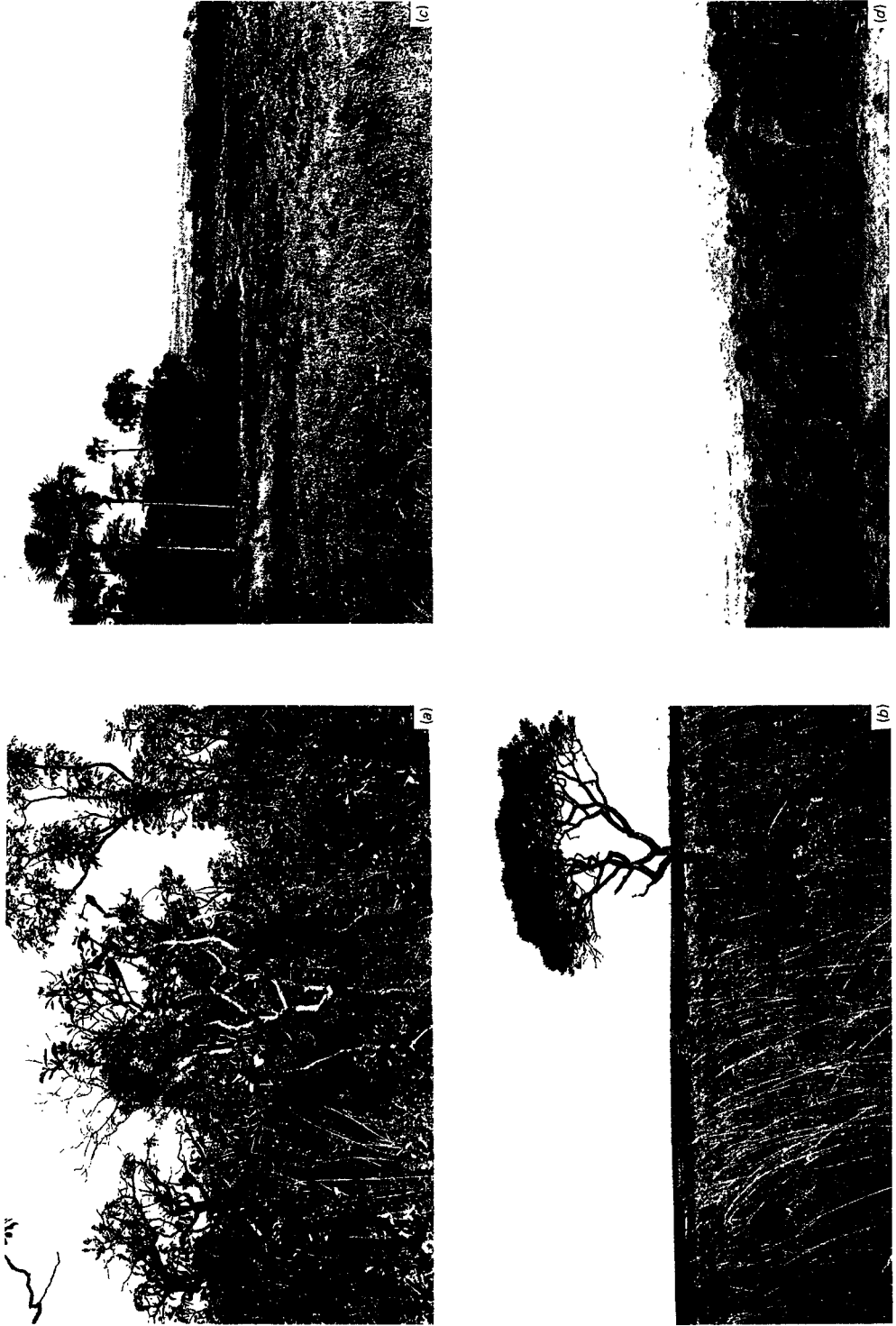


Figure 2. The major habitats of the central Brazilian cerrado: (a) cerrado, (b) campo, (c) brejo, (d) gallery forest.

47° 53' W). Although cerrado is poorly represented in this area, all other vegetation types were common. Most field work was done on the Ecological Reserve of the Instituto Brasileiro de Geografia e Estatística and the Fazenda Água Limpa research station of the Universidade de Brasília.

#### METHODS

Between August 1983 and November 1984, small mammals were sampled from all vegetation types: cerrado, cerrado (s.s.), and campo cerrado (4801 trap-nights); campo sujo, campo limpo, valley-side wet campo (4096 trap-nights); gallery forest (70 465 trap-nights); and brejo (5739 trap-nights). Sherman (23 × 8 × 9 cm) and Tomahawk (48 × 15 × 15 cm) live-traps were used to sample both the lower (<100 g) and upper (100 g - 2 kg) size classes of small mammals. Traps were placed at 10 or 15 m intervals along transect lines or in grids. Captured animals were anaesthetized with ether, and examined, measured and identified. Standard mark-recapture data were recorded, the animal was marked and, after recovery from anaesthesia, released at the point of capture. Although the number of trap-nights in gallery forest is far greater than that of the brejo and upland habitats, we feel that the latter are sufficient for the comparisons made in this paper. Voucher specimens for all species (except *Chironectes* and *Coendou*) were deposited in the Stovall Museum of Science and History, The University of Oklahoma, and the Departamento de Biologia Animal, Universidade de Brasília.

*Statistical analyses.* A species × habitat matrix was constructed to analyse similarity in rodent species composition between habitats. Zero (0) signified either the absence of a particular species from a habitat, or a habitat in which a species was only rarely caught, suggesting that the habitat was not preferred by that species. One (1) indicated presence of the species in preferred habitat. The unweighted pair-group method of clustering with arithmetic averaging (Sneath & Sokal 1973, UPGMA) was employed to summarize similarities between habitats based on the simple matching coefficients, and to summarize similarities between species.

A similar analysis was performed on a macroniche × habitat matrix. Macroniches (Eisenberg 1981) were defined as the locomotor adaptation-diet combination in each habitat. Zero (0) signified absence of a macroniche in a given habitat; one (1) indicated that at least one species occupied that macroniche in a given habitat. Again, UPGMA was used to summarize similarity between habitats based on simple matching coefficients.

*Taxonomic determination.* Whenever possible, series of study specimens (skin and skeleton) were made and compared with specimens in museums as well as with published descriptions of species. The taxonomic identifications are as precise as we can make them at the moment. However, two species, both members of the *Oryzomys nigripes* complex, are listed as *O. nigripes* A and *O. nigripes* B. Also, we have been unable as yet to determine with certainty the proper binomial for one species each of *Marmosa*, *Proechimys* and *Dasyprocta*.

RESULTS

Seven species of marsupials (family Didelphidae) and 18 species of rodents (families Muridae, Caviidae, Dasyproctidae, Echimyidae; Figure 3) were captured. Two additional rodent species (families Hydrochaeridae, Erethizontidae) were seen but not captured (the presence of *Hydrochaeris* also was detected by the unique footprints of this species). These mammals display a wide range of body masses, food habits, and locomotor adaptations (Table 1).

Table 1. Body mass, diet, locomotor adaptation and preferred habitat of marsupials and rodents captured or seen in the cerrado. Diets are: C, carnivore; F, frugivore; G, granivore; H, herbivore; I, insectivore; O, omnivore. Locomotor adaptations are: A, arboreal; Aq, aquatic; C, cursorial; S, scansorial; Saq, semiaquatic; T, terrestrial. Habitats are: B, brejo; C, cerrado; F, forest; M, campo.

Species	Body mass (g)	Diet	Locomotor adaptation	Habitat
<b>Didelphidae</b>				
<i>Chironectes minimus</i>	600-790[11]	C[11]	Aq[11]	F
<i>Didelphis albiventris</i>	700-2000*	O[3]	T/A[3]	F, B, M, C
<i>Marmosa agilis</i>	18-45*	O/I	A/T*	F
<i>Marmosa</i> sp.	36*	O/I	T	F
<i>Monodelphis americana</i>	35-70*	O/C	T*	F
<i>Monodelphis domestica</i>	50-155[6]	O/C	T	C
<i>Monodelphis kunsii</i>	9-15*	I[1]	T	C
<b>Muridae</b>				
<i>Akodon cursor</i>	30-55*	O[3]	T[3]*	F
<i>Bolomys lasiurus</i>	30-75*	O[10]	T[10]*	M, C
<i>Calomys callosus</i>	20-60*	G/I[14]	T*	M, C
<i>C. tener</i>	9-15*	G/O	T*	M, C
<i>Nectomys squamipes</i>	200-450*	O[3]	Saq*	F
<i>Oryzomys bicolor</i>	20-40*	O	A*	F
<i>O. capito</i>	40-75*	O[7]	T*	F
<i>O. concolor</i>	45-95*	O/F	A/T*	F
† <i>O. nigripes</i> A	16-35*	O[3]	T/A*	F
† <i>O. nigripes</i> B	12-25*	O	T/A*	B, M
<i>O. subflavus</i>	60-115*	F/O	T*	M, C
<i>Oxymycterus roberti</i>	50-95*	I[12, 13]	T*	B, M
<i>Rhipidomys mastacalis</i>	55-95*	O[13]	A[13]*	F
<i>Thalpomys lasiotus</i>	17-30*	O	T*	M, C
<b>Erethizontidae</b>				
<i>Coendou prehensilis</i>	1-5 kg[12]	H/F[8, 12]	A[12]	F
<b>Caviidae</b>				
<i>Cavia aperea</i>	400-1000[6]	H[12]	C	M
<b>Hydrochaeridae</b>				
<i>H. hydrochaeris</i>	27-80 kg[12]	H[12]	Aq	F, B
<b>Dasyproctidae</b>				
<i>Dasyprocta</i> sp.	1200-3000[12]	H/F[12]	C	F
<b>Echimyidae</b>				
<i>Proechimys</i> sp.	225-425*	H/F[5, 12]	T[13]*	F
<i>Thrichomys apereoides</i>	175-395*	H/F	T/S[14]	C

Citations: \* this study; 1 = Anderson 1982; 2 = Charles-Dominique *et al.* 1981; 3 = Crespo 1982; 4 = Davis 1947; 5 = Emmons 1982; 6 = Fadem *et al.* 1982; 7 = Fleming 1970; 8 = Mares & Ojeda 1982; 9 = Mares *et al.* 1981a; 10 = Mares *et al.* 1981b; 11 = Marshall 1978; 12 = Nowak & Paradiso 1983; 13 = O'Connell 1982; 14 = Streilein 1982.

† Added in proof. Identifications now known to be: *O. nigripes* A = *O. nigripes* (Olfers); *O. nigripes* B = *O. fornesi* Massoia.

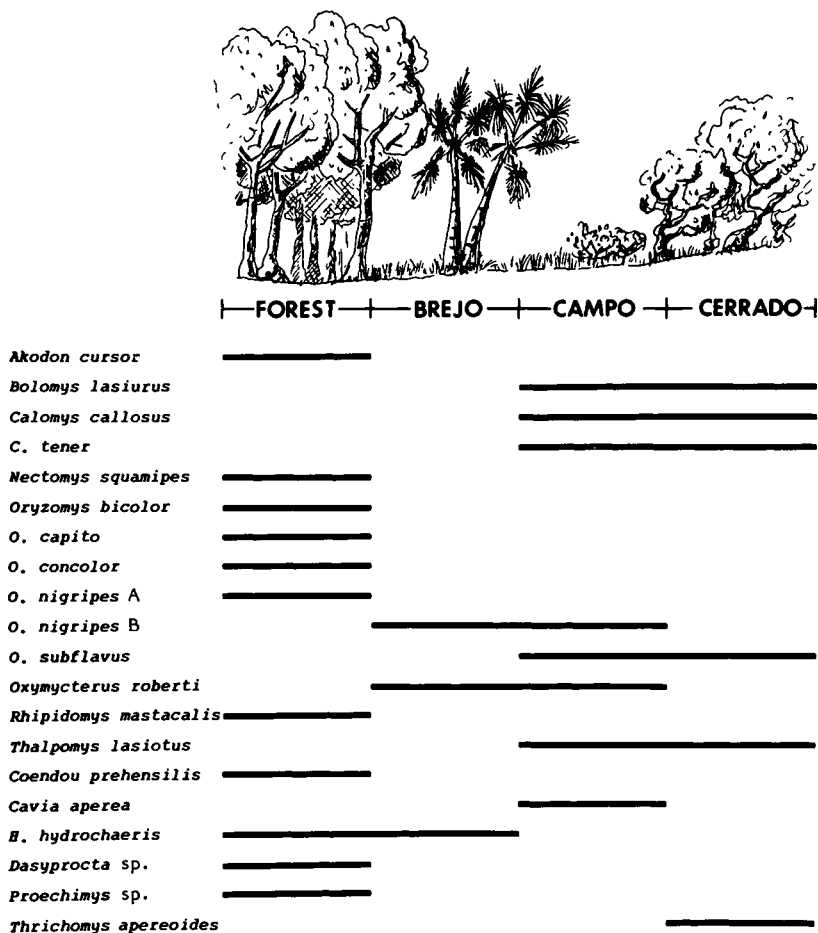


Figure 3. Preferred habitats of rodent species in the cerrado. Bars indicate presence or absence of rodents in the four major habitats considered.

Gallery forest showed the highest species richness of both marsupials (five species) and rodents (11 species). The latter were represented by seven murids and one species each of Erethizontidae, Hydrochaeridae, Dasyproctidae and Echimyidae. Brejo had the lowest rodent diversity: two murid species and *Hydrochaeris*. *Didelphis* was the only marsupial captured in brejo. Campo and cerrado were intermediate in diversity. Campo was a preferred habitat for six murid species and one caviid. Again, *Didelphis* was the only marsupial. Cerrado had five murids, one echimyid and three marsupials.

Rodent species clustered into two main groups (Figure 4A). The first group contained species that occurred in the forest. Campo, campo/brejo, campo/cerrado, and cerrado species were subsets that comprised the second group, the non-forest rodents.

Campo and cerrado were the most similar habitats in terms of rodent species composition (Figure 5). Sixty-two percent of the campo species also occurred



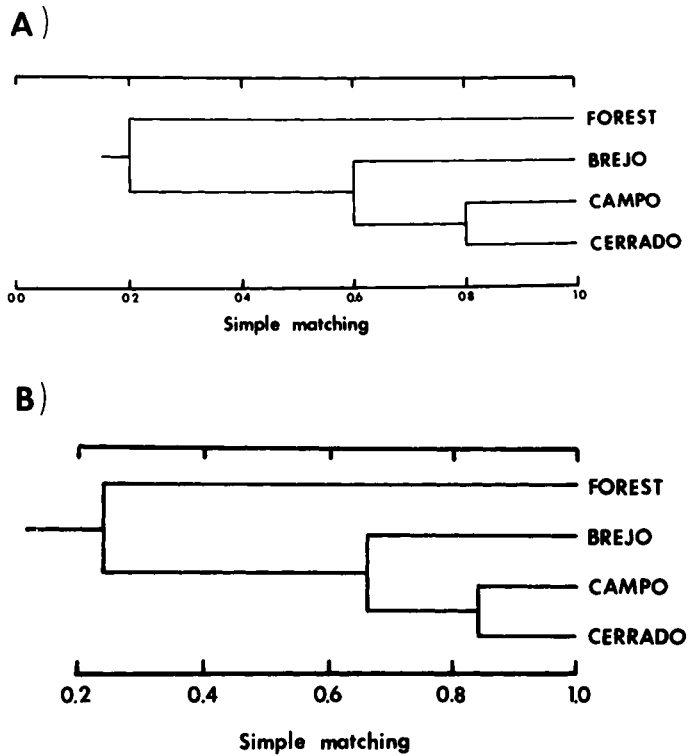


Figure 4. Dendrogram of habitat relationships: (A) based on presence or absence of rodent species, cophenetic correlation coefficient = 0.914; (B) when clustered by macroniches present or absent in each macrohabitat, cophenetic correlation coefficient = 0.966.

in cerrado, while 83% of cerrado species occurred in campo. Some overlap in rodent species was found between campo and brejo (two species), and forest and brejo (one species). Forest was the most distinctive habitat: only one of its 11 species (9%) was shared with another habitat.

Gallery forest supported the highest number of macroniches (Table 2), and was quite distinct from the other habitats in terms of macroniches filled (Figure 4B). Campo and cerrado supported intermediate numbers of macroniches, and were the most similar habitats. Brejo supported the fewest macroniches.

#### DISCUSSION

The Cerrado Province supports a very diverse small mammal fauna. Indeed, we collected 27 species of small mammals in our immediate area, and several other species have been reported from the cerrado of central Brazil (e.g. Didelphidae: *Philander opossum*; Muridae: *Akodon nigrita*, *Holochilus brasiliensis*, *Juscelynomyx candango*, *Kunsia fronto*, *Plectomys paludicola*; Caviidae: *Galea spixii*; Agoutidae: *Agouti paca*; Echimyidae: *Carterodon sulcidens*, *Clyomys laticeps*, *Euryzygomatomys spinosus*; Alho 1982a). If these species are included, the cerrado supports an exceedingly rich small mammal fauna. We must point out

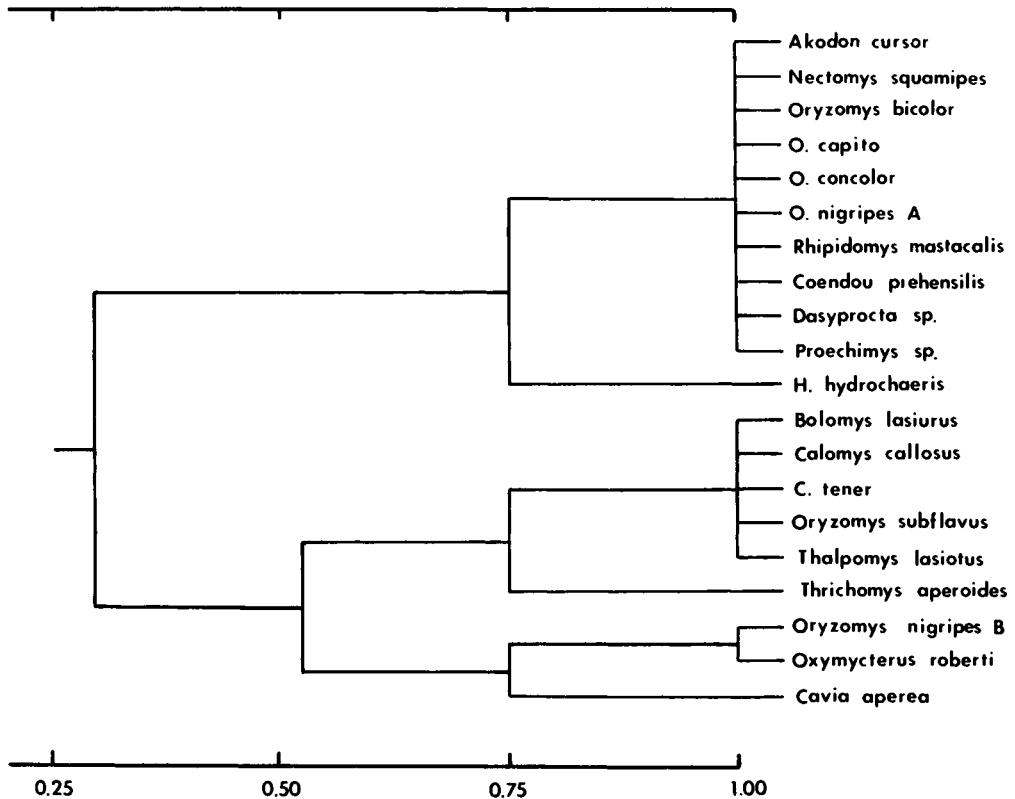


Figure 5. Dendrogram of rodent species relationships when clustered by presence or absence in the four major macrohabitats, cophenetic correlation coefficient = 0.952.

that such high richness is not found within any one habitat or even within a fairly extensive, but localized, area. Thus, while the cerrado does support a complex small mammal community, faunal lists reported in the literature (e.g. Alho 1982a, Redford & Fonseca, in press) are somewhat misleading. Very likely such lists accentuate diversity because they include species from throughout the extensive cerrado region, where numerous other microhabitats are found and where species from other phytogeographic provinces extend into the cerrado. In some cases, however, elevated species richness is assumed because of lack of sufficient field research to determine exactly which species occur in which habitats. Thus, we doubt that any other species occur in the gallery forests where our high-intensity trap grids were in operation. It is significant that all but one of the species (*Agouti paca*) we consider as potential inhabitants of the region are non-forest species: our more limited trap effort outside the forest makes us less definite about species occurrence in those habitats.

There was very little overlap between forest rodent species and those of the grassland habitats (Figures 3-5). The brejo had no species that was limited to that habitat, while both the cerrado and campo had one species that occurred only in that particular habitat. Campo and cerrado were more similar in their species composition than any other habitats (Figures 4 and 5), and the brejo

Table 2. Macroniches (locomotor adaptation-diet combinations) present in each habitat. Codes are combinations of the codes for diet and locomotor adaptations (see Table 1)

Macroniche	Habitat			
	Forest	Brejo	Campo	Cerrado
Aq-C	+	-	-	-
Aq-H	+	+	-	-
SAq-O	+	-	-	-
C-H/F	+	-	-	-
C-H	-	-	+	-
T-O/C	+	-	-	+
T-O	+	-	+	+
T-O/I	+	-	-	-
T-I	-	+	+	+
T-G/I	-	-	+	+
T-G/O	-	-	+	+
T-F/O	-	-	+	+
T-H/F	+	-	-	-
T/S-H/F	-	-	-	+
T/A-O	+	+	+	+
A/T-O/I	+	-	-	-
A/T-O/F	+	-	-	-
A-O	+	-	-	-
A-H/F	+	-	-	-
Number of macroniches	13	3	7	8

shared two species with the campo and only one, the capybara (*Hydrochaeris hydrochaeris*), with the forest. Thus when habitats and species were clustered, two main groups developed: the forest and the cerrado (*s. l.*).

Our analyses show that the gallery forest is quite distinct from all other cerrado habitats from the standpoint of the small mammal fauna. A macroniche analysis agreed almost perfectly with the cluster analysis based on species composition. This indicates that not only is the forest fauna more diverse in terms of number of species, but also in broad niche types. This can be viewed as supporting the idea that the gallery forest of central Brazil is an extension of both the Amazonian and Atlantic tropical forests into the uplands of the country (cf. Cerqueira 1982, Lovejoy *et al.* 1984, Redford & Fonseca, in press). This results in a situation where cerrado endemics, primarily grassland species such as *Plectomys* or *Juscelinomys*, live alongside rain forest elements such as *Rhipidomys*, *Oryzomys bicolor*, or *Coendou*. The interdigitation of such a rich community with complex grass/scrub habitats helps explain the elevated species richness of mammals, and presumably of other taxa as well, in the Cerrado Province.

The habitats we have considered in this report are macrohabitats in that each is made up of distinctive microhabitats. In this paper, we present the broad view, but preliminary analysis of our extensive data set for the gallery forest mammal community shows that microhabitat selection can be quite specific among the species considered in this report. Unpublished studies by L. Z. Nitikman and M. A. Mares have shown that the rodent species of gallery forest areas subdivide the forest into at least five principal microhabitats, and reveal

that species occurrence may differ greatly from one gallery forest patch to the next. Thus, the gallery forest fauna of the Cerrado Province allows for great diversification in niche types. Among the small mammals are found species that are arboreal or terrestrial, aquatic or scansorial, diurnal or nocturnal, insectivorous, herbivorous, frugivorous or omnivorous.

Our findings can be interpreted as supporting conservation efforts of gallery forest habitat in Brazil. The fauna of the cerrado is more than doubled by the presence of a forest mammal community. Any damage to the gallery forests, such as logging or burning, will greatly reduce diversity in the area. Other data we have gathered show that population sizes of forest mammals are frequently quite low, making them even more sensitive to habitat disruption.

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