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# The structure of Neotropical mammal communities: an appraisal of current knowledge

## La estructura de comunidades de mamíferos neotropicales: una apreciación del conocimiento actual

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## ABSTRACT

Patterns and processes of community organization in the tropics have intrigued biologists since the early development of theoretical ecology. Indeed, many of the major hypotheses about community structure were developed by ecologists attempting to understand the complexity of tropical systems. Hypotheses espousing the importance of competition, predation, resource allocation, or life history strategies in structuring tropical communities are frequently presented as if based on extensive data, yet data on tropical systems are few. We review available information on mammalian community ecology from most of the major ecosystems of the continent, including rain forests, Llanos, Cerrado, Caatinga, mediterranean scrub, and temperate forests.. Within each of these ecosystems studies of more than one year in duration have been conducted. Although a great deal of natural history data is now available on the species of these areas, important hypotheses about community structure remain virtually untested. Specifically, we know little about the effect of interspecific competition in molding tropical communities and even less about the role of predation in such systems. Feeding habits and habitat preference data are available for only a fraction of the mammalian species of the Neotropics. Long-term studies of representative tropical ecosystems are the only means of obtaining these data.

Key words: South America, community ecology, mammal surveys, species richness, diversity gradients.

## RESUMEN

Los patrones y procesos de organización comunitaria en los trópicos han intrigado a los biólogos desde el desarrollo de la ecología teórica. De hecho, muchas de las grandes hipótesis sobre estructura comunitaria fueron desarrolladas por ecólogos que intentaban entender la complejidad de los sistemas tropicales. Las hipótesis que enfatizan la importancia de competencia, depredación, asignación de recursos, o estrategias de historia de vida en la estructuración de comunidades tropicales se presentan frecuentemente como si estuvieran basadas en extensa información. Sin embargo, los datos sobre sistemas tropicales son pocos. Nosotros revisamos la información disponible sobre ecología comunitaria de mamíferos en la mayoría de los grandes ecosistemas del continente, incluyendo bosque húmedo, llanos, cerrado, caatinga, matorral mediterráneo y bosque templado. Dentro de cada uno de estos ecosistemas, estudios de más de un año de duración han sido realizados. Aunque existe una buena cantidad de información sobre historia natural de las especies en estas áreas, importantes hipótesis sobre estructura comunitaria permanecen sin ser puestas a prueba. Específicamente, sabemos poco sobre el efecto de la competencia interespecífica en la estructuración de comunidades tropicales, y aún menos sobre el rol de la depredación en tales sistemas. Datos sobre hábitos alimenticios y preferencias de hábitat existen para sólo una fracción de las especies de mamíferos de la región neotropical. Estudios de larga duración en ecosistemas tropicales representativos constituyen la única manera de obtener la información.

Palabras claves: Sudamérica, ecología comunitaria, estudios de mamíferos, riqueza de especies, gradientes de diversidad.

## INTRODUCTION

Ecosystems of South America have attracted the interest of ecologists because the continent straddles the equator; as such, many of the world's most complex and diverse communities are found there. This diversity is in sharp contrast to temperate zone communities of North America and Europe. Indeed, one of the great dogmas of ecology is that species diversity increases with decreasing latitude. It has been argued

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that this relationship holds for virtually all higher taxa (MacArthur 1972); it is certainly true for the class Mammalia (Simpson 1964).

Fleming (1973) and Wilson (1974) have noted that the increase in diversity that occurs with decreasing latitude is not a general pattern for all taxa of mammals and, in fact, seems largely restricted to bats. When the Chiroptera are excluded from the analysis, quadrupedal mammals do not show any marked decline in richness with increasing latitude until one reaches approximately 50° N latitude (Wilson 1974). Similarly, Mares & Ojeda (1982) examined the relationship between species richness of hystricognath rodents and latitude within South America and found latitude, per se, unimportant in explaining patterns of diversity. They contend that continental area was of overriding importance in explaining numbers of rodent species over the whole continent. Since different techniques and times are employed in surveying volant and quadrupedal mammals, few ecologists study both components of the mammlian community. There is, as a consequence, information available for some communities on their quadrupedal mammal components *or* their bats, but seldon is information collected on both groups during a single study.

Any relationship between species richness and latitude is clearly a question of pattern in ecology. The ways in which elevated diversities arise and are maintained is a question of process. Although resolving questions of pattern ecology is frequently quite difficult, it is generally easier than resolving question of process. There are a number of hypotheses that attempt to explain latitudinal gradients in diversity. We will review them briefly.

*Habitat specialization.*— The greater structural and floristic diversity of the tropics leads to a greater degree of specialization in habitat use, resulting in a narrow niche breadth along a habitat axis (MacArthur *et al.* 1966). This is reflected in more pronounced microhabitat selection.

*Food resource specialization.*— The greater resource productivity of the tropics results in abundant and stable resources which allow for greater specialization in resource use and a narrow niche breadth along the resource axis (Orians 1969). This is reflected in specialized food habits.

*Intense competition.*— Since tropical environments are presumably stable, tropical organisms have few adaptations to fluctuations in the physical environment (e.g., Janzen 1967). Most of their interactions are with the biotic environment, and organisms have evolved to be highly efficient competitors. This intense competition narrows niches, allowing more species to coexist (MacArthur & Wilson 1967). This is reflected in large competition coefficients (or any other measure that reflects the intensity of competition, e.g., Seifert & Seifert 1976, Hallett & Pimm 1979).

*Reduced competition.*— Abundant and stable food resources allow heterotrophs to specialize, thereby contracting their food resource niche breadth. This reduces competition for food resources, which permits coexistence of a greater number of species. It also reduces extinction rates (Ricklefs 1979).

*Predation.*— Increased levels of predation in the tropics, due to a larger proportional representation of predatory organisms in the fauna, depresses prey levels below their carrying capacity and thus effectively reduces competition. This allows for the coexistence of greater numbers of prey and an overall higher species richness (Paine 1966; Janzen 1970).

*Growth potential.*— This hypothesis is related to the ability of organisms to reach a competitive equilibrium. Low growth rates allow for maintenance of diversity by slowing the approach to competitive equilibrium and enhancing the effect of factors that tend to prevent competitive exclusion. Low growth rates, therefore, enhance diversity and high growth rates depress diversity (Huston 1979). Data needed to support or reject the hypothesis are population growth rates or any factors that are closely correlated with growth rates.

More detailed reviews of these hypotheses are available in Pianka (1966), Pielou (1975), Menge & Sutherland (1976), Krebs (1978), Ricklefs (1979), and Brown & Gibson (1983). These and other authors have evaluated the strengths and weaknesses of the hypotheses; however, few of these hypotheses have been accepted or rejected on the basis of empirical evidence.

Community ecology is a search for patterns and their causes and in this paper, we will review our progress in revealing patterns and processes in Neotropical mammalian communities.

## METHODOLOGY

We review information on the structure of the mammalian communities at seven sites in seven different Neotropical ecosystems. These were chosen because they represent areas that have been studied for more than one year; they have been well surveyed; and at least some community-level processes in each have been examined. All Neotropical sites will be compared to a Nearctic site with a similar climate and/or vegetation structure. The Neotropical/Nearctic comparisons are, at best, approximations. The ecosystems chosen are briefly described below.

Our procedure contains four steps. We first describe the faunas of all sites by order and family and then present the tropical-temperate comparison. Next, we evaluate the quality of the census at each site. This is particularly important, since the description of any pattern depends upon an accurate account of species composition for the area. Finally, we discuss whether or not community-level processes that are reputedly important in structuring communities have been evaluated. We will ascertain whether or not data appropriate to evaluate these hypotheses have been collected.

## SITES EXAMINED

### 1) *Dry Coastal Chaparral*

*Chilean Matorral.*— Matorral is a mediterranean semiarid scrub formation located in the temperate zone of central Chile. The area has a typical mediterranean climate of dry summers and wet, mild winters; it is climatically and floristically quite different from tropical scrub communities like the Caatinga of northeastern Brazil (see below). Descriptions of the habitat are available in Glanz (1977), Meserve & Glanz (1978), Glanz & Meserve (1982), and Meserve *et al.* (1982, 1983). Data used in this paper are drawn from these papers.

*California Chaparral.*— This is a mediterranean scrub community located in southern California that is quite similar to the Matorral. A description is available in Meserve (1976) and the data are from Glanz & Meserve (1982). Mooney (1977) compares various parameters of the Chilean and California chaparral scrub communities.

### 2) *Semiarid Scrub*

*Caatinga.*— The Caatinga is a semiarid, drought-deciduous tropical forest formation located in northeastern Brazil. It is described in Mares *et al.* (1985). Data are from Mares *et al.* (1981), Lacher (1981), Streilein (1982a, b, c, d, e), and Willig (1985).

*Mesquite Plains.*— The Caatinga is a unique biome; no temperate zone formation is comparable. We chose the mesquite plains of Texas as being most comparable, based upon rainfall and vegetation structure. Mesquite formations are described in Blair (1941, 1943, 1950, 1954), Ryan (1968), and Simpson (1977). The mammal data we used are from Blair (1954).

### 3) *Grassland*

*Cerrado.*— This is an extensive upland grassland that covers most of central Brazil. There are distinct wet and dry seasons, but the savanna is never inundated. Eiten (1972) presents an excellent description of the vegetation. The mammal information is from Alho (1981, 1982), Mares *et al.* (in press). Ernest (1985) and Nitikman (1985).

*Llanos.*— This grassland formation of Venezuela lies in the central lowlands along the Orinoco River. The habitat is described by Troth (1979) and the mammal list is from Eisenberg *et al.* (1979).

*Konza Prairie.*— The Konza is a remnant tall grass prairie of eastern Kansas in the United States. There is a hot dry summer and cold winter. Precipitation falls primarily as snow in winter and rain in spring. For description, see O'Connell (1982) and Kaufman *et al.* (1983). The list of mammals was published in Finck *et al.* (1986).

### 4) *Mesic Forests*

*Tropical Lowland Rain Forest: Panama Canal Zone.*— The lowland tropical forest of Barro Colorado Island and the surrounding mainland have been intensively studied for many years. We present data on Barro Colorado Island (Leigh *et al.* 1982) and an adjacent mainland site (Fleming 1973). The list of mammals is from Fleming (1973) and Glanz (1982).

*Tropical Lowland Rain Forest: Peru-1.*— This site is located in the Alto Marañón Basin of western Peru. It is lowland tropical forest, and the sampling site (Rio Cenepa) is situated at 210 m elevation. Site descriptions and species lists are in Patton *et al.* (1982).

*Tropical Lowland Rain Forest: Peru-2.*— The second Peruvian site is the Manú National Park. The park is a virgin tropical forest of 15,320 sq km with average elevation of 380 m. A description of the habitat and a list of mammals are presented in Terborgh *et al.* (1984). We have deleted all species listed as "hypothetical" from our list.

*Temperate Rain Forest.*— The coastal forests of the Pacific Northwest of the United States are referred to as temperate rain forests. They have cool wet winters and mild dry summers. We have selected the lower elevations of western Oregon (from 0-1000 ft.) as our site. Descriptions of the study area and a list of the mammals are presented in Harris (1984).

### 5) *Broadleaf Temperate Forest*

*Southern Beech Forest.*— These forests have a climate much like the forest of the Pacific Northwest. Unlike the Pacific Northwest, this region is dominated by broadleaf trees (*Nothofagus*) rather than conifers, although coniferous *Araucaria* trees are present in some areas. A list of mammals and a description of habitats is available in Greer (1968) for a forest site in Chile, and Pearson (1983) and Pearson & Pearson (1982) for a forest in southern Argentina.

*Mixed Mesophytic Forest.*— This deciduous forest formation of the eastern United States is similar to the southern beech forests in structure, although it differs somewhat in climate. Barbour (1951) presents a list of the mammals from a forest in the Appalachian Mountains in Kentucky. Fleming (1973) compared eastern deciduous forest to the rain forest of Panamá. In this paper, we compare it to the *Nothofagus* forest.

## RESULTS

### *Dry Coastal Chaparral*

Glanz & Meserve (1982) compared small mammal communities of dry coastal sites in California and Chile. We use their data in this report. The California site is clearly richer than the Chilean (Table 1). Only small mammals were used in this comparison, but a perusal of literature on larger mammal species present in these areas indicates that this difference exists if all mammals are included. Indeed, we suspect the difference would be even greater. Both sites were well surveyed as part of the Mediterranean Scrub Project of the International Biological Program (Mooney 1977). In terms of species richness, Chile is clearly depauperate.

TABLE 1

Small mammal community composition at two dry coastal chaparral sites. These data were not plotted in Fig. 1 due to the absence of survey information on bats and large mammals for each site

Composición de las comunidades de pequeños mamíferos en dos sitios de matorral tipo mediterráneo. Estos datos no fueron usados en Fig. 1 debido a la ausencia de datos sobre murciélagos y mamíferos grandes para estos dos sitios.

| TAXON | CHILEAN SCRUB | CALIFORNIA SCRUB |
|---|---|---|
| Marsupialia | | |
| Didelphidae | 1 | 0 |
| Insectivora | | |
| Soricidae | 0 | 1 |
| Rodentia | | |
| Heteromyidae | 0 | 3 |
| Muridae | 4 | 8 |
| Abrocomidae | 1 | 0 |
| Octodontidae | 1 | 0 |
| Total | 7 | 12 |

Glanz & Meserve (1982) also compared a number of important community-level processes between sites. Their study represents the only situation in which the methodology employed at both sites was fairly consistent. Meserve (1976, 1981a) and Glanz (1977) quantified microhabitat selection by small mammals in California and Chile. The similarity of procedures used allowed them to compare the sites. Percent shrub cover was one of the habitat variables considered. The mean percent shrub cover of all capture locations did not differ between sites; however, the manner by which species selected available habitat differed markedly. Small mammal species in California utilized a wider range of sites, with morphologically similar species showing significant differences in habitats used. Two species, *Dupodomys agilis* and *Peromyscus maniculatus,* preferred stations with low shrub cover (< 50 percent). The less-rich Chilean fauna used a narrower spectrum of available habitats and showed more overlap among species. All species were trapped at locations with moderate to high cover and no species preferred more-open habitats.

The same authors also examined food habits of the small mammals on their study sites. There were important differences in the two communities. Both sites have some large-bodied leaf eaters, but Chile lacks highly specialized granivores. California had no insectivores, whereas Chile had two insectivorous species. Both sites supported resources specialists and generalists, but Chilean mammals show less dietary overlap than do California mammals (Meserve 1981a). The competition, predation, and growth rate hypotheses were not evaluated in Chile. Data available allow for some conjecture. Meserve (1981a, b) concluded that niche overlap values were higher for Chilean mammals than for Californian mammals, based primarily on the large amount of overlap in microhabitat use. However, resources were more abundant in Chile, and this, coupled with the greater dietary specialization among Chilean small mammals, led Meserve to conclude that competition was less intense in the Chilean scrub. Populations at both sites show the potential for outbreaks and high rates of growth (Glanz & Meserve 1982). Other information on predation and competition deals almost exclusively with natural history (Fuentes & Le Boulengé 1977; Jaksic *et al.* 1980, 1981a, b; Meserve 1981a, b; Meserve *et al.* 1982, 1983; Meserve & Glanz 1978), but see Jaksic (this issue).

## *Broadleaf Forests*

The comparison of the Malleco Province site, the Patagonian site, and the Kentucky site is similar to the chaparral comparison (Table 2). The Chilean and Kentucky sites have equal richness, but the Patagonian site is depaurerate. The data on chaparral scrub and broadleaf forests suggest that Neotropical temperate zones are slightly less rich than Nearctic temperate formations. This is not particularly surprising, considering the restricted areal extent of Neotropical temperate formations (Eisenberg & Redford (1982).

Neither Greer (1968) nor Barbour (1951) present ecological information along with the survey data. Pearson (1983) discusses a number of life-history attributes of the small mammals in the *Nothofagus* forests of Patagonia. Reproductive rates are reported to be low, although many of the smaller cricetines reproduce at a young age and would seem to have the potential for rapid population growth. Aspects of competition and predation were not examined by Pearson.

TABLE 2

Mammalian community composition at three broadleaf forest sites

Composición de las comunidades de mamíferos en tres sitios de bosque meso-mórfico

| TAXON | MA-LLECO | PATA-GONIA | KENTU-CKY |
|---|---|---|---|
| Marsupialia | | | |
| Didelphidae | 1 | 0 | 1 |
| Microbiotheriidae | 1 | 1 | 0 |
| Insectivora | | | |
| Soricidae | 0 | 0 | 3 |
| Talpidae | 0 | 0 | 1 |
| Rodentia | | | |
| Sciuridae | 0 | 0 | 4 |
| Muridae | 10 | 7 | 9 |
| Zapodidae | 0 | 0 | 1 |
| Chinchillidae | 1 | 0 | 0 |
| Capromyidae | 1 | 0 | 0 |
| Octodontidae | 2 | 1 | 0 |
| Ctenomyidae | 1 | 0 | 0 |
| Lagomorpha | | | |
| Leporidae | 0 | 0 | 2 |
| Carnivora | | | |
| Mustelidae | 4 | 2 | 2 |
| Canidae | 2 | 1 | 1 |
| Procyonidae | 0 | 0 | 1 |
| Felidae | 2 | 2 | 0 |
| Artiodactyla | | | |
| Cervidae | 1 | 2 | 1 |
| Subtotal | 26 | 16 | 26 |
| Chiroptera | 5 | – | 5 |
| Total | 31 | * | 31 |

* Total number of species not available due to lack of information on bats.

Murua *et al.* (1978[1], 1980, ms[2]), Murua and Gonzalez (1981, 1982), and Meserve *et al.* (1982) have intensively studied the small-mammal community of a Chilean forest at a site farther south than Greer's. The three most common species of small mammals, *Oryzomys longicaudatus, Akodon olivaceus,* and *Akodon longipilis*, show distinct diets in the field (Murua & Gonzalez 1981) and similar macrohabitat, but different microhabitat, utilization patterns (Murua & Gonzalez 1982). Temporal activity patterns also differ to some degree (Murua *et al.* 1978[1]). In order to better interpret these patterns in light of competition theory, Murua *et al.* (ms[2]) conducted a series of removal experiments at the site. Results suggest that interspecific competition plays but a minor role in determining the structure of this small mammal community in southern Chile. Murua (this issue) has also been studying the population dynamics of *O. longicaudatus* and *A. olivaceus.* Like most small cricetines, both species possess reproductive attributes (moderate litter size, young age at first reproduction, multiple litters per breeding season) that would allow for rapid population growth. Both species have pronounced annual fluctuations.

### *Semiarid Scrub*

The previous two comparisons have contrasted two temperate Neotropical communities with structurally similar sites in North America. The semiarid scrublands allow us to make a true tropical (Caatinga)–temperate (Texas) comparison. The fauna of the Mesquite Plains is clearly much richer than the fauna of the Caatinga when only quadrupedal mammals are considered (Table 3). The surveys of both sites were conducted over long periods of time, and should be fairly complete. A few large species that could occur at the Caatinga site have almost certainly been extirpated.

When bats are added to the comparison (Table 3), the Caatinga is richer. This observation supports the contention of other authors (Fleming 1973; Wilson 1974) that the high species richness of tropical mammal faunas is largely attributable to the Chiroptera.

TABLE 3

Mammalian community composition at two semiarid scrub sites

Composición de las comunidades de mamíferos en dos sitios semiáridos de vegetación arbustiva

| TAXON | CAATINGA | MESQUITE PLAINS |
|---|---|---|
| Marsupialia | | |
| Didelphidae | 3 | 1 |
| Insectivora | | |
| Soricidae | 0 | 2 |
| Talpidae | 0 | 1 |
| Primates | | |
| Callithricidae | 1 | 0 |
| Cebidae | 1 | 0 |
| Edentata | | |
| Myrmecophagidae | 1 | 0 |
| Dasypodidae | 2 | 1 |
| Lagomorpha | | |
| Leporidae | 1 | 3 |
| Rodentia | | |
| Sciuridae | 0 | 5 |
| Geomyidae | 0 | 2 |
| Heteromyidae | 0 | 6 |
| Castoridae | 0 | 1 |
| Muridae | 5 | 12 |
| Erethizontidae | 0 | 1 |
| Echimydae | 1 | 0 |
| Caviidae | 2 | 0 |
| Dasyproctidae | 1 | 0 |
| Carnivora | | |
| Mustelidae | 2 | 5 |
| Canidae | 1 | 3 |
| Procyonidae | 1 | 2 |
| Felidae | 3 | 2 |
| Artiodactyla | | |
| Cervidae | 1 | 2 |
| Antilocapridae | 0 | 1 |
| Bovidae | 0 | 1 |
| Subtotal | 26 | 51 |
| Chiroptera | 47 | 5 |
| Total | 73 | 56 |

A number of community processes have been studied in the Caatinga. Lacher (1981) and Streilen (1982d) examined microhabitat selection in a number of small– to mid-sized mammals. Numerous species

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[1] MURUA R, LA GONZALEZ & C JOFRE (1978) Determinación de los ritmos de actividad en cinco especies de roedores silvestres en el laboratorio. Archivos de Biología y Medicina Experimental (Santiago, Chile) 11: 199.

[2] MURUA R, LA GONZALEZ, PL MESERVE & C JOFRE (ms) Small mammal community structure and competition in a Chilean temperate rain forest.

(*Kerodon rupestris, Thrichomys apereoides, Monodelphis domestica*) are largely restricted to isolated boulder piles. One bat (*Mollosops mattogrossensis*) roots exclusively in boulder-pile habitat (Willig 1985). This high degree of microhabitat specialization seems more related to the unusual climate of the region, rather than to the fact that these species occur in the tropics (Mares *et al.* 1985).

Food habits were studied by Lacher (1981), Lacher *et al.* (1982) and Streilein (1982a, c). These studies did not measure niche breadth; most of the information deals with basic natural history. Although some species, like *Kerodon rupestris*, have fairly specialized feeding behavior there are no data to indicate that Caatinga mammals are any zone specialized than their temperate zone counterparts. Information on competition and predations is largely inferential, and nothing is known about the importante of these processes in structuring even a portion of the mammalian community. Many of the smaller cricetines show a high growth potential (Streilein 1982c), but this seems more related to phylogeny than to ecological adaptation.

## *Grasslands*

The observed pattern of species richness in the grassland comparison is shown in Table 4. The richest fauna is the Cerrado, and the least rich is the Llanos: both are tropical savannas. The tall grass prairie of temperate Kansas is intermediate in richness. When bats are considered, the Llanos greatly exceed Kansas in richness. All three sites are well surveyed. Data on the Cerrado are from two adjacent biological reserves (the Fazenda Agua Limpa of the University of Brasilia and the biological reserve of the Brazilian Institute of Geography and Statistics); the Cerrado may be richer than reported (da Fonseca & Redford 1984; Redford & da Fonseca 1986).

The is some information available on community-level processes in tropical grasslands. Microhabitat selection and competition in the Llanos was studied by Eisenberg *et al.* (1979), August (1981, 1983, 1984) and O'Connell (1982). Similar information was collected in the Cerrado by Alho (1981, 1982, de Paula (1983), Lacher *et al.* (1984, in press), Ernest (1985), Nitikman (1985) and Mares *et al.* (in press). Different methodologies were used in virtually all of these studies, and comparisons among these sites, and among tropical and temperate sites, are tenuous at best.

August (1981, 1984) showed that most of the six species of small mammals that he studied in the Llanos were all effectively

TABLE 4

Mammalian community composition at three grassland sites

**Composición de las comunidades de mamíferos en tres sitios de sabana**

| TAXON | CERRA-DO | LLA-NOS | KAN-SAS |
|---|---|---|---|
| Marsupialia | | | |
| Didelphidae | 8 | 2 | 1 |
| Insectivora | | | |
| Soricidae | 0 | 0 | 2 |
| Talpidae | 0 | 0 | 1 |
| Primates | | | |
| Cebidae | 2 | 2 | 0 |
| Callithricidae | 1 | 0 | 0 |
| Edentata | | | |
| Myrmecophagidae | 2 | 2 | 0 |
| Dasypodidae | 5 | 1 | 0 |
| Lagomorpha | | | |
| Leporidae | 1 | 1 | 1 |
| Rodentia | | | |
| Sciuridae | 0 | 1 | 5 |
| Geomyidae | 0 | 0 | 1 |
| Heteromyidae | 0 | 1 | 1 |
| Castoridae | 0 | 0 | 1 |
| Muridae | 14 | 4 | 10 |
| Erethizontidae | 1 | 1 | 0 |
| Caviidae | 1 | 0 | 0 |
| Hydrochaeridae | 1 | 1 | 0 |
| Dasyproctidae | 1 | 1 | 0 |
| Agoutidae | 0 | 1 | 0 |
| Echimyidae | 2 | 1 | 0 |
| Zapodidae | 0 | 0 | 1 |
| Carnivora | | | |
| Canidae | 3 | 1 | 3 |
| Procyonidae | 1 | 1 | 1 |
| Mustelidae | 1 | 3 | 5 |
| Felidae | 1 | 3 | 1 |
| Artiodactyla | | | |
| Tayassuidae | 0 | 1 | 0 |
| Cervidae | 2 | 1 | 2 |
| Subtotal | 47 | 29 | 36 |
| Chiroptera | – | 42 | 9 |
| Total | * | 71 | 45 |

* Total number of species not available due to lack of information on bats.

separated by some combination of arboreal/terrestrial behavior and microhabitat use. He also used a multiple regression technique to estimate competition coefficients, but this techniques showed no evidence of interspecific competition. In order to gather additional information on competition, August (1981) conducted a series of removal experiments on two potential competitors, *Zygodontomys brevicauda* and *Sigmomys alstoni.* The results conditionally supported the conclusions drawn from the multiple regression procedure; competition did not seem important.

Lacher *et al.* (in press) used a multiple regression technique to evaluate microhabitat use and competition in a community of four species of grassland rodents in central Brazil. Results showed that both microhabitat preferences and interspecific competition are important. Some species are microhabitat specialists (e.g., *Oxymycterus roberti*), yet seem to compete strongly with habitat generalists like *Bolomys lasiurus.* This study was conducted during the dry season only; it is not known if the situation holds year round.

No systematic research on food habits or resources use has been carried out in either the Cerrado or the Llanos. And, as with the Caatinga, many small cricetines of tropical grasslands show potentially high rates of increase (Alho & Souza 1982; Pereira 1982), but this again seems related to phylogeny, rather than ecology. O'Connell (1979, 1982) argues that seasonal inundation in the Llanos places constraints on the kinds of mammals that can colonize these habitats. High fecundity is typical of grassland species; those species with low reproductive rates are arboreal or scansorial and largely restricted to gallery forests. Here, differences in reproductive rates are related not to latitude, but to patterns of habitat selection.

### *Mesic Forest*

This set involves the most comparisons and, like the previous ones, shows no clear trend. The two Peruvian sites are clearly very rich in both non-volant and volant mammals. When considering only quadrupedal mammals, however, one tropical site, the Canal Zone, is less rich than the coastal forests of western Oregon (Table 5). All four areas seem very well surveyed, although the Oregon data may exaggerate species richness.

The two Peruvian sites have been very poorly studied at the community-level, beyond basic natural history. We know of

TABLE 5

Mammalian community composition at four mesic forest sites

Composición de las comunidades de mamíferos en cuatro sitios de bosque húmedo

| TAXON | PANAMA | PERU-1 | PERU-2 | OREGON |
|---|---|---|---|---|
| Marsupiala | | | | |
| Didelphidae | 6 | 9 | 8 | 0 |
| Insectivora | | | | |
| Soricidae | 0 | 0 | 0 | 5 |
| Talpidae | 0 | 0 | 0 | 2 |
| Primates | | | | |
| Callithricidae | 1 | 0 | 4 | 0 |
| Cebidae | 4 | 5 | 9 | 0 |
| Edentata | | | | |
| Myrmecophagidae | 2 | 3 | 3 | 0 |
| Bradypodidae | 2 | 2 | 2 | 0 |
| Dasypodidae | 2 | 3 | 2 | 0 |
| Rodentia | | | | |
| Aplodontidae | 0 | 0 | 0 | 1 |
| Castoridae | 0 | 0 | 0 | 1 |
| Sciuridae | 2 | 3 | 4 | 6 |
| Heteromyidae | 1 | 0 | 0 | 0 |
| Geomyidae | 0 | 0 | 0 | 1 |
| Muridae | 5 | 7 | 9 | 10 |
| Zapodidae | 0 | 0 | 0 | 1 |
| Erethizontidae | 1 | 1 | 1 | 1 |
| Echimyidae | 2 | 3 | 5 | 0 |
| Hydrochaeridae | 0 | 1 | 1 | 0 |
| Dasyproctidae | 1 | 2 | 2 | 0 |
| Agoutidae | 1 | 1 | 1 | 0 |
| Dinomyidae | 0 | 1 | 1 | 0 |
| Lagomorpha | | | | |
| Leporidae | 1 | 1 | 1 | 2 |
| Carnivora | | | | |
| Mustelidae | 2 | 3 | 3 | 8 |
| Canidae | 0 | 2 | 0 | 1 |
| Ursidae | 0 | 1 | 0 | 1 |
| Procyonidae | 3 | 4 | 4 | 2 |
| Felidae | 1 | 4 | 4 | 2 |
| Perissodactyla | | | | |
| Tapiridae | 1 | 1 | 1 | 0 |
| Artiodactyla | | | | |
| Tayassuidae | 1 | 2 | 2 | 0 |
| Cervidae | 2 | 1 | 2 | 2 |
| Subtotal | 41 | 60 | 69 | 46 |
| Chiroptera | 30 | 26 | 25 | 11 |
| Total | 71 | 86 | 94 | 57 |

no ecological data from the Rio Cenepa site. Terborgh *et al.* (1984) present general information on macrohabitats, foraging position in the forest, and diurnal versus nocturnal activity, although there are not sufficient data for testing hypotheses on processes of species diversity. Terborgh (1984) presents detailed information on five species of primates from the site, but these species represent only a fraction of the total number of mammal species present.

The Canal Zone is one of the best studied of all tropical sites. Most of the research has been done at the Smithsonian's Tropical Research Institute on Barro Colorado Island. Leigh *et al.* (1982) summarize research that began there as early as 1916. The island has been a reserve since 1925 and has been a tropical research institute since 1966. Relevant work on mammals includes Enders (1935), Eisenberg & Thorington (1973), Froehlich & Thorington (1982), Glanz (1982), Glanz *et al.* (1982), Milton (1982), Oppenheimer (1982), Russell (1982), and Smythe *et al.* (1982). Little work on mammals there has specifically addressed the question of pattern and process in diversity gradients (but see Fleming 1973). Glanz (1982) emphasizes the difficulty in censusing even a small area like Barro Colorado Island.

The difficulties associated with the study of complex community-level processes like competition and predation are greatly exacerbated in the tropical mesic forest sites. Species richness is so great that even basic natural history parameters are unknown for the majority of the species present.

### *Patterns in Richness of Non-volant Mammals*

Our analysis of species richness is based upon on-site censuses, rather than an examination of distribution maps (e.g., Wilson 1974). Our conclusions however, are the same as Wilson's (Fig. 1). There is no

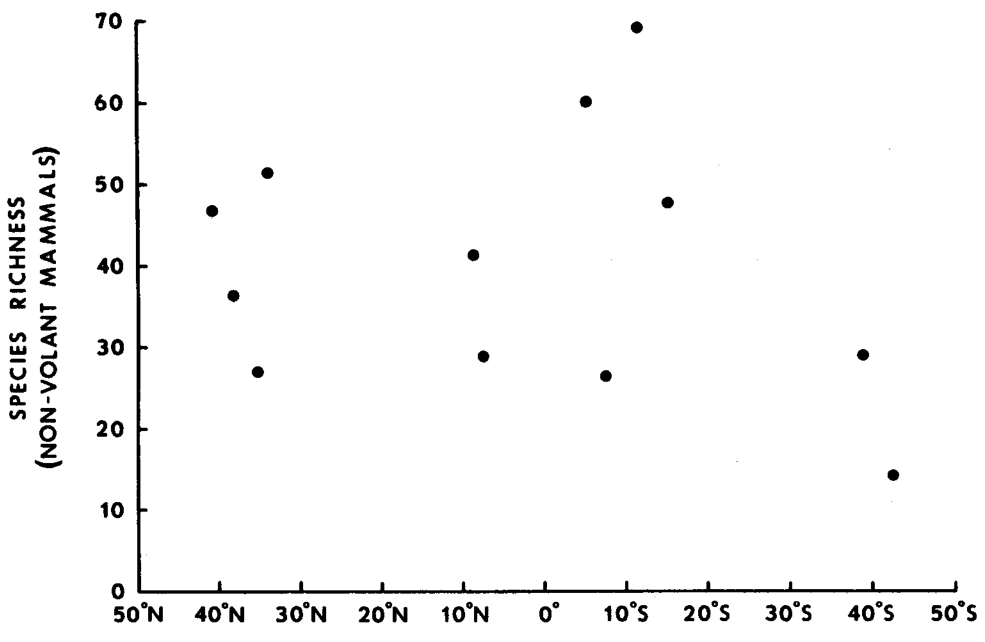

*Fig. 1.* The relationship between species richness of non-volant mammals and latitude for the sites examined in our study. Latitude for each site is as follows: Oregon, 41° N; Kansas, 39° N; Kentucky, 35° N; Texas, 33° N; Panama 9° N; Venezuela, 8° N; Peru 1, 5° S; Caatinga, 8° S; Peru 2, 11° S; Cerrado, 15° S; Chilean forest, 38° S; Argentine forest, 41° S.

Relación entre el número de especies de mamíferos no voladores y latitud para los sitios examinados en nuestro estudio. La latitud para cada sitio es la siguiente: Oregón, 41° N; Kansas, 39° N; Kentucky, 35° N; Texas, 33° N; Panamá, 9° N; Venezuela, 8° N; Peru 1, 5° S; Caatinga, 8° S; Peru 2, 11° S; Cerrado, 15° S; Chilean forest, 38° S; Argentine forest, 41° S.

apparent pattern in richness of non-volant mammals as one moves from temperate North America to temperate South America. As others have shown (Fleming 1973), when bats are considered (Tables 3, 4, and 5), tropical regions attain a high species richness.

## DISCUSSION

### *Patterns of Latitudinal Diversity*

Our data show that, for the sites examined, there is no latitudinal trend in diversity for the non-volant mammal fauna (Fig. 1). Our comparisons of the entire mammal fauna of specific sites (Fig. 2) support the more general results of previous authors (Fleming 1973; Wilson 1974): the tropics are clearly more diverse.

This raises an interesting point. Most systematists, biogeographers, and ecologists study either non-volant mammals or bats, but rarely both. Available data clearly show that quadrupedal mammals do not become more diverse as latitude decreases. Bats are clearly an important component of neotropical mammal communities. In terms of number of species, they are by far the most important order. Many species of bats, especially frugivores, carnivores, nectarivores and gleaning insectivores, probably compete directly for food resources with arboreal and terrestrial small mammals. Both small mammals and bats are almost exclusively nocturnal. Bats are generally excluded from studies of mammalian community structure by convenience, and not by ecological wisdom. Their exclusion likely biases our perception of community structure and community-level processes.

Indeed, Fleming (1979) argues that diffuse competition for fruits may exist among species of different classes (birds and mammals), although he feels that it is rare. Mares & Rosenzweig (1978) have shown that rodents, birds and ants may

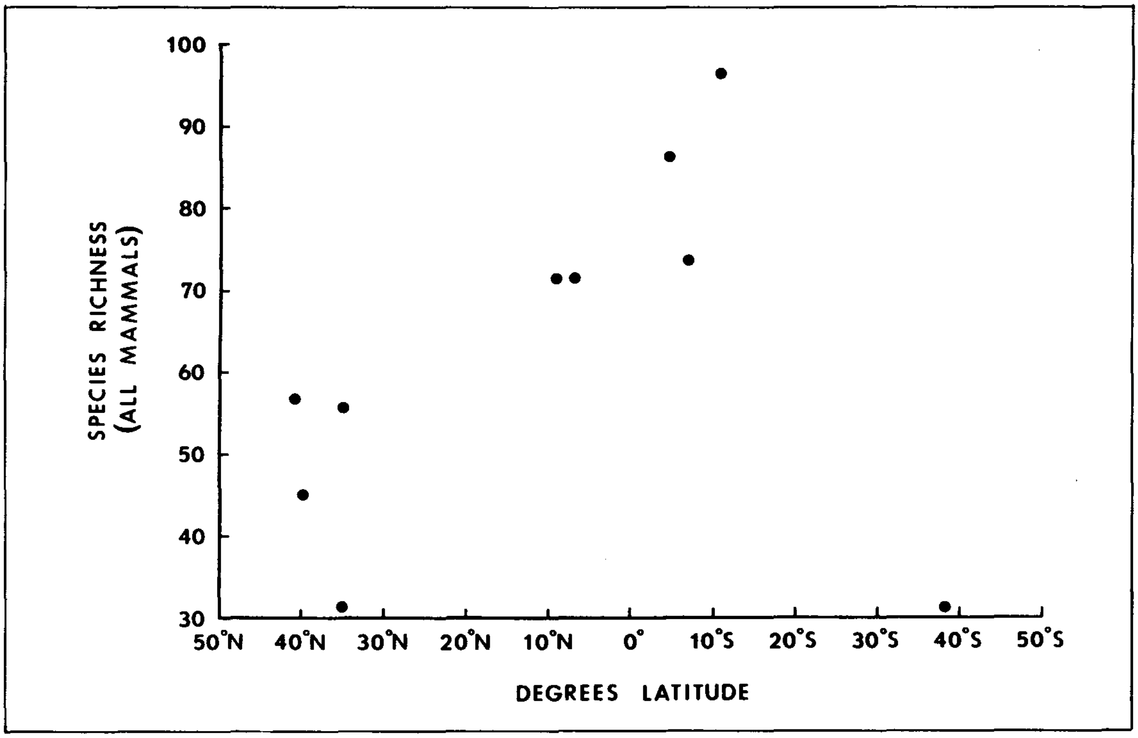

*Fig. 2.* The relationship between species richness of all mammals and latitude for the sites from our study for which data are available. Latitude for each site is as follows: Oregon, 41° N; Kansas, 39° N; Kentucky, 35° N; Texas, 33° N; Panama, 9° N; Venezuela, 8° N; Peru 1, 5° S; Caatinga, 8° S; Peru 2, 11° S; Chilean forest, 38° S.

Relación entre el número de especies de mamíferos y latitud para los sitios en nuestro estudio que tienen estos datos. La latitud para cada sitio es la siguiente: Oregón, 41° N; Kansas, 39° N; Kentucky, 35° N; Texas, 33° N; Panamá 9° N; Venezuela, 8° N; Perú 1, 5° S; Caatinga, 8° S; Perú 2, 11° S; Chilean forest, 38°S.

compete for seeds in arid ecosystems. Given the diversity and complexity of interactions that characterize tropical systems, a synecological approach may prove to be particularly appropriate for research on tropical systems; one that combines the study of birds, ectothermic vertebrates, and insects along with mammals. However, this will require more resources, both human and financial, than are likely to be available in the near future.

### *Ecological Processes*

As we have emphasized, there are incomplete data available on important community-level processes for all tropical sites examined. August & Fleming (1984) have discussed the paucity of empirical research that has been done on competition in Neotropical mammal communities. We have shown that this is true for virtually all important community processes. To further complicate matters, even temperate zone sites lack the requisite data, and when data are available, their comparative utility is limited.

Microhabitat selection is documented in most tropical and temperate communities. There has been only one direct comparison of the degree of microhabitat selection in temperate versus tropical communities (Glanz & Meserve 1982), but even in this case, the methodologies differed slightly.

Food habit studies show that there are numerous resource specialists among tropical mammals; possibly such specialists are more common in the tropics than in the temperate zone. No rigorous comparisons have been made, however.

We know little about the importance of competition and predation in structuring tropical communities, but most patterns are not strikingly different from those observed in the temperate zones. Indeed, we lack good comparative information for much of the temperate zone. Competition has proven to be an elusive quantity to estimate, regardless of habitat (Connell 1983). Also, the notion that predators maintain proportionately higher species richness in the tropics than in the temperate zone is not supported by our data on quadrupedal mammals (Tables 1-5).

Data on population growth rates are available for a number of species of Neotropical mammals, but Huston's(1979) hypothesis will be difficult to test. Any mammal community is a mix of orders and families having different phylogenetic histories. Reproductive characteristics, including litter size, parental care, and population growth rates differ dramatically among taxa that live in the same habitat. The contrast between hystricognath and muroid rodents is a good example. Hystricognaths give birth to small litters of precocial young. This holds even when hystricognaths and muroids coexist. The necessity to control for historical and evolutionary differences requires large, complete data sets for entire faunas, which thus far are not available.

The different taxa that make up tropical and temperate mammal assemblages complicate comparative research. Tables 1-5 show that some taxa are largely temperate (Insectivora, Sciuridae, Heteromyidae, Mustelidae), whereas others are largely tropical (Marsupialia, Primates, Edentata, hystricognaths). A solution to the problem of different evolutionary histories is to restrict the study of latitudinal gradients to trends within continents. However, even this does not completely resolve the complicating factor of history. Temperate Chile, for example, is isolated from the rest of the continent by the Andes, and might be expected to be depauperate, independent of latitudinal effects. The Llanos of Venezuela is a tropical habitat that is depauperate in nin-volant mammals because of seasonal disturbance like flooding and fire. Eisenberg & Redford (1979) argue that historical factors are also responsible for the depauperate Llanos fauna.

Although the general pattern of enhanced species richness with decreasing latitude is well supported for some taxa, the processes that determine the pattern are not well understood. Biologists have always assumed that complex ecological processes are typical of tropical systems and cause the high diversity. But there are also important historical and phylogenetic differences between tropical and temperate systems that may, in part, be responsible for the enhanced diversity of tropical systems. As such, complex ecological interactions may result from high diversity, and not necessarily be causative. We need to evaluate the relative importance of ecology, phylogeny, and history through comparisons of tropical and temperate systems, where critical ecological processes are studied with consistent methodology and procedures. Our current piecemeal approach seems unlikely to increase significantly our understanding of tropical community ecology.

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## LITERATURE CITED

ALHO CJR (1981) Small mammal populations of Brazilian cerrado: the dependence of abundance and diversity on habitat complexity. Revista Brasileira de Biologia 41: 223-230.

ALHO CJR (1982) Brazilian rodents: their habitats and habits. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 143-166. Special Publication Series, Pymatuning Laboratory of Ecology, Volume 6, Pittsburgh, Pennsylvania.

ALHO CJR & MJ SOUZA (1982) Home range and use of space in *Zygodontomys lasiurus* (Cricetidae, Rodentia) in the Cerrado of central Brazil. Annals of the Carnegie Museum 51: 127-132.

AUGUST PV (1981) Population and community ecology of small mammals in northern Venezuela. Ph.D. Dissertation, Boston University, Boston, Massachusetts.

AUGUST PV (1983) The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64: 1495-1507.

AUGUST PV (1984) Population ecology of small mammals in the Llanos of Venezuela. Special Publications of the Museum of Texas Tech University Nº 22: 71-104.

AUGUST PV & TH FLEMING (1984) Competition in Neotropical small mammals. Acta Zoologica Fennica 172: 33-36.

BARBOUR RW (1951) The mammals of Big Black Mountain, Harlan County, Kentucky. Journal of Mammalogy 32: 100-110.

BLAIR WF (1941) Annotated list of mammals of the Tularosa Basin, New Mexico. American Midland Naturalist 26: 218-229.

BLAIR WF (1943) Ecological distribution of mammals in the Tularosa Basin, New Mexico. Contributions from the Laboratory of Vertebrate Biology, University of Michigan 20: 1-24.

BLAIR WF (1950) The biotic provinces of Texas. Texas Journal of Science 2: 93-117.

BLAIR WF (1954) Mammals of the mesquite plains biotic district in Texas and Oklahoma, and speciation in the central grasslands. Texas Journal of Science 6: 235-264.

BROWN JH & AC GIBSON (1983) Biogeography. Mosby, St. Louis, Missouri.

CONNELL JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122: 661-696.

DA FONSECA GAB & KH REDFORD (1984) The mammals of IBGE's ecological reserve and an analysis of the role of gallery forests in increasing diversity. Revista Brasileira de Biologia 44: 517-523.

DE PAULA AC (1983) Relaçoes espaciais de pequenos mamíferos em uma comunidade de mata de galeria do Parque Nacional de Brasília. MS thesis, Universidades de Brasília, Brasília.

EISENBERG JF, MA O'CONNELL & PV AUGUST (1979) Density, productivity, and distribution of mammals in two Venezuela habitats. In: Eisenberg JF (ed) Vertebrate ecology in the northern Neotropics: 187-207. Smithsonian Institution Press, Washington, D.C.

EISENBERG JF & KH REDFORD (1979) A biogeographic analysis of the mammalian fauna of Venezuela. In: Eisenberg JF (ed) Vertebrate ecology in the northern Netropics: 31-36. Smithsonian Institution Press, Washington, D.C.

EISENBERG JF & KH REDFORD (1982) Comparative niche structure and evolution of the mammals of the Nearctic and southern South America. In: Mares MA & HH Genoways (eds) Mammalian biology in South America; 77-93. Special Publications Series, Pymatuning Laboratory of Ecology, Volume 6, Pittsburgh, Pennsylvania.

EISENBERG JF & RW THORINGTON Jr (1973) A preliminary analysis of a Neotropical mammal fauna. Biotropica 5:150-161.

EITEN G (1972) The Cerrado vegetation of Brazil. Botanical Review 38: 201-341.

ENDERS RF (1935) Mammalian life histories from Barro Colorado Island, Panama. Bulletin of the Museum of Comparative Zoology 78: 383-502.

ERNEST KA (1985) Ecology of *Nectomys squamipes*, the Neotropical water rat, in central Brazil: home range, habitat selection, reproduction, and behaviour. MS thesis, University of Oklahoma, Norman, Oklahoma.

FINK EJ, DW KAUFMAN, GA KAUFMAN, SK GURTZ, BK CLARK, LJ McLELLAN & BS CLARK (1986) Mammals of the Konza Prairie Research Natural Area, Kansas. Prairie Naturalist 18: 153-166.

FLEMING TH (1973) Numbers of mammal species in North and Central American communities. Ecology 54: 555-563.

FLEMING TH (1979) Do tropical frugivores compete for food? American Zoologist 19: 1157-1172.

FROEHLICH JW & RW THORINGTON Jr (1982) The genetic structure and socioecology of howler monkeys (*Alouatta palliata*) on Barro Colorado Island. In: Leigh EG Jr AS Rand & DM Windsor (eds) The ecology of a tropical forest: 291-305. Smithsonian Institution Press, Washington, D.C.

FUENTES ER & PY LE BOULENGE (1977) Prédation et compétition dans la dynamique d'une communauté herbacée secondaire du Chili central. La Terre et al Vie 31: 104-117.

GLANZ WE (1977) Comparative ecology of small mammal communities in California and Chile. Ph.D dissertation, University of California, Berkeley, California.

GLANZ WE (1982) The terrestrial mammal fauna of Barro Colorado Island: census and long-term changes. In: Leigh EG Jr, AS Rand & DM Windsor (eds) The ecology of a tropical forest: 405-468. Smithsonian Institution Press, Washington, D.C.

GLANZ WE & PL MESERVE (1982) An ecological comparison of small mammal communities in California and Chile. In: Conrad CE & WC Oechel (eds) Dynamics and management of mediterranean-type ecosystems. U.S. Department of Agriculture, Forest Service General Technical Report PSW-58: 220-226.

GLANZ WE, RW THORINGTON Jr, J GIACALONE-MADDEN & LR HEANEY (1982) Seasonal food use and demographic trends in *Sciurus granatensis*. In: Leigh EG Jr, AS Rand & DM Windsor (eds) The ecology of a tropical forest: 239-252. Smithsonian Institution Press, Washington, D.C.

GREER JK (1968) Mamíferos de la provincia de Malleco. Publicación Nº 12 del Museo Dillman S. Bullock, El Vergel, Angol, Chile.

HALLETT JG & SL PIMM (1979) Direct estimation of competition. American Naturalist 113: 593-600.

HARRIS LD (1984) The fragmented forest. University of Chicago Press, Chicago, Illinois.

HUSTON M (1979) A general hypothesis of species diversity. American Naturalist 113: 81-101.

JAKSIC FM, HW GREENE & JL YAÑEZ (1981b) The guild structure of a community of predatory vertebrates in central Chile. Oecologia 49: 21-28.

JAKSIC FM, RP SCHLATTER & JL YAÑEZ (1980) Feeding ecology of central Chilean foxes, *Dusicyon culpaeus* and *Dusicyon griseus*. Journal of Mammalogy 61: 254-260.

JAKSIC FM, JL YAÑEZ & ER FUENTES (1981a) Assessing a small mammal community in central Chile. Journal of Mammalogy 62: 391-396.

JANZEN DH (1967) Why mountain passes are higher in the tropics. American Naturalist 101: 233-249.

JANZEN DH (1970) Herbivore and the number of tree species in tropical forests. American Naturalist 104: 501-528.

KAUFMAN DW, GA KAUFMAN & EJ FINCK (1983) Effects of fire on rodents in tallgrass prairie of the Flint Hills region of eastern Kansas. Prairie Naturalist 15: 49-56.

KREBS CJ (1978) Ecology: the experimental analysis of distribution and abundance. Second edition, Harper & Row, New York.

LACHER TE Jr (1981) The comparative social behavior of *Kerodon rupestris* and *Galea spixii* and the evolution of behavior in the Caviidae. Bulletin of the Carnegie Museum of Natural History 17: 1-71.

LACHER TE Jr, GAB DA FONSECA, C ALVES Jr & B MAGALHAES-CASTRO (1984) Parasitism of trees by marmosets in a central Brazilian gallery forest. Biotropica 16: 202-209.

LACHER TE Jr, MA MARES & CJR ALHO (in press) The structure of the small mammal community of a central Brazilian savanna. In: Mammals of the Americas, University of Florida Press, Gainesville, Florida.

LACHER TE JR, MR WILLIG & MA MARES (1982) Food preference as a function of resource abundance with multiple prey types: an experimental analysis of optimal foraging theory. American Naturalist 120: 297-316.

LEIGH EG Jr, AS RAND & DM WINDSOR, eds (1982) The ecology of a tropical forest. Smithsonian Institution Press, Washington, D.C.

MACARTHUR RH (1972) Geographical ecology. Harper & Row, New York.

MACARTHUR RH, H RECHER & M CODY (1966) On the relation between habitat selection and species diversity. American Naturalist 100: 319-332.

MACARTHUR RH & EO WILSON (1967) The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

MARES MA, KA ERNEST & DD GETTINGER (in press) Small mammal community structure and composition in Cerrado (*sensu lato*) of central Brazil. Journal of Tropical Ecology.

MARES MA & RA OJEDA (1982) Patterns of diversity and adaptation in South American hystricognath rodents. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 393-432. Special Publication Series, Pymatuning Laboratory of Ecology, Volume 6, Pittsburgh, Pennsylvania.

MARES MA & ML ROSENZWEIG (1978) Patterns of granivory in North and South American deserts: rodents, birds, and ants. Ecology 59: 235-241.

MARES MA, MR WILLIG & TE LACHER Jr (1985) The role of the Brazilian Caatinga in South American biogeography: tropical mammals in a dry region. Journal of Biogeography 12: 57-69.

MARES MA, MR WILLIG, KE STREILEIN & TE LACHER Jr (1981) The mammals of northeastern Brazil. Annals of the Carnegie Museum 50: 80-137.

MENGE BA & JP SUTHERLAND (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110: 351-369.

MESERVE PL (1976) Food relationships of a rodent fauna in a California coastal sage scrub community. Journal of Mammalogy 57: 300-319.

MESERVE PL (1981a) Resource partitioning in a Chilean semi-arid small mammal community. Journal of Animal Ecology 50: 745-757.

MESERVE PL (1981b) Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy 62: 304-314.

MESERVE PL & WE GLANZ (1978) Geographical ecology of small mammals in the northern Chilean arid zone. Journal of Biogeography 5: 135-148.

MESERVE PL, RE MARTIN & J RODRIGUEZ M (1983) Feeding ecology of two Chilean caviomorphs in central mediterranean savanna. Journal of Mammalogy 64: 322-325.

MESERVE PL, R MURUA, O LOPETEGUI & JR RAU (1982) Observations on the small mammal fauna of a primary temperate rain forest in southern Chile. Journal of Mammalogy 63: 315-317.

MILTON K (1982) Dietary quality and population regulation in a howler monkey population. In: Leigh EG Jr, AS Rand and DM Windsor (eds) The ecology of a tropical forest: 273-290. Smithsonian Institution Presss, Washington, D.C.

MOONEY HA, ed (1977) Convergent evolution in Chile and California. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

MURUA R & LA GONZALEZ (1981) Estudios de preferencia y hábitos alimentarios en dos especies de roedores cricétidos. Medio Ambiente (Valdivia, Chile) 5: 115-124.

MURUA R & LA GONZALEZ (1982) Microhabitat selection in two Chilean cricetid rodents. Oecologia 52: 12-15.

MURUA R, LA GONZALEZ & C JOFRE (1980) Experimental food preferences of two southern Chilean rodents. Journal of Mammalogy 61: 138-140.

NITIKMAN LZ (1985) Ecology of small mammals in a gallery forest of central Brazil. MS thesis, University of Oklahoma, Norman, Oklahoma.

O'CONNELL MA (1979) Ecology of didelphid marsupials from northern Venezuela. In: Eisenberg JF (ed) Vertebrate ecology in the northern Neotropics: 73-87. Smithsonian Institution Press, Washington, D.C.

O'CONNELL MA (1982) Population biology of North and South American grassland rodents: a comparative review. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 167-186. Special Publication Series, Pymatuning Laboratory of Ecology, Volume 6, Pittsburgh, Pennsylvania.

OPPENHEIMER JR (1982) *Cebus capucinus:* home range, population dynamics, and interspecific relationships. In: Leigh EG Jr, AS Rand & DM Windsor (eds) The ecology of a tropical forest: 253-272. Smithsonian Institution Press, Washington, D.C.

ORIANS GH (1969) The number of bird species in some tropical forests. Ecology 50: 783-801.

PAINE RT (1966) Food web complexity and species diversity. American Naturalist 100: 67-76.

PATTON JL, B BERLIN & EA BERLIN (1982) Aboriginal perspectives of a mammal community in Amazonian Peru: knowledge and utilization patterns among the Aguaruna Jívaro. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 111-128. Special Publication Series, Pymatuning Laboratory of Ecology, Volume 6, Pittsburgh, Pennsylvania.

PEARSON OP (1983) Characteristics of a mammalian fauna from forests in Patagonia, southern Argentina. Journal of Mammalogy 64: 476-492.

PEARSON OP & AK PEARSON (1982) Ecology and biogeography of the southern rain forests of Argentina. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 129-142. Special Publications Series, Pymatuning Laboratory of Ecology, Volume 6, Pittsburgh, Pennylvania.

PEREIRA LA (1982) Uso ecológico do espaço de *Zygodontomys lasiurus* (Rodentia, Cricetidae) em habitat natural de Cerrado do Brasil Central. MS thesis, Universidade de Brasília, Brasília.

PIANKA ER (1966) Latitudinal gradients in species diversity: a review of concepts. American Naturalist 100: 33-46.

PIELOU EC (1975) Ecological diversity. John Wiley & Sons, New York.

REDFORD KH & GAB DA FONSECA (1986) The role of gallery forests in the zoogeography of the Cerrado's non-volant mammalian fauna. Biotropica. 19: 126-135.

RICKLEFS RJ (1979) Ecology. Second edition, Chiron Press, New York.

RUSSELL JK (1982) Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. In: Leigh EG Jr, AS Rand & DM Windsor (eds) The ecology of a tropical forest: 413-431. Smithsonian Institution Press, Washington, D.C.

RYAN RM (1968) Mammals of Deep Canyon. The Desert Museum, Palm Springs, California.

SEIFERT RP & FH SEIFERT (1976) A community matrix analysis of *Heliconia* insect communities. American Naturalist 110: 461-483.

SIMPSON BB, ed (1977) Mesquite: its biology in two desert ecosystems. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

SIMPSON GG (1964) Species density of North American recent mammals. Systematic Zoology 13: 57-73.

SMYTHE N, WE GLANZ & EF LEIGH Jr. (1982) Population regulation in some terrestrial frugivores. In: Leigh EG Jr, AS Rand & DM Windsor (eds) The ecology of a tropical forest: 227-238. Smithsonian Institution Press, Washington, D.C.

STREILEIN KE (1982a) The ecology of small mammals in the semiarid Brazilian Caatinga. I. Climate and faunal composition. Annals of the Carnegie Museum 51: 79-107.

STREILEIN KE (1982b) The ecology of small mammals in the semiarid Brazilian Caatinga. II. Water relations. Annals of the Carnegie Museum 51: 109-126.

STREILEIN KE (1982c) The ecology of small mammals in the semiarid Brazilian Caatinga. III. Reproductive biology and population ecology. Annals of the Carnegie Museum 51: 251-269.

STREILEIN KE (1982d) The ecology of small mammals in the semiarid Brazilian Caatinga. IV. Habitat selection. Annals of the Carnegie Museum 51: 331-343.

STREILEIN KE (1982e) The ecology of small mammals in the semiarid Brazilian Caatinga. V. Agonistic behavior and overview. Annals of the Carnegie Museum 51: 345-369.

TERBORGH JW (1984) Five New World primates. Princeton University Press, Princeton, New Jersey.

TERBORGH JW, JW FITZPATRICK & L EMMONS (1984) Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. Fieldiana, Zoology 21: 1-29.

TROTH RG (1979) Vegetational types on a ranch in the central Llanos of Venezuela. In: Eisenberg JF (ed) Vertebrate ecology in the northern Neotropics: 17-30. Smithsonian Institution Press, Washington, D.C.

WILLIG MR (1983) Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from northeast Brazil. Bulletin of the Carnegie Museum of Natural History 23: 1-131.

WILLIG MR (1985) Ecology, reproductive biology, and systematics of *Neoplatymops mattogrossensis* (Chiroptera: Molossidae). Journal of Mammalogy 61: 618-628.

WILSON JW III (1974) Analytical zoogeography of North American mammals. Evolution 28: 124-140.