

## THE ROLE OF HABITAT COMPLEXITY AND HETEROGENEITY IN STRUCTURING TROPICAL MAMMAL COMMUNITIES<sup>1</sup>

PETER V. AUGUST

*Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881 USA*

**Abstract.** The relationship between mammal community structure and vertical variation in habitat physiognomy (complexity) and horizontal variation in habitat form (heterogeneity) was examined on five study areas in the llanos of Venezuela. Data on the small mammals (<1 kg) of the study sites were obtained through a mark-recapture trapping program of >38 000 trap nights from 1976–1978. Data on the distribution of large, nonvolant mammals were obtained during 24 mo of field observation. Measures of habitat complexity and habitat heterogeneity were derived using principal components analysis. There was little association between habitat structure and the richness, diversity, abundance, and biomass of small mammals. Abiotic factors, such as the degree of wet-season flooding, probably play an important role in patterns of small mammal distribution and abundance. The total number of mammal species was positively correlated with habitat complexity but not correlated with habitat heterogeneity. Increasing species richness across the complexity gradient was probably accommodated by increasing potential food resources. New species were added to complex communities primarily through guild expansion rather than guild addition.

**Key words:** *community structure; diversity; habitat complexity; habitat heterogeneity; species richness; tropical mammals.*

### INTRODUCTION

Following Mac Arthur and Mac Arthur's (1961) demonstration of a positive association between bird species diversity and foliage height diversity, ecologists have spent a considerable amount of time testing the geographic and taxonomic ubiquity of this relationship. Generally, such studies set out to test the hypothesis that species diversity increases with increasing habitat complexity. It is reasoned that highly complex habitats offer more potential niches than structurally simpler habitats (Klopfer and Mac Arthur 1960). Many have found that species diversity is related to habitat complexity (Mac Arthur et al. 1966, Karr 1968, Recher 1969, Rosenzweig and Winakur 1969, Karr and Roth 1971, Murdoch et al. 1972, Willson 1974, Cody 1975, Terborgh 1977) while others have failed to find similar relationships (Power 1971, Lovejoy 1972, Brown 1973, Pearson 1975, Roth 1976). Species diversity/habitat profile associations are often obscured by biogeographical or historical factors affecting subsets of the diversity sample (Brown 1973, Cody 1975, Karr 1980, Pearson 1975, Pianka 1975, Rosenzweig 1975).

The terms "complexity" and "heterogeneity" have been used in the past to describe a number of different aspects of habitat form. Some authors have used "heterogeneity" interchangeably with "complexity" (Pianka 1966, Kohn 1967, Heck and Wetstone 1977, Reed 1978, Rohde 1978) while others use heterogeneity to indicate horizontal variation or patchiness

(Willson et al. 1973, Wiens 1974, 1976, Willson 1974, Roth 1976, Rotenberry and Wiens 1980). Complexity, as used in this report, describes the development of vertical strata within a habitat. Complex habitats have many and well-developed vertical strata. Simple habitats have fewer and less developed vertical strata. Mac Arthur and Mac Arthur's (1961) foliage height diversity index (hereafter denoted FHD) is one measure of habitat complexity as I have defined it. Heterogeneity, or patchiness, represents horizontal variation in habitat physiognomy. A small patch of tropical forest can be extremely complex but very homogeneous, whereas woodland savanna may be less complex but highly patchy. Both increasing complexity and increasing heterogeneity can be hypothesized to increase species diversity by providing more niches in a unit of space (Mac Arthur et al. 1962, Levins 1968). Potential niches are distributed vertically in complex habitats and both horizontally and vertically in patchy habitats.

The distinction between patchiness and complexity is an important one if we are to understand fully the relationship between species diversity and habitat structure. The ecological and geographic relevance of the role that habitat form plays in structuring animal communities will be apparent only after studies are completed on a variety of organisms in a variety of habitats. I present here an analysis of the relationship between habitat structure and mammal diversity in the Venezuelan llanos. Principal components analysis is used to derive estimates of complexity and patchiness and FHD is included as an additional measure of habitat complexity. Two data sets on mammal diversity

<sup>1</sup> Manuscript received 7 June 1982; revised 6 December 1982; accepted 8 December 1982.

are examined. One includes only small mammals ( $<1$  kg adult body mass) and is based on 2 yr of live-trapping data. The other includes total nonvolant (i.e., all mammals except bats) mammal faunas of the study areas and is based on field observations by myself and the participants of the Smithsonian Institution–Venezuela Wildlife Research Project. The results are evaluated in view of the natural history of llanos mammals and recent hypotheses on species packing.

#### MATERIALS AND METHODS

Five habitats were studied over an 8-km transect on a large ( $>3000$ -ha) ranch in the Venezuelan llanos. I deliberately kept the total sampling area (the ranch) small so as to reduce between-site differences in factors that might affect diversity patterns, such as climate, evolutionary history, and barriers to colonization by the local pool of mammals. All mammals occurring on the study area have the dispersal potential to colonize each of the habitats studied. I assume that rainfall and temperature are similar across the five sites. Any differences observed in the number and diversity of mammals occurring on the grids are considered to be due to habitat features.

##### *Study areas and trapping methods*

This study was done on Fundo Pecuario Masaguaral, 45 km south of Calabozo, Estado Guarico, Venezuela ( $8^{\circ}33'N$ ,  $67^{\circ}36'W$ ). Masaguaral is a working cattle ranch, and the owner, Tomas Blohm, has maintained the area as a wildlife sanctuary with minimal induced burning and hunting over the last 25 yr.

The total annual rainfall is  $\approx 1500$  mm with  $>90\%$  falling in the wet season (May to November). The general vegetation type is dry tropical forest (Ewell and Madriz 1968). Detailed description of the flora, fauna, and climate of Masaguaral are given in Eisenberg (1979).

Five sites representing four of the major habitat types on Masaguaral were chosen for study. In each study area, I established a  $10 \times 10$  grid of mammal traps with 20-m intervals between grid stations (except grid DFI which had an inter-trap distance of 15 m). At each station a Sherman live trap was placed on the ground. Additional Sherman traps and small National traps were set at various heights above the ground in standing vegetation. Traps were baited with crushed corn or dry dog food pellets. Banana or plantain was also used in the tree traps. On each grid, traps were run five consecutive days each month (unless otherwise noted). Traps were checked and rebaited each morning between 0700 and 1000. For each captured mammal, the following data were recorded: trap station, species, individual toe-clip number, sex, age, mass, and breeding condition. Details of trapping procedures and the population ecology of llanos small mammals are presented in August (*in press*).

The "Savanna" grid was set in palm-grass savanna

on the west side of Masaguaral. This grid was run from January 1978 to May 1978 for a total of 3660 trap nights. The dominant plants of the grid were grasses and sedges (*Panicum*, *Leersia*, *Eleocharis*) with scattered palms (*Copernicia tectorum*) and thorny shrubs (*Acacia* sp.) at the base of many palms. This habitat is sometimes called estero habitat (Troth 1979) and is flooded for much of the wet season.

The "Flooded" grid was set in bajio habitat (Troth 1979) and was trapped from January to June 1978 for a total of 4400 trap nights. This study site was a mosaic of grass field and forest patches. Palms (*Copernicia*), figs (*Ficus*), and legumes were dominant components of the wooded patches. Lower portions of the grid flood in the wet season.

The "Dry" grid was set in medano habitat (Troth 1979) in September 1976 and trapped for seven consecutive days monthly until December 1977 for a total of 15 344 trap nights. Medano habitat is found on the higher portions of the ranch (higher and lower reflect subtle differences in elevation, usually only a few metres) and characteristically occurs on sandy, well-drained soils. Medano is a mosaic of short-tree/tall-shrub woodland (*Annona*, *Byrsonima*, *Casearia*) and grass/herb field (*Ipomea*, *Mimosa*, *Hyptis*) and remains dry throughout the rainy season.

Two grids were set in deciduous forest habitat near a permanent stream, the Cano Caracol, on the east side of Masaguaral. Grid "DFI" was approximately 1.2 km from the Cano and was run from January 1977 to April 1978 for a total of 11 200 trap nights. Grid "DFII" was adjacent to the Cano and was run from January 1978 to May 1978 for a total of 3725 trap nights. Deciduous forest habitat had a moderately continuous and well-developed canopy. The understory was either open or cluttered with shrubs and vines. Deciduous forest habitat was not flooded extensively in the wet season. A complete list of the trees in this study site can be found in Troth (1979).

##### *Measurement of mammal diversity*

Five variables were used to characterize small-mammal communities. These were: species richness or the number of species present on a grid; species diversity; species evenness or equitability; the total number of individuals; and small-mammal biomass per grid. I used the Shannon-Wiener information index ( $H'$ ) as a measure of diversity and Pielou's index ( $J'$ ) as a measure of evenness. Natural logs were used in the computation of both indices. The number of individuals present on each grid was the sum of the mean monthly density of each species. Small-mammal biomass was determined by summing across species the mean monthly density multiplied by the mean adult mass.

Diversity and evenness indices were calculated for small mammals captured on each grid. Unequal sampling effort among sites can affect diversity values

(Sanders 1968, Fager 1972, Simberloff 1972, Heck et al. 1975, James and Rathbun 1981). The grids Dry and DFI were sampled for 16 mo, while grids DFII, Savanna, and Flooded were only sampled for 5 or 6 mo. To minimize any sampling biases in estimating small-mammal diversity, I recalculated small-mammal fauna parameters using only 6 mo of trapping data for grids DFI and Dry. Only dry season results were used (January to June 1977) in these subsamples so as to avoid any seasonal biases in grid censusing.

A second data set was developed that consisted of the total mammal fauna of each grid (excluding bats). This list (see Appendix) is based on my own mammal sightings, sightings made by colleagues studying mammal ecology on Masaguaral (J. Eisenberg, J. Robinson, and R. Rudran), and data reported in Eisenberg et al. (1979). For each grid, mammal richness could be calculated, but since density estimates for each species on the five grids are not available, I was unable to determine diversity or evenness.

Two measures of ecological diversity, locomotor and foraging, were derived from the total mammal data set. The three locomotor classes reflect the vertical habitat space utilized by llanos mammals. Each species was classified as arboreal, scansorial (utilizing tree and ground aspects of the habitat), or terrestrial. I recognized six trophic classes: carnivores, insectivores, frugivores or granivores foraging on fruits or seeds of arborescent vegetation, herbivores foraging on leaves or flowers of trees, browsers or grazers feeding on herbaceous vegetation or small shrubs, and myrmecophages feeding on ants or termites. Any species can forage on one or more food types. Locomotor and foraging class data were based on observations by myself and the persons noted above as well as the data of Enders (1935), Eisenberg and Thorington (1973), Fleming (1973), and Eisenberg (1980). Foraging and locomotor diversity and evenness were computed from these data.

A measure of mammalian ecological diversity based on both foraging and locomotor diversity was derived. A matrix consisting of foraging types along the columns and locomotor types along the rows was made for each grid. The cells of the matrix were the number of mammal species showing each locomotor-foraging type combination. The grand sum was the total number of ecological types present, and this is termed ecological richness. Ecological diversity was calculated using the Shannon-Wiener index,

$$H'_{eco} = -\sum(c_{ij}/\Sigma\Sigma) \ln (c_{ij}/\Sigma\Sigma),$$

where  $c_{ij}$  is the total of each cell of the matrix and  $\Sigma\Sigma$  is the grand sum. Ecological evenness was simply ecological diversity divided by the natural logarithm of the number of occupied cells. Each cell of the matrix represents a foraging-locomotor guild of mammals, and the number of occupied cells of the matrix is the number of guilds present in a habitat.

### *Measurement of habitat complexity and heterogeneity*

Habitat measurements were made at each trap station on each grid. The following variables were recorded (abbreviations in parentheses): (1) canopy height (CANHT) in metres directly above each station; (2) subjective estimates of the vegetation density in the canopy layer (CAN), midstory (MID), and shrub layer (SHRUB) around and above each trap station (a zero score indicated no vegetation in the stratum and a score of four indicated a dense, closed stratum); (3) continuity (CONNECT) of arborescent vegetation on a scale of 0–4 (a zero score indicated no arboreal routes to adjacent trap stations while a four indicated that foliage at all adjacent trap stations was continuous; this variable was recorded to estimate the development of above-ground vegetation, a factor that may affect the distribution of small arboreal or scansorial mammals); (4) representative height (in centimetres) of herbaceous vegetation (GCHT) in a 3.5 m radius circle around each trap station; (5) mean diameter at breast height (DBH) of all trees and shrubs with a DBH >3.2 cm in a 3.5 m radius circle around each trap station; (6) number of individual trees and shrubs in the DBH sample (NDBH); (7) number of species (NSPP) of trees and shrubs in the DBH sample; (8) percent herb and grass cover (TGC) in a 3.5 m radius circle around each trap station; and (9) percent canopy cover (TPCAN) above each trap station. Habitat measurements were made in the dry season to avoid the confounding effects of seasonal foliage change in describing study sites. All percent variables were arcsine transformed for statistical analyses (Sokal and Rohlf 1969). Additional details of the habitat measurements are given in August (*in press*).

My definition of habitat complexity states that complex habitats have many vegetational strata with dense foliage and simple habitats have few vegetational strata. An increasing value for each of the habitat variables I measured reflects increasing complexity. A maximally complex habitat would have dense and tall ground cover, many large trees and shrubs, and a dense canopy and midstory. An index of habitat complexity should reflect the relative magnitude of each habitat variable. I derived such an index using principal components analysis (PCA).

One of the uses of PCA is dimension reduction. The objective of such an analysis is to reduce a data set of many (and possibly redundant) variables to a new data set of fewer (and orthogonal) variables, yet containing the same amount of information as the original set of measures (Neff and Marcus 1980). The first principal component (PCI) is a weighted linear combination of the original variables. The variable weights are taken from the elements of the eigenvector derived from the correlation matrix. PCI describes a plane through the greatest amount of variation present in the raw data. The second principal component (PCII) is a new set

of weights that, when multiplied by the original data, explains the maximum amount of variation not correlated with PCI (Kleinbaum and Kupper 1978). The number of principal components can equal the number of raw variables. However, only the first few components are generally used as new variables, since they often explain most of the total sample variance. PCA can be done on the variance-covariance matrix or the correlation matrix of the raw data. Because different variables had different scaling factors, I used the correlation matrix in my analyses (Neff and Marcus 1980). No statistical assumptions regarding the raw data need to be made when PCA is used for purely descriptive purposes (Neff and Smith 1979).

Interpretation of each principal component is done by examining the magnitude of factor loadings on each component. Systematists have found that PCI is often a size factor explaining the variation imposed by having a gradation of large and small specimens in a sample (Robinson and Hoffman 1975, Neff and Smith 1979). Factor scores resulting from PCI condense all of the original variables into one measure of overall size. This is precisely the type of measure necessary to estimate habitat complexity on each grid. My index of habitat complexity was simply the grid mean of the factor scores from PCI. If a grid was complex and homogeneous, all the factor scores would be of large magnitude. A patchy grid would have considerable variation in the calculation of within-grid mean factor I. The standard deviation of the mean factor score for PCI was used as a measure of habitat heterogeneity or patchiness.

A measure of foliage height diversity (Mac Arthur and Mac Arthur 1961) was derived using four vegetational strata: canopy, midstory, shrub, and herb layers. I converted percent herb cover (GC is the untransformed variable TGC) to a 0–4 scale identical to that used in rating vegetation density in the variables CAN, MID, and SHRUB. A zero score indicated 0–19% ground cover, a score of one was 20–39% ground cover, etc. The sum of the scores for the variables CAN, MID, SHRUB, and scaled GC was calculated and the relative proportion of each stratum was used to estimate FHD. Both FHD and the index of complexity derived from PCA are sensitive to increasing number of foliage strata and even partitioning of vegetation among strata. The two indices differ in that FHD does not take into account foliage dimension (DBH) or plant diversity (NSPP), whereas the PCA index of complexity does. Holmes et al. (1979) found these variables important in correlating forest physiognomy with avian community structure.

## RESULTS

### *Habitat form*

Habitat profiles differed among the study grids (Table 1, Fig. 1). The Savanna grid was structurally sim-

TABLE 1. Habitat complexity, patchiness, and foliage height diversity (FHD) values, derived from principal components analysis, for five llanos study areas. DFI and DFII are the two study areas in deciduous forest habitat.

	Study areas				
	Savanna	Dry	Flooded	DFI	DFII
Complexity	-6.39	-4.20	-0.90	5.33	6.37
Patchiness	1.17	4.18	6.09	2.09	2.55
FHD	0.00	0.39	1.14	1.37	1.14

ple and homogeneous, with a well-represented herb layer but little arborescent vegetation. The Dry grid was not very complex but was quite patchy. The herb layer was well represented, while the shrub, midstory, and canopy layers were sparse. The high heterogeneity index resulted from the mosaic nature of this grid; woodland was intermixed with field. The Flooded grid was moderately complex relative to the other sites and was extremely heterogeneous. Herbaceous vegetation was abundant and there were patches of dense arborescent vegetation. Grids DFI and DFII were structurally complex and homogeneous. Both grids had dense and continuous canopy, midstory, and shrub strata. Grid DFI had more herbaceous vegetation than DFII. The complexity and heterogeneity indices of each grid corresponded well with my perception of these aspects of habitat profile that were apparent in the field.

The pattern of factor loadings on PCI (Table 2) shows that all of the weights were of the same approximate magnitude and all but TGC and GCHT were of the same sign. This indicates that PCI is a size factor (Neff and Smith 1979) and represents the abundance of vegetation in forest strata. Usually all of the loadings are of the same sign when PCI represents a size gradient. However, this would be biologically impossible with the present set of habitat variables. The negative signs of TGC and GCHT show that as the density of arborescent vegetation increases, herbaceous cover

TABLE 2. Factor loadings for the first (PCI) and the second (PCII) principal components.

Habitat variable (abbreviation)	PCI	PCII
Canopy height (CANHT)	0.84	-0.13
Canopy density (CAN)	0.86	-0.16
Midstory density (MID)	0.82	-0.21
Shrub density (SHRUB)	0.75	-0.20
Continuity of foliage (CONNECT)	0.91	0.12
Ground cover height (GCHT)	-0.53	-0.03
Number of trees in DBH sample (NDBH)	0.69	0.34
Diameter at breast height (DBH)	0.41	0.76
Number of tree and shrub species (NSPP)	0.84	0.35
Percent ground cover (TGC)	-0.79	0.04
Percent canopy cover (TPCAN)	0.68	-0.22
Eigenvalue	6.25	1.02
Percent variation explained	56.8	9.2
Cumulative percent variation explained	56.8	66.0

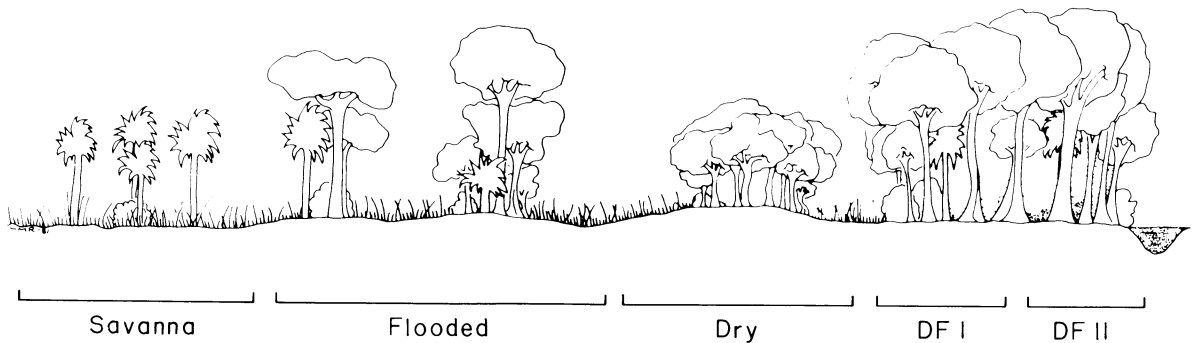


FIG. 1. Habitat structure of five study sites. The vertical scale indicates the relative differences in forest height. The depression to the right of grid DFII (deciduous forest II) represents the Cano Caracol, a small permanent stream.

decreases because of shading. James and Wamer's (1982) principal components analysis describing habitat form of north temperate forest also resulted in a PCI that represented a gradation of simple to complex vegetation types.

The five grids represent a gradation of habitat complexity and can be ranked in order of increasing complexity as Savanna < Dry < Flooded < DFI < DFII. Increased complexity is achieved by adding foliage strata (Fig. 1). Habitat complexity measured by FHD

is similar to the gradient resulting from the PCA index of complexity except that the Flooded grid and grid DFII are equally complex (Table 1). The gradient observed for habitat patchiness is quite dissimilar to the complexity gradient and can be ranked in order of increasing heterogeneity as Savanna < DFI < DFII < Dry < Flooded. Complexity and heterogeneity show independent trends among grids (Spearman's rank correlation coefficient,  $r_s = 0.20$ ,  $P > .70$ ), and this makes it possible to test which is the better predictor of mammal species richness and diversity.

#### Small-mammal diversity

Small-mammal faunas differed among the study grids (Table 3). The Savanna grid had a depauperate fauna consisting of only one species, *Oryzomys bicolor*, while the Dry grid and grid DFI had six species each (Appendix). The diversity of small mammals in either total or 6-mo samples showed no meaningful correlation with habitat complexity or heterogeneity (Table 4, Fig. 2). Small-mammal evenness showed little correlation with the habitat measures. Variation in  $H'$  was associated with variation in species number (Spearman's  $r_s = 0.95$ ,  $P < .01$ ) rather than  $J'$  (Spearman's  $r_s = 0.70$ ,  $P > .10$ ). Increasing  $H'$  due to increasing species richness has been observed in numerous studies of avian diversity (Tramer 1969, Power 1971, Lovejoy 1974, Aus-

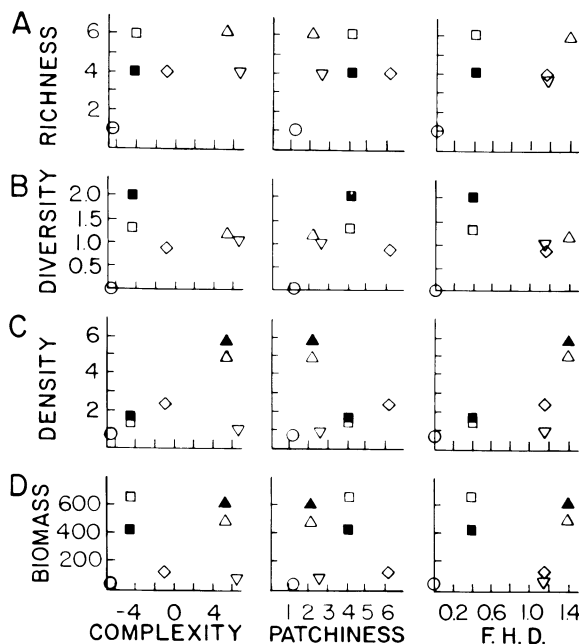


FIG. 2. Associations between measures of habitat profile and (A) small-mammal species richness, (B) small-mammal diversity, (C) small-mammal density (species pooled, no./ha), (D) small-mammal biomass (species pooled, g/ha). The different study areas are represented by ○ Savanna, ◇ Flooded, □ Dry, △ DFI, and ▽ DFII. Closed symbols represent the parameter value of a 6-mo, dry-season subsample of the total data per grid (open symbols) when the two values differ.

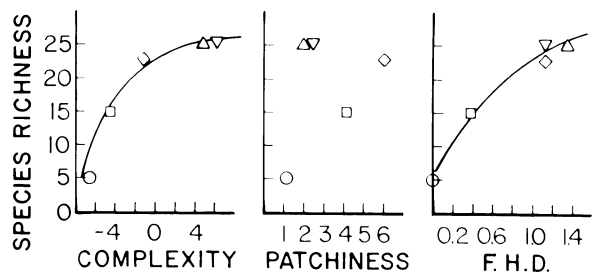


FIG. 3. Associations between total nonvolant mammal species richness and measures of habitat profile. The different study areas are represented by ○ Savanna, ◇ Flooded, □ Dry, △ DFI, and ▽ DFII. Curves are fit by eye.

TABLE 3. Measures of small-mammal richness, diversity, and evenness. Values outside of the parentheses are based on total samples. Values inside parentheses represent a 6-mo dry-season subsample.

	Study area				
	Savanna	Dry	Flooded	DFI	DFII
Total no. species	1 (1)	6 (4)	4 (4)	6 (6)	4 (4)
Diversity	0.00 (0.00)	1.33 (1.20)	0.90 (0.90)	1.24 (1.24)	1.09 (1.09)
Evenness	0.00 (0.00)	0.74 (0.87)	0.65 (0.65)	0.69 (0.69)	0.79 (0.79)
Biomass (g/ha)	28 (28)	647 (429)	126 (126)	489 (613)	67 (67)
Number of individuals/ha	0.7 (0.7)	1.4 (1.7)	2.3 (2.3)	4.9 (5.7)	0.9 (0.9)

tin and Tomoff 1978, James and Rathbun 1981), although other studies have shown  $H'$  to be a function of  $J'$  and not species number (Tramer 1969, Kricher 1972, Rotenberry 1978, Rotenberry et al. 1979).

#### Total mammal faunas

**Species richness.**—In contrast to the small mammals, total mammal species richness was highly correlated with habitat complexity and FHD (Table 4, Fig. 3). A trend toward increasing species number with increasing patchiness was evident among grids Savanna, Dry, and Flooded. However, the two highly complex yet homogeneous grids DFI and DFII were extreme outliers. This suggests that, overall, habitat complexity is better than habitat patchiness in predicting species richness. For moderately simple habitats, patchiness may also be correlated with species richness.

**Ecological groups.**—The numbers of terrestrial, scansorial, and arboreal mammals were significantly correlated with habitat complexity and FHD but not with patchiness (Table 5, Fig. 4). However, the number of species in each locomotor class was also highly correlated with the total number of species present on a grid (Table 5). To determine the rate at which new

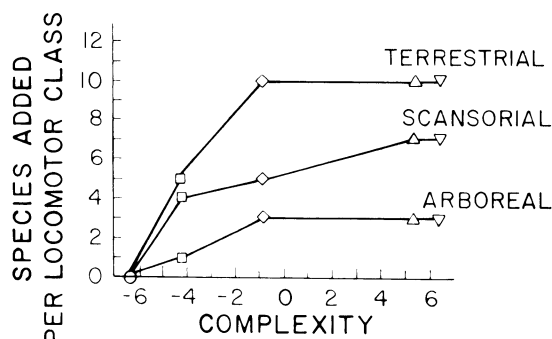


FIG. 4. Accumulation rates of species within each locomotor class across the complexity gradient. The values on the vertical axis represent the number of species not found on the Savanna grid that occur on each of the other four study areas. This standardizes the accumulation rates of all three locomotor classes to a common origin, the Savanna study site. The different study areas are represented by  $\circ$  Savanna,  $\diamond$  Flooded,  $\square$  Dry,  $\triangle$  DFI, and  $\nabla$  DFII.

TABLE 4. Spearman correlation coefficients of mammal fauna parameters vs. habitat complexity, patchiness, and foliage height diversity (FHD). Numeric values are given only for significant correlations. Statistical significance of correlation coefficients are: NS =  $P > 0.10$ ,  $\dagger P < 0.10$ ,  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.005$ ; Prop. = proportion of;  $n = 5$  in all cases.

	Complexity	Patchiness	FHD
	Spearman's $r_s$		
Total small-mammal sample			
Diversity	NS	NS	NS
Evenness	NS	NS	NS
No. species	NS	NS	NS
Biomass (g/ha)	NS	NS	NS
No. individuals/ha	NS	NS	0.82†
Six-month small-mammal sample			
Diversity	NS	NS	NS
Evenness	NS	NS	NS
No. species	NS	NS	0.92*
Biomass (g/ha)	NS	NS	NS
No. individuals/ha	NS	NS	0.82†
All nonvolant mammals			
Total no. species	0.97**†	NS	0.92*
No. arboreal	0.89*	NS	0.92*
Prop. arboreal	NS	NS	NS
No. scansorial	0.97**†	NS	0.92*
Prop. scansorial	NS	NS	NS
No. terrestrial	0.89*	NS	0.92*
Prop. terrestrial	-0.87†	NS	NS
Locomotor diversity	0.95*	NS	0.87†
Locomotor evenness	0.95*	NS	0.87†
No. carnivores	0.97**†	NS	0.92*
Prop. carnivores	NS	-0.95*	NS
No. insectivores	0.95*	NS	0.87†
Prop. insectivores	NS	NS	NS
No. frugivores	0.97**†	NS	0.92*
Prop. frugivores	NS	NS	NS
No. arboreal herbivores	NS	NS	NS
Prop. arboreal herbivores	-0.87†	NS	NS
No. browser-grazers	NS	NS	NS
Prop. browser-grazers	NS	0.87†	NS
No. myrmecophages	NS	NS	NS
Prop. myrmecophages	-0.97**†	NS	-0.92*
Foraging diversity	NS	0.87†	NS
Foraging evenness	NS	0.87†	NS
Ecological richness	0.97**†	NS	0.92*
Ecological diversity	0.87†	NS	NS
Ecological evenness	NS	NS	NS
No. guilds	0.87†	NS	NS
Species/guild	NS	NS	NS

TABLE 5. Characteristics of mammal communities based on all nonvolant mammal species occurring on the five llanos study grids. Numbers of mammals of a foraging or locomotor class are given outside the parentheses and the proportion of the total mammal fauna per grid in the foraging or locomotor class is given inside the parentheses.

	Study area				
	Savanna	Dry	Flooded	DFI	DFII
Total no. species	5	15	23	25	25
No. arboreal	1 (0.20)	2 (0.13)	4 (0.17)	4 (0.16)	4 (0.16)
No. scansorial	1 (0.20)	5 (0.33)	6 (0.26)	8 (0.32)	8 (0.32)
No. terrestrial	3 (0.60)	8 (0.53)	13 (0.57)	13 (0.52)	13 (0.52)
Locomotor diversity ( $H'$ )	0.95	0.97	0.97	0.99	0.99
Locomotor evenness ( $J'$ )	0.86	0.88	0.88	0.90	0.90
No. carnivores	2 (0.25)	4 (0.17)	6 (0.17)	9 (0.22)	9 (0.22)
No. insectivores	2 (0.25)	6 (0.25)	6 (0.17)	9 (0.22)	9 (0.22)
No. frugivores	2 (0.25)	5 (0.21)	10 (0.29)	12 (0.29)	12 (0.29)
No. arboreal herbivores	1 (0.13)	2 (0.08)	4 (0.11)	3 (0.07)	3 (0.07)
No. browser-grazers	0 (0.00)	5 (0.21)	7 (0.20)	6 (0.15)	6 (0.15)
No. myrmecophages	1 (0.13)	2 (0.08)	2 (0.06)	2 (0.05)	2 (0.05)
Foraging diversity	1.57	1.71	1.69	1.65	1.65
Foraging evenness	0.88	0.95	0.94	0.92	0.92
Ecological diversity	1.94	2.31	2.24	2.38	2.38
Ecological evenness	1.00	0.93	0.93	0.93	0.93
No. guilds	7	12	11	13	13
No. species/guild	1.14	2.00	3.18	3.15	3.15

species were added to each locomotor class across the complexity gradient, I plotted the number of species per class per grid minus the minimum number found on any grid (Fig. 4). The increase in species number across the complexity gradient is mainly due to the increasing number of terrestrial and scansorial taxa. Habitat complexity increases when foliage strata increase in number and vegetation density. With a well-represented canopy and midstory, I would predict an increase in space for arboreal taxa, but Fig. 4 indicates that this is not true. Apparently, the addition of new foliage strata provides resources other than additional living space for terrestrial and scansorial taxa.

The significant positive correlations between the diversity and evenness of locomotor types and com-

plexity measures (Table 4) is rather meaningless in view of the small variation in locomotor  $H'$  and  $J'$  among grids (Table 5). Indeed, all of the grids were within 0.04 units of each other for both indices.

To examine the rate at which species were added to each of the foraging classes across the complexity gradient, I standardized all grids such that the number of species in each foraging category was the number above the minimum value in the gradient (Fig. 5). Species number increased along the complexity gradient because of increasing numbers of frugivores, insectivores, carnivores, and browser-grazers. A similar pattern is evident in the correlation analysis (Table 4). Apparently, well-developed foliage strata characterizing complex habitats provides greater food resources for frugivorous mammals and substrates for insect prey. Because of the general increase in species numbers associated with complex habitats, carnivores would have a more diverse prey base.

Foraging  $H'$  and  $J'$  were not correlated with habitat complexity and were marginally associated with patchiness. However, it is difficult to place heavy emphasis on these patterns in view of the small amount of among-grid variation in these indices (Table 5). Ecological diversity, a composite variable of both locomotor and foraging classes, was marginally correlated with complexity and FHD but not patchiness. Ecological evenness was not correlated with habitat structure and was relatively constant among grids.

In spite of the five-fold difference in species richness between savanna habitat and deciduous forest, the proportions of feeding and locomotor classes were remarkably consistent among grids (Table 5). This suggests that increasing species richness is accommodated by expanding mammalian guilds rather than the

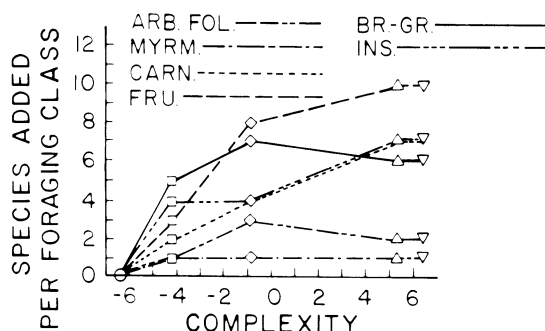


FIG. 5. Accumulation rates of species within each foraging class across the complexity gradient. The values on the vertical axis represent the number of species not found on the Savanna grid and occur on each of the other four study areas. This standardizes the accumulation rates of all six foraging classes to a common origin, the Savanna study site. The different study areas are represented by ○ Savanna, ◇ Dry, △ Flooded, and ▽ DFI.

addition of new guilds to complex habitats. Species number increased 67% between the relatively simple habitat of the Dry grid and the complex deciduous forest habitats, yet the complex habitats had only one additional guild of mammals. The number of species within guilds varied more than guild number across the complexity gradient (Fig. 6). These results are consistent with Cody's (1975) observations on patterns of avian community structure in mediterranean habitats but contrary to the results of Willson (1974) who found that species packing in temperate bird faunas was accomplished through guild addition rather than expansion.

## DISCUSSION

### *Small mammals*

By both temperate and tropical standards, the llanos has a depauperate small-mammal fauna. Fleming (1973) has shown a sharp increase in mammal species richness with decreasing latitude due to increased bat diversity in equatorial habitats. Many deserts of the southwestern United States have richer small-mammal faunas than the llanos, some containing as many as 11 trappable species (August et al. 1979). Similarly, other tropical habitats often have more small-mammal species than the llanos (Harrison 1969, Fleming 1970, Eisenberg et al. 1979). In general, the llanos has a rather limited mammalian fauna compared with other biogeographic regions of Venezuela. The llanos has no endemic mammals; most mammals in the area derive from the North Coastal Range and Guyana Highlands (Eisenberg and Redford 1979). A harsh Pleistocene climate characterized by periods of extreme aridity likely played an important historical role in the evolution of llanos biota (Simpson and Haffer 1978, Webb 1978, Eisenberg and Redford 1979).

Seasonal flooding likely limits the distribution and abundance of terrestrial small mammals in the llanos. For example, *Zygodontomys brevicauda* shows a distinct habitat shift at the start of the wet season (August, *in press*). Dry season habitat for this species is grassland that can become inundated after heavy and prolonged rainfall. Wet season activity is most apparent in wooded areas that remain above the flood line. The only species occurring on the Savanna grid is the arboreal *Oryzomys bicolor*, perhaps because this habitat is extensively flooded in the wet season.

Species richness and the number of individuals of small mammals showed positive trends with FHD but little correlation with heterogeneity. Both complexity and FHD are highly correlated with the number of individuals if grid DFII data are removed. This grid had especially low values for this variable. Perhaps the relationship between habitat complexity and small-mammal density is real, and grid DFII does not provide a representative sample of the deciduous forest small-mammal fauna. Censusing on grid DFII was done

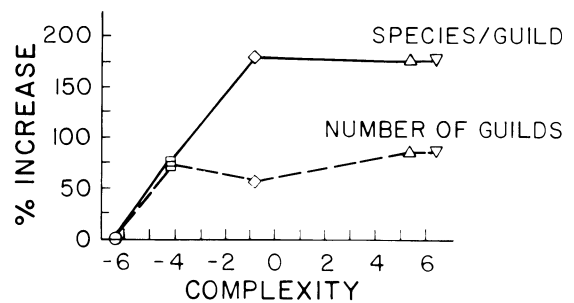


FIG. 6. Variation in guild size (number of species per guild) and guild number across the complexity gradient. The values represent the percent increase over that found on the Savanna study site. The different study areas are represented by ○ Savanna, ◇ Flooded, □ Dry, △ DFI, and ▽ DFII.

during the dry season of 1978. Grid DFII differed from the others because of its close proximity to year-round standing water (the Cano Caracol). The Cano is one of the few sources of free water in the deciduous forest during the dry season, and the abundance of large mammals was notably greater near the Cano during my censusing of grid DFII. This was especially apparent in *Cebus*, *Eira*, *Tayassu*, and *Dasyprocta*. *Cebus* and *Eira* are predators of small mammals, and the density of these taxa on grid DFII during the dry season was far greater than on grid DFI, in the same forest patch but >1.2 km from the Cano. In every census period, a group of over 20 *Cebus* monkeys was seen (on the ground and in the canopy) on or near grid DFII. *Cebus* monkeys are omnivores (J. G. Robinson 1981 and *personal communication*) and have been observed feeding on lizards and squirrels as well as attempting to remove a captured *Marmosa robinsoni* from a tree trap (J. G. Robinson, *personal communication*). Soon after the start of the wet season, the *Cebus* left the vicinity of the Cano and moved to other portions of the forest. This, as well as data showing a marked increase in urine-washing behavior in the absence of rainfall, suggest that these monkeys are under considerable water and thermal stress during the dry season (Robinson 1979). It is possible that grid DFII had so few small mammals because of the high density of predators in the dry season.

In general, community parameters of llanos small-mammal faunas showed little association with habitat complexity or patchiness. Rosenzweig and Winakur (1969) were able to develop an index of habitat complexity that was positively correlated with rodent diversity. However, Bond et al. (1980) found a negative correlation between rodent diversity and a simplified version of Rosenzweig and Winakur's complexity index. Bond et al. (1980) found no relationship between habitat heterogeneity and rodent species diversity, but M'Closkey (1976) reported that variables representing habitat patchiness explained a significant amount of variation in rodent species diversity. Do these conflict-

ing results suggest that habitat profile is not consistently important in structuring small-mammal communities? Perhaps, but it would not be surprising if small-mammal communities from as geographically distinct regions as the Venezuelan llanos (this study), the African fynbos (Bond et al. 1980), the Sonoran desert (Rosenzweig and Winakur 1969), and coastal sage scrub of southern California (M'Closkey 1976) followed different assembly rules. Geographic variation in the association between habitat form and community structure may be due to sampling phenomena as well. Small-mammal populations can exhibit considerable within- and between-year variation in density, and studies of small-mammal communities rarely last more than a few years, at most. Wiens (1981) has argued that it may simply be fortuitous to sample a community when species composition and abundance correlate with habitat structure.

#### *Total mammal faunas*

The present analysis suggests that the number of mammal species in different llanos habitats is associated with the structural complexity of vegetation in each habitat. Furthermore, abiotic factors, such as the intensity of wet-season flooding, likely affect the distribution of small terrestrial mammals (e.g., *Zygodontomys*, *Heteromys*, and *Sigmomys*). The presence or absence of most taxa on the study sites is generally consistent with what little we know of the natural history of each species. For example, the diversity of scansorial and arboreal mammals abruptly increases with the addition of arborescent vegetation in a habitat. Arborescent vegetation not only provides a locomotor substrate for "tree-living" mammals but also provides a substrate for a diversity of food types rarely available in savanna habitat. Examples include nasutitermine termites for *Tamandua*; herbage for *Coendou* and *Alouatta*; insects for *Marmosa* and *Cebus*; and fruits and seeds for many species (Appendix). The number of mammalian carnivores is highest in those habitats with considerable arborescent vegetation. In this study, complex habitats have a larger and more diverse prey base and provide the vertical space necessary for hunting and resting behavior seen in many mammalian carnivores (e.g., *Eira barbara*, *Felis concolor*, and *F. pardalis*).

Generally, the number of species in each foraging class was correlated with total species number per grid (Table 5). Consistent trends were not evident in the correlations between the proportion of species in each foraging class and measures of habitat profile. The highly significant negative association between the proportion of anteaters and habitat complexity is due to their decreasing proportion as species number increases. Indeed, the maximum number of llanos anteaters (two species) occurred on four out of five habitats sampled. I would not predict a linear increase in the number of anteater species with increasing habitat

complexity for two reasons. One, there are few ways that the ant-eating niche could be further subdivided. *Tamandua* and *Myrmecophaga* can probably coexist because one is well adapted for foraging in the canopy (*Tamandua*) while the other is well adapted for excavating large surface nests and travelling long distances to find them (*Myrmecophaga*) (Montgomery and Lubin 1977). Second, only three genera of mammals (*Myrmecophaga*, *Tamandua*, and possibly *Prionotes*) specializing in ant-eating occur north of the Orinoco River in Venezuela (Handley 1976), and two are present in the llanos.

The maximum number of canopy-foraging herbivores on any grid was four (Flooded grid). Considering the large amount of vegetation present in the forest canopy, I would have expected the arboreal herbivore guild to contain more species. A number of factors likely contribute to the depauperate nature of this guild. An important consideration is the highly deciduous nature of canopy vegetation in the dry season. Folivorous llanos mammals must be able to exploit a wide range of food resources to sustain themselves through the dry season or they will be especially stressed during this portion of the year (e.g., *Alouatta*, R. Rudran, *personal communication*). On a global basis, the arboreal folivore niche is narrow (Eisenberg 1978). Indeed, all of the genera of arboreal folivores in Venezuela, except sloths (Bradypodidae), occur on my study site (Handley 1976, Eisenberg 1978). Llanos habitat is probably unsuitable for sloths because the low availability of utilizable herbage in the dry season and the risk of hyperthermia (McNab 1978) may preclude the colonization of llanos forests by these obligate folivores (Montgomery and Sunquist 1978).

#### *Sampling considerations*

This study was designed to determine if the number and diversity of llanos mammals were associated with increasing habitat complexity or heterogeneity. By limiting the number of habitats sampled to those occurring in a small area, biogeographic and historical biases between sampling points have been minimized. This limited the total number of habitats available for study. Had I followed Brown's (1973, 1975) sampling procedure of 200 trap nights per location, this analysis would not have been possible. Indeed, my overall trap success was only 1% (August, *in press*) indicating that in a 200-trap-night sampling effort, I would have had only two captures. I am not criticizing Brown's methodology, but emphasize that tropical deciduous forests are not deserts, and different methodologies are necessary for different communities (Rudd 1979). Nevertheless, trends were apparent in the five habitats examined that are consistent with those shown by other researchers for different groups of organisms in different geographic areas.

The diversity of animals in some communities may be a function of plant diversity. While some research-

ers have found a positive association between plant and animal diversity (Pianka 1971, Murdoch et al. 1972), others have not (Mac Arthur and Mac Arthur 1961, Pianka 1967, Karr 1968, Rosenzweig and Winakur 1969, M'Closkey 1976, Heck and Wetstone 1977). Habitat grain (Levins 1968) and the degree of ecological specialization among the animals involved probably play an important role in explaining these conflicting data. Does plant diversity dictate animal diversity or is the reverse true? An unequivocal answer cannot be given for this very basic question, and logical arguments can be made in support of both options. On my study site, a fruiting fig tree (*Ficus*) increases the local diversity of birds and bats in the vicinity of the tree as long as fruits are ripe (Morton 1979, August 1981). In this case, vegetational productivity is the cause of animal diversity, albeit for a short period of time in an isolated location. However, figs are extremely dense in certain habitats in the llanos and their distribution is intimately associated with the animals dispersing fig seeds (Janzen 1979, August 1981). Many factors that are extremely important in structuring plant communities are not directly important to structuring animal communities; the depth of the water table might be an example. Although the abiotic and biotic factors governing plant and animal diversity may be different, ecological processes, such as competition, disequilibrium, disturbance rates, and colonization patterns can affect both (Mac Arthur and Wilson 1967, Horn 1975, Connell 1978, Fox 1979, Huston 1979).

A number of recent studies have shown positive correlations between patchiness and measures of species diversity (Wiens 1974, Willson 1974, Roth 1976), a result contrary to mine. Does this indicate that heterogeneity is not an important habitat parameter in structuring mammal communities in the llanos, or might it be an artifact of my method of measuring patchiness? Without additional data on the effects of habitat patchiness in other mammal communities, it is impossible to answer these questions unequivocally. I am confident that my use of PCA to estimate horizontal variation (patchiness) in habitat structure does in fact accomplish this. However, patch size (or grain, Levins 1968) does not figure in my index, and this is probably of tremendous importance to mammals. Grain dimension is a function of the size and mobility of the animal under consideration (Levins 1968). An ecologically significant habitat patch to a 40-g *Zygodontomys* is probably trivial to a 40-kg *Odocoileus*. The lack of association between total nonvolant mammal species richness and habitat patchiness could very well be due to the difficulty inherent in scaling patch size when considering mammals ranging in mass from 40 g to 40 kg. This bias should have been minimal, however, in my analysis of small-mammal communities.

Why was habitat heterogeneity poorly correlated with the diversity of mammals in the same size range? The answer again probably involves patch dimension.

Two different habitat profiles would yield identical patchiness values in my study. A grid that is divided in half with deciduous forest on one side and continuous field on the other would be as patchy as a grid with every other sampling station in forest and the remaining stations in open field. The first example would reflect a coarse-grained habitat with two large patches, while the second would be a fine-grained habitat with numerous small patches. The grain size of proper habitat would assuredly affect small-mammal distributions. Arboreal species, such as *Echimys*, *Rhipidomys*, and *Oryzomys*, would expend considerable time and energy commuting on the ground between fine-grain forest patches. Terrestrial small mammals such as *Zygodontomys* and *Sigmomys* could incur substantial predation risks by leaving the cover of one grass patch and commuting across the open forest floor to reach another grass patch. The potential energetic cost and predator risks inherent in crossing suboptimal patch types might contribute to making a fine-grain habitat extremely inhospitable to such taxa. Conversely, coarse-grain habitats would have sufficient continuous optimal habitat to support populations of both arboreal and terrestrial taxa. In the future, investigators of mammalian diversity might find it profitable to incorporate grain dimension in their measures of habitat heterogeneity.

Habitat profile was better correlated with total mammal species richness than small-mammal richness or diversity. It may be misleading to draw general conclusions about the role of habitat structure and faunal diversity using only a small subset of the animals occurring over a complexity or heterogeneity gradient. As mentioned earlier, grid DFII may have had a reduced number of individuals of small mammals because of intense predation by *Cebus* and *Eira*. In this case, predation reduced species diversity (Kushlan 1976) rather than promoting it (Paine 1966). Competition or predation by taxonomically distant groups of organisms probably plays an important role in structuring communities (Pearson 1975, 1977, Karr 1976, Brown and Davidson 1977, Brown et al. 1979, Munger and Brown 1981, August and Fleming, *in press*). Future studies of community diversity based on ecological rather than taxonomic types will provide considerable insight into the composition and maintenance of natural ecosystems.

#### ACKNOWLEDGMENTS

My research in Venezuela was generously supported by a Predoctoral Fellowship from the Smithsonian Institution. A Graduate Fellowship from the Department of Biology, Boston University, and the Albert R. and Alma Shadle Fellowship in Mammalogy (administered by the American Society of Mammalogists) provided financial support during the data analysis and writing phase of this study. John Eisenberg and Thomas Kunz provided guidance and direction over the course of the project. If it were not for the dedication to wildlife conservation shown by Sr. Tomas Blohm, the owner of Fundo Pecuario Masaguaral, the study sites and their spectacular

faunas would not exist. His warm hospitality established a comfortable and productive atmosphere for field research. The investigators and families of the Smithsonian Institution-Venezuela Cooperative Wildlife Research project all gave friendly scientific and social counsel. John Eisenberg, R. Rudran, and John Robinson provided substantial information concerning the distribution and ecology of llanos mammals. Eduardo Mondolfi, Juan Gomez-Nunez, Josephina Figueroa, Miguel Carballo, R. Rudran, Margaret O'Connell, and Betty Howser gave logistic aid throughout the project. Christopher Burnett provided expert advice on multivariate statistics. I thank Thomas Kunz, John Eisenberg, Robert Tamarin, Fred Wasserman, Jim Brown, Ted Fleming, and an anonymous reviewer for their comments on the manuscript. Lastly, I thank Lynn August for the field assistance, moral support, and encouragement given throughout the study.

## LITERATURE CITED

- August, P. V. 1981. Fig fruit consumption and seed dispersal by *Artibeus jamaicensis* in the llanos of Venezuela. *Biotropica* 13:70-76.
- . *In press*. Population ecology of small mammals in the llanos of Venezuela. Special Publications, The Museum, Texas Tech University, Lubbock, Texas, USA.
- August, P. V., J. Clarke, M. H. McGaugh, and R. L. Packard. 1979. Demographic patterns of small mammals, a possible use in impact assessment. In R. J. Baker and H. H. Genoways, editors. Biological investigations in the Guadalupe Mountains National Park. National Park Service Proceedings and Transactions 4:333-340.
- August, P. V., and T. H. Fleming. *In press*. Competition in neotropical small mammals. *Acta Zoologica Fennica*.
- Austin, G. T., and C. S. Tomoff. 1978. Relative abundance in bird populations. *American Naturalist* 112:695-699.
- Bond, W., M. Ferguson, and G. Forsyth. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape Mountains. *South African Journal of Zoology* 15:34-43.
- Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. *Ecology* 54:775-787.
- . 1975. Geographical ecology of desert rodents. Pages 315-341 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap, Cambridge, Massachusetts, USA.
- Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880-882.
- Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979. An experimental study of competition between seed-eating rodents and ants. *American Zoologist* 19:1129-1143.
- Cody, M. L. 1975. Towards a theory of continental species diversity. Pages 214-257 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap, Cambridge, Massachusetts, USA.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Eisenberg, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. Pages 135-152 in G. G. Montgomery, editor. *Ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- . 1979. Vertebrate ecology in the northern Neotropics. Smithsonian Institution Press, Washington, D.C., USA.
- . 1980. The density and biomass of tropical mammals. Pages 35-55 in M. Soule and B. Wilcox, editors. *Conservation biology*. Sinauer, Sunderland, Massachusetts, USA.
- Eisenberg, J. F., M. A. O'Connell, and P. V. August. 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. Pages 187-207 in J. F. Eisenberg, editor. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C., USA.
- Eisenberg, J. F., and K. Redford. 1979. A biogeographic analysis of the mammalian fauna of Venezuela. Pages 31-36 in J. F. Eisenberg, editor. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C., USA.
- Eisenberg, J. F., and R. W. Thorington. 1973. A preliminary analysis of a neotropical mammal fauna. *Biotropica* 5:150-161.
- Enders, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panama. *Bulletin of the Museum of Comparative Zoology, Harvard* 78:383-502.
- Ewell, J. J., and A. Madriz. 1968. Zonas de vida de Venezuela. Ministerio Agricultura y Cria, Caracas, Venezuela.
- Fager, E. W. 1972. Diversity: a sampling study. *American Naturalist* 106:293-310.
- Fleming, T. H. 1970. Notes on the rodent faunas of two Panamanian forests. *Journal of Mammalogy* 51:473-490.
- . 1973. Numbers of mammal species in North and Central American forest communities. *Ecology* 54:555-563.
- Fox, J. F. 1979. Intermediate disturbance hypothesis. *Science* 204:1344-1345.
- Handley, C. O. 1976. Mammals of the Smithsonian Venezuela Project. *Brigham Young University Science Bulletin* 20:1-89.
- Harrison, J. L. 1969. The abundance and population density of mammals in Malayan lowland forests. *Malayan Nature Journal* 22:174-178.
- Heck, K. L., G. van Belle, and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* 56:1459-1461.
- Heck, K. L., and G. S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4:135-142.
- Holmes, R. T., R. E. Bonney, and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* 60:512-520.
- Horn, H. S. 1975. Markovian processes of forest succession. Pages 196-211 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap, Cambridge, Massachusetts, USA.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.
- James, F. C., and S. Rathbun. 1981. Rarefaction, relative abundance, and diversity of avian communities. *Auk* 98:785-800.
- James, F. C., and N. O. Wamer. 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63:159-171.
- Janzen, D. H. 1979. How to be a fig. *Annual Review of Ecology and Systematics* 10:13-51.
- Karr, J. R. 1968. Habitat and avian diversity on strip mined land in east-central Illinois. *Condor* 70:348-357.
- . 1976. Within- and between-habitat avian diversity in African and neotropical lowland habitats. *Ecological Monographs* 46:457-481.
- . 1980. Geographical variation in the avifaunas of tropical forest undergrowth. *Auk* 97:283-298.
- Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. *American Naturalist* 105:423-435.
- Kleinbaum, D. G., and L. L. Kupper. 1978. *Applied regression analysis and other multivariable methods*. Duxbury Press, North Scituate, Massachusetts, USA.
- Klopfer, P. H., and R. Mac Arthur. 1960. Niche size and faunal diversity. *American Naturalist* 94:293-300.
- Kohn, A. J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-west Pacific reef platforms. *American Naturalist* 101:251-259.

- Kricher, J. C. 1972. Bird species diversity: the effect of species richness and equitability on the diversity index. *Ecology* **53**:278–282.
- Kushlan, J. A. 1976. Environmental stability and fish community diversity. *Ecology* **57**:821–825.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, USA.
- Lovejoy, T. E. 1972. Bird species diversity and composition in Amazonian rain forest. *American Zoologist* **12**:711–712.
- . 1974. Bird diversity and abundance in Amazon forest communities. *Living Bird* **13**:127–191.
- Mac Arthur, R. H., and J. W. Mac Arthur. 1961. On bird species diversity. *Ecology* **42**:594–598.
- Mac Arthur, R. H., J. W. Mac Arthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *American Naturalist* **96**:167–174.
- Mac Arthur, R. H., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. *American Naturalist* **100**:319–332.
- Mac Arthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- McCloskey, R. T. 1976. Community structure in sympatric rodents. *Ecology* **57**:728–739.
- McNab, B. K. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. Pages 153–162 in G. G. Montgomery, editor. *Ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- Montgomery, G. G., and Y. D. Lubin. 1977. Prey influences on movements of neotropical anteaters. Pages 103–131 in R. Phillips and C. Jonkel, editors. *Proceedings of the 1975 Predator Symposium*. Montana Forest and Conservation Experiment Station, Missoula, Montana, USA.
- Montgomery, G. G., and M. E. Sunquist. 1978. Habitat selection and use by two-toed and three-toed sloths. Pages 329–359 in G. G. Montgomery, editor. *Ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- Morton, E. S. 1979. A comparative survey of avian social systems in northern Venezuelan habitats. Pages 233–259 in J. F. Eisenberg, editor. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C., USA.
- Munger, J. C., and J. H. Brown. 1981. Competition in desert rodents: an experiment with semipermeable enclosures. *Science* **211**:510–512.
- Murdoch, W. M., F. C. Evans, C. H. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology* **53**:819–829.
- Neff, N. A., and L. Marcus. 1980. *A survey of multivariate methods for systematics*. Neff and Marcus (privately published), New York, New York, USA.
- Neff, N. A., and G. R. Smith. 1979. Multivariate analysis of hybrid fishes. *Systematic Zoology* **28**:176–196.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Pearson, D. L. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. *Condor* **77**:453–466.
- . 1977. A pantropical comparison of bird community structure on six lowland forest sites. *Condor* **79**:232–244.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* **100**:33–46.
- . 1967. On lizard species diversity: North American flatland deserts. *Ecology* **48**:333–351.
- . 1971. Lizard species diversity in the Kalahari desert. *Ecology* **52**:1024–1029.
- . 1975. Niche relations of desert lizards. Pages 292–314 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap, Cambridge, Massachusetts, USA.
- Power, D. M. 1971. Warbler ecology: diversity, similarity, and seasonal differences in habitat segregation. *Ecology* **52**:434–443.
- Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. *American Naturalist* **103**:75–80.
- Reed, C. 1978. Species diversity in aquatic microecosystems. *Ecology* **59**:481–488.
- Robinson, J. G. 1979. Correlates of urine washing in the wedge-capped capuchin, *Cebus nigrivittatus*. Pages 137–143 in J. F. Eisenberg, editor. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C., USA.
- . 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Animal Behaviour* **29**:1036–1056.
- Robinson, J. W., and R. S. Hoffman. 1975. Geographical and interspecific variation in big-eared ground squirrels (*Spermophilus*): a multivariate study. *Systematic Zoology* **24**:79–88.
- Rohde, K. 1978. Latitudinal gradients in species diversity and their causes. II. Marine parasitological evidence for a time hypothesis. *Biologisches Zentralblatt* **97**:405–418.
- Rosenzweig, M. L. 1975. On continental steady states of species diversity. Pages 121–140 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap, Cambridge, Massachusetts, USA.
- Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* **50**:558–572.
- Rotenberry, J. T. 1978. Components of avian diversity along a multifactorial climatic gradient. *Ecology* **59**:693–699.
- Rotenberry, J. T., R. F. Fitzner, and W. H. Rickard. 1979. Seasonal variation in avian community structure: differences in mechanisms regulating diversity. *Auk* **96**:499–505.
- Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. *Ecology* **61**:1228–1250.
- Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* **57**:773–782.
- Rudd, R. L. 1979. Is the tropical small mammal collector a fruiting tree? *Malayan Nature Journal* **33**:71–74.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* **102**:243–282.
- Simberloff, D. 1972. Properties of the rarefaction diversity measurement. *American Naturalist* **106**:414–418.
- Simpson, B. B., and J. Haffer. 1978. Speciation patterns in the Amazonian forest biota. *Annual Review of Ecology and Systematics* **9**:497–518.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* **58**:1007–1019.
- Tramer, E. J. 1969. Bird species diversity: components of Shannon's formula. *Ecology* **50**:927–929.
- Troth, R. G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. Pages 17–30 in J. F. Eisenberg, editor. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C., USA.
- Webb, S. D. 1978. A history of savanna vertebrates in the New World. Part II: South America and the great interchange. *Annual Review of Ecology and Systematics* **9**:393–426.
- Wiens, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. *American Midland Naturalist* **91**:195–213.
- . 1976. Population responses to patchy environ-

- ments. Annual Review of Ecology and Systematics 7:81–120.
- . 1981. Single-sample surveys of communities: are the revealed patterns real? American Naturalist 117:90–98.
- Willson, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017–1029.
- Willson, M. S., S. H. Anderson, and B. G. Murray. 1973. Tropical and temperate bird species diversity: within-habitat and between-habitat comparisons. Caribbean Journal of Science 13:81–90.

## APPENDIX

Summary of nonvolant mammal species known to occur on the five llanos habitats. Abbreviations are as follows: DF, deciduous forest; Sav, savanna; Loco, locomotor type; Forag, foraging type; T, terrestrial; S, scansorial; A, arboreal; C, carnivore; I, insectivore; Ft, fruits or seeds of arboresecent vegetation; Ht, foliar and floral vegetation of trees and shrubs; BG, browser-grazer; M, myrmecophagous; \*, present on grid; X, trapped on grid.

Family/species	Grid					Ecology	
	Dry	DFI	Flood	DFII	Sav	Loco	Forag
<b>Didelphidae</b>							
<i>Didelphis marsupialis</i>	X	X	*	*		S	C, I, Ft
<i>Marmosa robinsoni</i>	X	X	X	X		S	I, Ft
<b>Dasypodidae</b>							
<i>Dasypus novemcinctus</i>	*	*	*	*	*	T	I
<b>Myrmecophagidae</b>							
<i>Tamandua tetradactyla</i>	*	*	*	*		S	M
<i>Myrmecophaga tridactyla</i>	*	*	*	*	*	T	M
<b>Cebidae</b>							
<i>Cebus nigrivittatus</i>		*		*		A	C, I, Ft
<i>Alouatta seniculus</i>		*	*	*		A	Ft, Ht
<b>Mustelidae</b>							
<i>Conepatus semistriatus</i>	*	*	*	*		T	I, BG
<i>Eira barbara</i>		*	*	*		S	C, Ft, I
<i>Galictis vittata</i>		*	*	*		T	C
<b>Procyonidae</b>							
<i>Procyon cancrivorus</i>		*	*	*		T	C, I, Ft
<b>Canidae</b>							
<i>Cerdocyon thous</i>	*	*	*	*	*	T	C, I, Ft
<b>Felidae</b>							
<i>Felis yagouaroundi</i>	*	*	*	*	*	S	C
<i>F. pardalis</i>	*	*	*	*		S	C
<i>F. concolor</i>		*	*	*		S	C
<b>Leporidae</b>							
<i>Sylvilagus floridanus</i>	*	*	*	*		T	BG
<b>Sciuridae</b>							
<i>Sciurus granatensis</i>		X	*	X		S	Ft
<b>Heteromyidae</b>							
<i>Heteromys anomalus</i>		X	*	X		T	BG
<b>Cricetidae</b>							
<i>Rhipidomys</i> sp.			X			A	Ft, Ht
<i>Oryzomys bicolor</i>	X		*		X	A	Ft, Ht
<i>Zygodontomys brevicauda</i>	X	X	X	X		T	BG
<i>Sigmomys alstoni</i>	X		X			T	BG
<b>Erethizontidae</b>							
<i>Coendou prehensilis</i>		*	*	*		A	Ht
<b>Echimyidae</b>							
<i>Echimys semivillosus</i>	X	X		*		A	I, Ft, Ht
<i>Dasypsecta aguti</i>		*	*	*		T	Ft
<i>Agouti paca</i>		*		*		T	Ft
<b>Cervidae</b>							
<i>Odocoileus virginianus</i>	*	*	*	*		T	BG
<b>Tayassuidae</b>							
<i>Tayassu tajacu</i>		*	*	*		T	BG, Ft