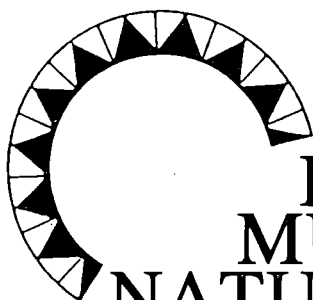


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THE MAMMAL SPECIES OF NORTH-CENTRAL VENEZUELA

John F. Eisenberg and John R. Polisar

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Plate 1. Female jaguar (*Panthera onca*) near prestamo. La Candelaria, Hato Piñero, Estado Cojedes. Eye shine of young caiman (*Caiman crocodilus*) in background.



Plate 2. Giant anteater (*Myrmecophaga tridactyla*) along dry savanna/dry forest ecotone. Las Penitas, Hato Piñero, Estado Cojedes.



Plate 3. White-lipped peccaries (*Tayassu pecari*) exiting mud wallow. Dry season, Caño Caujaral, Hato Piñero.



Plate 4. Puma (*Puma concolor*) traveling along foot-transect. Caño Caujaral, Hato Piñero.



Plate 5. Capybara (*Hydrochaeris hydrochaeris*) carcass killed by a jaguar. Rio Pao, Hato Piñero.

THE MAMMALS OF NORTH-CENTRAL VENEZUELA

John F. Eisenberg¹ and John R. Polisar²

ABSTRACT

The terrestrial mammal fauna of Venezuela includes 327 species. In this paper we examine the mammal fauna from the six north-central states and the federal district. This area includes the Caribbean coast, the north coastal ranges, the interior ranges, and the northern llanos. A diverse array of habitats are represented in this area: xeric scrub forests, montane rain forests, cloud forests, deciduous forests, and the savannas of the llanos.

This north-central portion of Venezuela contains 180 species which have been vouchered and deposited in museums. The forested north coastal ranges include sites such as Guatopo National Park with some 95 species, while llanos sites, when gallery forests are included, may have up to 75 species. Some bat species have ranges restricted to specific vegetation complexes and/or altitudes.

Representative examples of all major habitat types in this area currently receive some protection. National parks perform this role in the north coastal ranges and interior ranges. To-date the most successful protection of llanos flora and fauna seems to have been the result of private initiatives, on ranches such as Hato Piñero and Hato Masagual. In the llanos, maintenance of large mammals such as white-lipped peccaries (*Tayasu pecari*), jaguar (*Panthera onca*), and puma (*Puma concolor*) will depend on linked networks of large ranches and parks in which habitats are intact and hunting levels low to nonexistent.

RESUMEN

Se han registrado 327 especies de mamíferos terrestres para Venezuela. En este trabajo analizamos la mastozoofauna de los seis estados del norte central y del distrito federal. Se incluyen por lo tanto, la costa del Caribe, el ramal norteño de la Cordillera de la Costa, los ramales sureños de la Cordillera de la Costa y los llanos norteños. Están representadas una variedad de habitats: matorral desértico, bosques húmedos montanos, bosques de neblina, bosques deciduos y las sabanas de los llanos.

Esta región de Venezuela alberga 180 especies de mamíferos que cuentan con especímenes depositados en algún museo. La Cordillera de la Costa incluye sitios como el Parque Nacional de Guatopó que alberga 95 especies, mientras que en los llanos, en localidades que incluyen bosques de galería se pueden llegar a registrar hasta 75 especies. Algunas especies de quirópteros tienen rangos de distribución restringidos a un tipo de vegetación específico y/o a un rango de altitudes.

En esta región muestras representativas de todos los hábitats importantes están bajo alguna forma de protección. En la Cordillera de la Costa la protección está dada por parques nacionales. En los llanos la protección más efectiva de especies de flora y fauna ha sido debido a la iniciativa privada, por ejemplo en ranchos como Hato Piñero y Hato Masagual. Es por eso que en los llanos para la protección de mamíferos

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grandes como Báquiro Cachete Blanco (*Tayassu pecari*), el jaguar (*Panthera onca*) y el puma (*Puma concolor*), se debe considerar una red integrada por grandes ranchos y parques que contengan hábitats prístinos sin presión o una presión muy baja de caza.

Introduction

As of 1998 roughly 337 species of mammals have been recorded within the political boundaries of Venezuela and within its coastal waters. Excluding strictly aquatic forms (Sirenia, Cetacea), there is a terrestrial fauna of some 327 species (Linares, 1998). The order Chiroptera includes 154 species and Rodentia 84 species; thus, seventy-two percent of the species are accounted for by just these two orders. This is a rich fauna by temperate-zone standards. Whitaker and Hamilton (1998) listed (exclusive of exotics and feral domesticates) 106 species for the twenty-seven states east of the Mississippi River in the U.S.A. Of this total, fifty-four percent belong to the Chiroptera and Rodentia.

Eisenberg and Redford (1979) conducted a comparative analysis of the Venezuelan mammal fauna across seven broad biogeographical regions. The northern coast ranges contain a number of peaks over 2,000 m. Much of this terrain is covered by evergreen forests, which are partially isolated from similar forests in the Andes by lowlands which contain dry deciduous forest and grasslands. Complex folding has resulted in a series of ranges roughly parallel along an east-west axis. It is possible to refer to two major components: (1) the coastal range abutting the sea and (2) a series of interior ranges separate from the former by the valley of Caracas and the Lake Valencia valley (Fig. 1). Protected areas in the front coastal range include Parque Nacional El Ávila (852 km²), Parque Nacional Henri Pittier (1078 km²) and Parque Nacional San Esteban (440 km²). Protected areas in the interior of the coast range include Parque Nacional Guatopo (1224 km²), Parque Nacional Macarao (150 km²) and Parque Nacional Tirgua (910 km²). A partially isolated inland range, the Sierra Aroa, contains Parque Nacional Yurubí (236.7 km²). Elevations gradually decrease as these mountains undulate into another, lower, biographic region, los llanos. The southern drainage from the mountains forms streams and rivers that meander south through los llanos, all eventually draining into major rivers, such as the Apure, and ultimately exiting into the Atlantic via the Orinoco.

The llanos are usually divided into llanos altos (above 100 m), and further south, los llanos bajos. Both are characterized by a habitat mosaic of low, seasonally flooded grasslands and gallery forests. The gallery forests provide a "ribbon of life" for forest forms. In los llanos altos, these gallery forests are augmented by large patches of semi-deciduous forest not associated with rivers. These connected forest corridors and patches maintain mammalian diversity in a savanna dominated landscape. Cattle ranching is the dominant land use throughout los llanos. In some cases, enlightened management by private owners

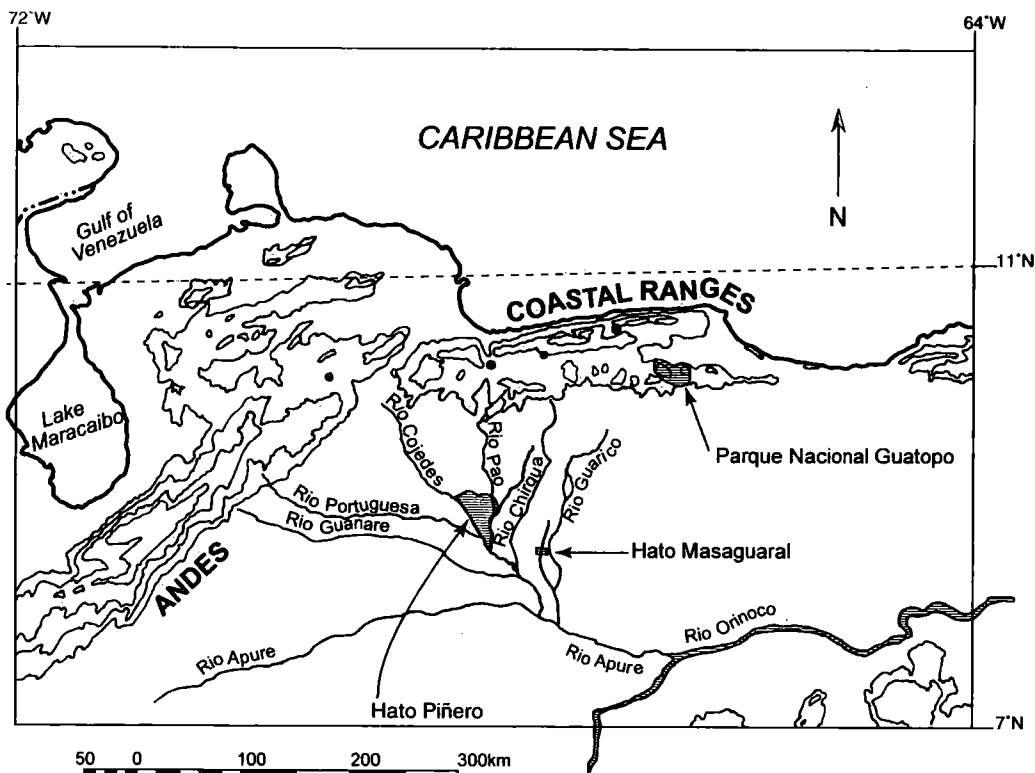


Figure 1. The moist forest zones of north-central Venezuela are associated with the higher elevation of the coastal ranges (Ewel and Madriz, 1968). Contour lines are at intervals of 500, 1000, 2000, and 3000 m. The llanos lie to the east of the Andes and south of the coastal ranges. Black dots indicate major centers of urbanization. The major study areas are shaded.

has resulted in wildlife refuges that rival national parks in efficacy. The aggregated forests and savannas of Hatos Piñero, Mata Clara, Socorro in Estado Cojedes and Hato Corralito in Guarico constitute an area of over 1,500 km². This is larger than any one effective national park in our entire study area (Estados Aragua, Carabobo, Cojedes, Guarico, Miranda, and Yaracuy, and the Distrito Federal). The fauna retained (jaguars, tapirs, white-lipped peccaries) reflect that. Two well-studied llanos sites include Hato Masaguaral (3000 ha) in Estado Guarico and Hato Piñero (84,000 ha) in Estado Cojedes.

Overall, habitat diversity is high. There are xeric habitats along the Caribbean Coast, humid and dry forest types in the northern mountains, and additional heterogeneity to the south in los llanos. Holdridge Life Zone classifications adequately describe the forests of the northern part of the study area (Wet Tropical, Dry Tropical, Very Dry Tropical, Very Wet Montane Tropical, Wet Montane Tropical, and Dry Montane Tropical Forests), but fail to adequately explain habitat variation in los llanos (Ewel and Madriz, 1968). Falling entirely

within a Holdridge Tropical Dry Forest classification, los llanos actually contain diverse habitats: seasonally burnt chaparrales, dry deciduous forests on low hills, semi-deciduous forests in valleys, palm forests along savanna edges, pockets of evergreen forests, and a wide variety of savanna types. Small changes in elevations, combined with variation in soils and hydrology, create a strong horizontal heterogeneity. The entire study area experiences strong seasonality. A wet season runs from May through October, the dry season from December through March, and April and November are transitional months. Low elevations, high temperatures, clay soils, and impeded drainage in los llanos result in exceptionally strong seasonality: annual cycles of flooding and dessication there greatly affect both flora and fauna.

The mammals of Venezuela were characterized in Handley (1976) and summarized by Linares (1998). Original ecological research in Parque Nacional Guatopo and Hato Masaguaral is included in Eisenberg (1979b). This paper aggregates information regarding the terrestrial mammal fauna of the north-central portion of Venezuela (Estados Aragua, Carabobo, Cojedes, Guarico, Miranda, Yaracuy, and the Distrito Federal). This area was chosen because of the depth of the studies that have taken place in this area, and its high diversity owing to a juxtaposition of biogeographic regions. The area is unique for another reason. Despite inclusion of several large cities, large scale industrial centers, and widespread agricultural activities, this area retains much of its original fauna. We document that situation and hope that this contribution helps perpetuate it (Fig. 2).

The mammal fauna of the area defined in the previous paragraphs includes 180 terrestrial species; 108 are Chiroptera and 27 belong to the Rodentia. The area is comparable to about seventy percent of the state of Georgia, U. S. A. The fauna is typical of the lowland Neotropics, although not as species-rich as comparable areas in the western Amazon region of Peru and Ecuador. A "list" of 161 species is included in Table 1 and represents the efforts of Handley (1976) and Eisenberg et al. (1979) with some amendments. Some marginal bat species are not included in Table 1 but are listed in Table 2. Combining Tables 1 and 2 could yield 180 species.

No one sampling effort in the major study areas discussed in Eisenberg et al. (1979) included the full faunal complement. This occurred for a variety of reasons. For example, let us consider Guatopo and vicinity. Handley (1976) collected 39 species of bats and 13 species of rodents. Eisenberg, O'Connell, and August (1979) recorded 18 species of bats and 13 species of rodents. The lists were not identical, reflecting different collecting efforts. When the lists are combined, the totals would be 50 species of bats and 17 species of rodents. Combining all collection efforts in Guatopo would yield about 95 species of mammals or about 55 percent of the total estimated fauna for the defined 113,430 km² six-state area; Guatopo covers 1,224 km².

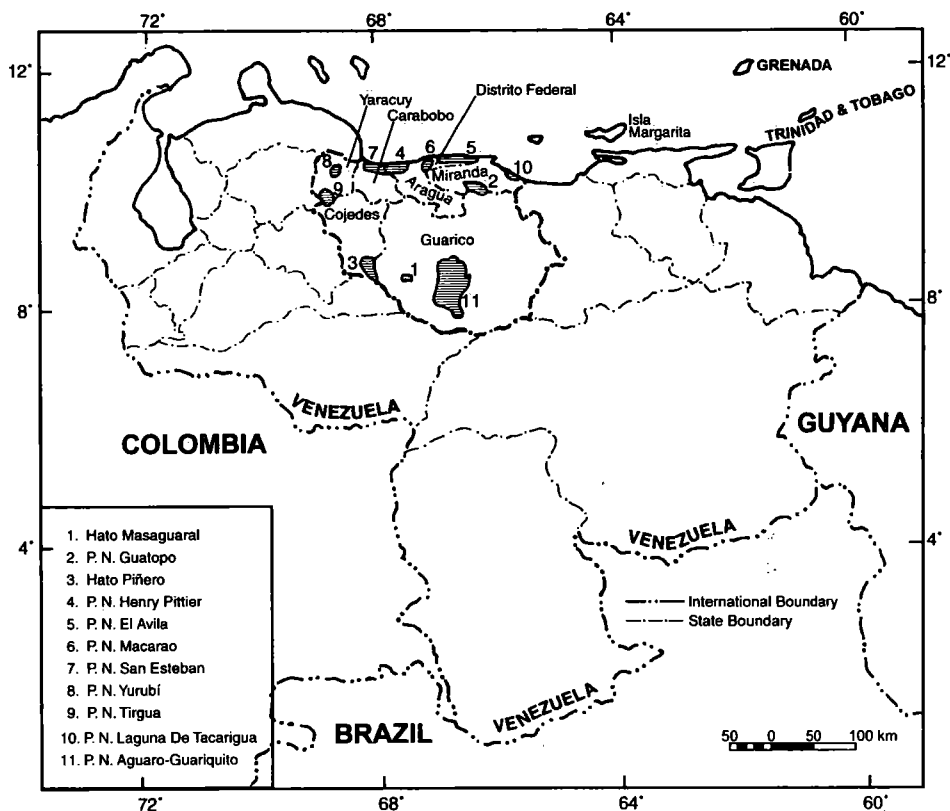


Figure 2. The six states of north-central Venezuela plus the federal district. Study and protected areas and parks are represented by the numbers.

Proceeding south, from the montane forests to the llanos, species richness declines somewhat. Where gallery forests are present, species numbers remain elevated, but the stochastic loss of species contributes to an uneven distribution. For example, in the savanna woodlands and gallery forests of Hato Masaguaral, seventy-four species of mammals were tabulated of which forty-two were bats and twelve rodents. The areas surveyed included some 3000 ha. The level of species richness is typical for woodland savannas in the Neotropics (Voss and Emmons, 1997).

Trapping effort, microhabitats sampled, and genuine differences between the "front" range and the "back" ranges of the north coast all contribute to differences in species numbers recorded. The figure of 180 species for the total area of six

Table 1. The Mammals of North-Central Venezuela (1976-1998).

Taxa	A ¹	B ²	C ³
Didelphimorphia (10)			
Didelphidae			
<i>Caluromys philander</i>	x, g	g	
<i>Chironectes minimus</i>	x, g	g	
<i>Didelphis marsupialis</i>	x, g	g, m	
<i>Marmosops fuscata</i>	x, g	g	
<i>Marmosa murina</i>	x, g	g	
<i>M. robinsoni</i>	x, g	g, m	
<i>Micoureus demararae (cinerea)</i>	x, g	g	
<i>Gracilinanus marica</i>	x	o	Perez Hernandez, 1989
<i>Monodelphis brevicaudata</i>	x, g	g	
<i>M. orinoci</i>	o	o	Perez-Hernandez, 1989
Insectivora			
Soricidae			
<i>Cryptotis meridensis</i>	o	o	Linares, 1998
Xenarthra (Edentata) (7)			
Myrmecophagidae			
<i>Myrmecophaga tridactyla</i>	o	m	
<i>Tamandua tetradactyla</i>	x, g	m, g	
Bradypodidae			
<i>Bradypus variegatus</i>	x, g	g	
Dasypodidae			
<i>Cabassous unicinctus</i>	o	g	
<i>Dasypus novemcinctus</i>	x, g	g, m	
<i>D. sabanicola</i>	o	o	Wetzel, 1985
<i>Priodontes maximus</i>	o	o	Wetzel, 1985
Primates (3)			
Cebidae			
<i>Cebus olivaceus (nigrivittatus)</i>	x, g	g, m	
<i>Alouatta seniculus</i>	x, g	g, m	
<i>Ateles belzebuth</i>	o	g	Mondolfi and Eisenberg, 1979
Chiroptera (88)			
Emballonuridae (7)			
<i>Pteropteryx kappleri</i>	x, g	o	
<i>P. macrotis</i>	x, g	o	
<i>P. trinitatus</i>	x, g	o	
<i>Rhynchonycteris naso</i>	x, g	m	
<i>Saccopteryx bilineata</i>	x, g	g, m	
<i>S. canescens</i>	x, g	o	
<i>S. leptura</i>	x, g	g, m	
Noctilionidae (2)			
<i>Noctilio leporinus</i>	x, g	m	
<i>N. albiventris</i>	x, g	m	
Mormoopidae (4)			
<i>Pteronotus davyi</i>	x, g	g	
<i>P. parnellii</i>	x, g	g	
<i>P. personatus</i>	x, g	o	

Table 1 Continued.

Taxa	A ¹	B ²	C ³
<i>P. suapurensis</i>	x, g	o	
<i>Mormoops megalophylla</i>	x, g	o	
Phyllostomatidae (45)			
Phyllostomatinae			
<i>Chrotopterus auritas</i>	x, g	g	
<i>Lonchorchina aurita</i>	x, g	g	
<i>Macrophyllum macrophyllum</i>	x, g	g	
<i>Micronycteris brachyotis</i>			
<i>M. megalotis</i>	x, g	m	
<i>M. nicefori</i>	x, g	g	
<i>M. minuta</i>	x, g	m	
<i>Mimon crenulatum</i>	x, g	m	
<i>Phyllostomus discolor</i>	x, g	g, m	
<i>P. elongatus</i>	x, g	m	
<i>P. hastatus</i>	x, g	g, m	
<i>Tonatia bidens</i>	x, g	o	
<i>T. brasiliense</i>	x, g	m	
<i>Tonatia sylvicola</i>	o	o	Linares, 1998
<i>Trachops cirrhosis</i>	x, g	m	
<i>Vampyrum spectrum</i>	x, g	o	
Glossophaginae			
<i>Anoura caudifer</i>	x, g	g	
<i>A. culturata</i>	x, g	o	
<i>A. geoffroyi</i>	x, g	o	
<i>Glossophaga longirostris</i>	x, g	m	
<i>G. soricina</i>	x, g	g, m	
Carollinae			
<i>Carollia brevicauda</i>	x, g	o	
<i>C. perspicillata</i>	x, g	g, m	
Sturnirinae			
<i>Sturnira erythromos</i>	x, g	g	
<i>S. lilium</i>	x, g	g, m	
<i>S. ludovici</i>	x, g	g, m	
Stenodermatinae			
<i>Chiroderma salvini</i>	x	g	
<i>C. villosam</i>	x, g	o	
<i>Uroderma bilobatum</i>	x, g	g	
<i>U. magnirostrum</i>	x, g	g, m	
<i>Vampyressa pusilla</i>	x, g	g	
<i>Vampyrodes caraccioli</i>	x	g	
<i>Platyrrhinus helleri</i>	x, g	g	
<i>P. umbratus</i>	x, g	o	
<i>P. vittatus</i>	x	o	
<i>Ametrida centurio</i>	x, g	g	
<i>Artibeus cinereus</i>	x, g	g, m	
<i>A. harti</i>	x		
<i>A. phaeotis</i>	o	g	
<i>A. jamaicensis</i>	x, g	g, m	
<i>A. lituratus</i>	x, g	g	
<i>Centurio senex</i>	o	o	Linares, 1986

Table 1 Continued.

Taxa	A ¹	B ²	C ³
<i>Sphaeronycteris toxophyllum</i>	x	g, m	
Desmodontinae			
<i>Desmodus rotundus</i>	x, g	m	
<i>Diphylla ecaudata</i>	x	o	
Vespertilionidae (14)			
<i>Eptesicus brasiliensis</i>	x	o	
<i>E. diminutus</i>	x	o	
<i>E. furinalis</i>	x, g	g, m	
<i>E. fuscus</i>	x	o	
<i>Histiotus humboldti</i>	x	o	
<i>Lasiurus blossevillei</i>	x	g, m	
(<i>L. borealis</i>)			
<i>L. cinereus</i>	x	o	
<i>L. ega</i>	x, g	m	
<i>Myotis albescens</i>	x, g	m	
<i>M. keaysi</i>	x, g	o	
<i>M. nigricans</i>	x, g	m	
<i>Myotis simus</i>	o	g	
<i>M. oxyotus</i>	x	o	
<i>Rhogeessa tumida</i>	x, g	g, m	
Natalidae (1)			
<i>Natalus tumidirostris</i>	x	o	
Molossidae (15)			
<i>Eumops auripendulus</i>	x	m	
<i>E. bonairiensis</i>	o	m	
<i>E. dabbenei</i>	x	m	
<i>E. glaucinus</i>	x	m	
<i>E. hansae</i>	o	m	
<i>Molossops greenhalli</i>	o	m	
<i>M. parvus</i>	x	o	
<i>M. temminckii</i>	o	m	
<i>Molossus ater</i>	x	o	
<i>M. azteus</i>	x	o	
<i>M. bondae</i>	x	o	
<i>M. mollosus</i>	x, g	m	
<i>M. sinaloae</i>	x	o	
<i>Nyctinomops laticaudatus</i>	x	o	Linares, 1998
<i>Tadarida brasiliensis</i>	o	o	Linares, 1998
Carnivora (17)			
Canidae			
<i>Urocyon cinereoargenteus</i>	x	o	
<i>Cerdocyon thous</i>	x	g, m	
<i>Speothos venaticus</i>	o	o	Bisbal, 1989
Procyonidae			
<i>Procyon cancrivorus</i>	x, g	g, m	
<i>Potos flavus</i>	x, g	g	
Mustelidae			
<i>Mustela frenata</i>	o	o	Bisbal, 1989
<i>Eira barbara</i>	o	g, m	
<i>Galictis vittata</i>	o	m	

Table 1 Continued.

Taxa	A ¹	B ²	C ³
<i>Conepatus semistriatus</i>	o	g, m	
<i>Lontra longicaudis</i>	o	o	Bisbal, 1989
<i>Pteronura brasiliensis</i>	o	o	Bisbal, 1989
Felidae			
<i>Puma concolor</i>	o	m	Hato Piñero
<i>Panthera onca</i>	o	g	Hato Piñero
<i>Herpailurus yagouaroundi</i>	o	g, m	
<i>Leopardus pardalis</i>	x, g	g, m	
<i>Leopardus wiedii</i>	o	o	Bisbal, 1989
<i>Leopardus tigrina</i>	x	o	
Perissodactyla (1)			
Tapiridae			
<i>Tapirus terrestris</i>	o	g	
Artiodactyla (5)			
Tayassuidae			
<i>Tayassu pecari</i>	o	o	Hato Piñero
<i>Tayassu tajacu</i>	o	g, m	
Cervidae			
<i>Odocoileus virginiana</i>	x, g	g, m	
<i>Mazama americana</i>	x	g	
<i>Mazama gouazoubira</i>	o	o	Bisbal, 1991
Rodentia (27)			
Sciuridae			
<i>Sciurus granatensis</i>	x, g	g, m	
Heteromyidae			
<i>Heteromys anomalus</i>	x, g	g, m	
Muridae			
Sigmonotinae			
Oryzomyini			
<i>Oecomys bicolor</i> (see text)			
<i>O. concolor</i> (see text)			
<i>O. speciosus</i>	x, g	m	
<i>O. trinitatis</i>	x, g	g	
<i>Oryzomys albigularis</i>	x	g	
<i>O. capito</i> (see text, gt)			
<i>O. megocephalus</i> (see text)			
<i>O. talamancae</i>	x	g	
<i>Microryzomys minutus</i>	x	o	
<i>Oligoryzomys fulvescens</i>	x, g	m	
<i>Neacomys tenuipes</i>	x, g	g	
Thomasomyini			
<i>Rhipidomys venustus</i>	x	o	
<i>R. venezuelae</i>	x, g	g, m	
Phyllotini			
<i>Calomys hummelinki</i>	o	o	Linares, 1998
Ichthyomyini			
<i>Ichthyomys pittieri</i>	o	o	Handley and Mondolfi, 1963
Akodontini			
<i>Akodon urichi</i>	x, g	g	
Zygodontomyini			

Table 1 Continued.

Taxa	A ¹	B ²	C ³
<i>Zygodontomys brevicauda</i>	x, g	m	
Sigmodontini			
<i>Sigmodon hispidus</i>	x, g	o	
<i>S. alstoni</i>	x	m	
<i>Holochilus sciureus</i>	x	o	
Erethizontidae			
<i>Sphiggurus pruinosus</i>	o	o	CEBRG
<i>Couendou prehensilis</i>	x, g	g, m	
Caviidae			
<i>Cavia aperea</i>	x, g	o	
Hydrochaeridae			
<i>Hydrochaeris hydrochaeris</i>	o	m	
Agoutidae			
<i>Agouti paca</i>	x, g	g	
Dasyproctidae			
<i>Dasyprocta agouti</i> (leporina)	x, g	g, m	
Echimyidae			
<i>Echimys semivillosus</i>	x	g, m	
<i>Proechimys guairae</i>	x, g	g	
Lagomorpha (2)			
Leporidae			
<i>Sylvilagus brasiliensis</i>	x	g	
<i>S. floridanus</i>	x	m	

¹ x = occurs in one or more of the six states of north-central Venezuela, g = collected at or near Guatopo; as documented in Handley (1976).

² Found in g (Guatopo) and/or m (Masaguaral) as documented in Eisenberg et al. (1979) or Sunquist, Sunquist, and Daneke (1989) (vouchers of Chiroptera and Rodentia at the Museum, Texas Tech University, Lubbock).

³ Other vouchered localities either by site, museum reference, or Linares, 1998.

Also see Tables 2 and 3 for additional Chiroptera records.

states comprising north-central Venezuela is probably still low. Taxonomic revisions will inflate the value and new discoveries may await us, but this present value of 180 species is probably representative of our knowledge of Neotropical mammals from comparable areas in Latin America at the close of the 20th Century.

Venezuelan mammalogists have been enormously productive in the last twenty years (Aguilera, 1985; Fernandez-Badillo et al., 1988; Linares, 1998). A new journal, *Marmosana*, was established in 1995, and specific references within the text attest to their activity.

Throughout the text abbreviations for collections will be employed: AMNH, American Museum of Natural History; USNM, National Museum of Natural History; CEBRG, Colección de la Estación Biológica de Rancho Grande; CMNHNS, Colección Museo Historia Naturales, La Salle; CMCN, Colección Museo

Ciencias Naturales, Caracas. The three Venezuelan collections contain more than 22,000 specimens (Aguilera, 1985).

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ANNOTATED LIST OF TERRESTRIAL SPECIES

The annotated list does not include the ubiquitous *Homo sapiens*. The numerous feral populations it has introduced are also excluded: *Felis catus*, *Canis familiaris*, *Equus caballus*, *E. asinus*, *Sus scrofa*, *Capra hircus*, *Bos taurus*, *Bubalus bubalis*, *Mus musculus*, *Rattus rattus*, and *R. norvegicus*. Also excluded are the strictly aquatic manatee (*Trichechus manatus*) and two species of freshwater dolphins (*Inia* and *Sotalia*).

ORDER POLYPROTODONTA

The marsupials of Venezuela have received monographic treatment by Perez-Hernandez, Soriano, and Lew (1994).

FAMILY DIDELPHIDAE

The distribution of the didelphids in Venezuela was reviewed by Perez-Hernandez (1989). O'Connell (1979) described the ecology of the common marsupials in northern Venezuela. The absence of the widespread *Philander* and *Metachirus* from north-central Venezuela is suggestive of the "insular" character of the north coastal ranges and llanos.

Didelphis marsupialis

Common Opossum

The opossum is widespread in the neotropics below 1500 m. It is tolerant of human disturbance. It prefers forested habitats and is most abundant in evergreen forest although it exploits dry, deciduous forest that occurs near permanent water. It can achieve densities of 50-100/km² in optimum habitat. Home ranges overlap and adult females have the smallest range at 16 ha; males can range over 120 ha (Sunquist, Austad, and Sunquist, 1987).

Chironectes minimus

Water Opossum

In north-central Venezuela the species is confined to streams in the north mountain ranges.

P. August trapped several individuals in Guatopo.

Marmosops fuscata

This species is more terrestrial than other mouse opossums. It prefers premontane forests and is most abundant at about 1000 m elevation. O'Connell (1979) studied it in Guatopo.

Marmosa murina

The species occurs in only a few locations in northern Venezuela. Handley (1976) assigned specimens from Yaraguy to the species. It is strongly associated with lowland, tropical evergreen forest. Perez-Hernandez et al. (1994) recorded specimens from Cojedas and Aragua; Eisenberg et al. (1979) recorded specimens in Guatopo.

Marmosa robinsoni

The common lowland mouse opossum in northern Venezuela is tolerant of dry, deciduous forest. It was studied extensively at Hato Masaguaral (O'Connell, 1979, 1983).

Gracilinanus marica

This diminutive mouse opossum is found in the north coast range of Venezuela. Most specimens are taken between 1500 and 2000 m in moist, tropical, montane forest.

Micoureus demararae (*Marmosa cinerea*)

In northern Venezuela it is confined to moist, lowland tropical forest and is widely present in the coast ranges. It has been studied in Guatopo by O'Connell (1979).

Monodelphis brevicaudata

Short-tailed opossum

In north-central Venezuela it is confined to the moist forests of the northern and southern coastal ranges. It has been studied in Guatopo by O'Connell (1979).

Monodelphis orinoci

Reig et al. (1977) separated specimens of *Monodelphis* from the llanos into the species *orinoci* while retaining *brevicaudata* for specimens taken in the coastal ranges. Perez-Hernandez (1989) and Perez-Hernandez, Soriano, and Lew (1993) retained the separation and plot locations in Cojedas, Guarico, and Bolivar. It is apparently smaller in size than *M. brevicaudata* (see also Ventura, Perez-Hernandez, and Lopez Fuster, 1988).

Caluromys philander

Wooly Opossum

This species is widespread in northern Venezuela but is strongly associated with lowland, tropical evergreen forest and is highly arboreal. It was studied by O'Connell (1979) in Guatopo.

Note: Linares (1998) notes records based on single specimens of *Gracilinanus agilis* and *G. emiliae* from north-central Venezuela which were not noted by Perez-Hernandez et al. (1994) nor Perez-Hernandez (1989). Further study is necessary since these records are distant from defined centers of their geographical distribution.

ORDER XENARTHRA (EDENTATA)**FAMILY DASYPODIDAE****GENUS DASYPUS**

Long-nosed Armadillos

The long-nosed armadillos have been reviewed by Wetzel and Mondolfi (1979 and Wetzel (1985). Redford (1985b) summarized feeding ecology.

Ferguson-Laguna (1984) studied dasypodid ecology in the savannas of northern Venezuela.

Dasypus novemcinctus
Nine-banded Armadillo

A highly adaptable species, it is found in most lowland habitats of north-central Venezuela. No specific studies have been made in northern Venezuela but it is well studied elsewhere (see McBee and Baker, 1982). It is widely hunted for its meat and could be managed as a small game species. Density estimates range from 5 to 30.4/km². Individual home ranges have been measured at 3.45-13.8 ha in the southern United States.

Dasypus sabanicola
Savanna Armadillo

This species exhibits a fragmented distribution in the llanos north of the Orinoco, and is primarily associated with los llanos bajos. It was first described by Mondolfi in 1968; the ecology was studied by Ferguson-Laguna (1984).

Cabassous unicinctus
Naked-tail Armadillo

The genus *Cabassous* was reviewed by Wetzel (1980). The fossorial habits of naked-tail armadillos means they are seldom seen or collected. Records of occurrence are scattered in the literature. A specimen was collected in Guatopo in 1967 and deposited with E. Mondolfi.

Priodontes maximus

This species has been hunted to extinction over much of its range in northern Venezuela. It is still to be found in Apure but is probably extinct in Guarico (Mondolfi pers. comm.).

FAMILY MYRMECOPHAGIDAE

Myrmecophaga tridactyla
Giant Anteater

Although the giant anteater is tolerant of a range of lowland tropical habitats, it appears to be most abundant in the open woodlands of the llanos. It was studied by Montgomery and Lubin (1977) at Masaguaral. Home ranges were large,

exceeding 25 km². Redford (1985a) summarized its feeding ecology. Because it is vulnerable to hunting, it is under threat.

Tamandua tetradactyla

Tamandua Anteater

This species is found in a variety of lowland habitats in northern Venezuela. It seldom ranges above 500 m. It is abundant in dry, deciduous forest but also is found in moist evergreen forests. The species has been studied by Montgomery and Lubin (1977) at Hato Masaguaral. Home ranges of 375 ha were recorded.

FAMILY BRADYPODIDAE

Bradypus variegatus

Three-toed Sloth

This species is confined to forested areas, especially moist, evergreen forest. It can extend to dry forest but always near permanent water. The sloth is common in Guatopo but is absent from the llanos, except where there is extensive evergreen forest near permanent water. The species has been well studied in Panama (see Montgomery and Sunquist [1974, 1975, 1978] and Sunquist and Montgomery [1973]). In appropriate habitats the three-toed sloth may reach high densities (3-4/ha). The home range is quite small, usually less than 1.0 ha.

ORDER INSECTIVORA

FAMILY SORICIDAE

Cryptotis meridensis

Short-tailed Shrew

Linares (1998) notes two vouchered specimens from the north coastal range in the state of Aragua.

ORDER PRIMATES

The isolated nature of the north-central mountain ranges and associated llanos is dramatically illustrated by the distribution of primates. The area covered in this paper has just three primate species (see also Eisenberg, 1979a; Bodini and Perez-Hernandez, 1987).

FAMILY CEBIDAE*Cebus olivaceus***Wedge-capped Capachin Monkey**

Handley (1976) and others have employed the name *C. nigrivittatus*, but see Groves (1993). This species is tolerant of a range of lowland forest types but is never found far from permanent water. It penetrates the llanos through forests associated with major rivers. Within the llanos, it primarily uses gallery and semi-deciduous forests, but will make forays into more open forest types and even savannas at times. This species was intensively studied at Hato Masaguaral and to a lesser extent at Hato Piñero. Foraging, diet, and social structure were studied by Robinson (1981, 1984a, 1986, 1987); vocalization by Robinson (1984b and Norris (1992); grouping tendencies by Ruiter (1986) and O'Brien and Robinson (1993); development by Fragaszy (1990); all at Masaguaral. Miller (1996) has initiated a long-term study at Hato Piñero.

*Alouatta seniculus***Red Howler Monkey**

One of the most adaptable species of New World primates, it enjoys a wide distribution. It has colonized the llanos occupying open woodlands and tree islands (matas) within the grasslands. This is one of the best studied species. Braza (1980) conducted a major study at Hato El Frio, Apure. The species was worked on for two decades at Hato Masaguaral (see Neville, 1972, Rudran, 1979, Mack, 1979). Vocalizations were studied by Sekulic (1981, 1982b, 1982c) and Sekulic and Chivers (1986); locomotion and anatomy by Schön-Ybarra (1984); demography by Rumiz (1992); population genetics by Pope (1989, 1990, 1992, 1998); and finally a classic series of papers on demography and infanticide by Crockett (1984, 1996), Crockett and Eisenberg (1987), Crockett and Pope (1984, 1988), Crockett and Rudran (1987a, b) and Crockett and Sekulic (1984).

*Ateles belzebuth***Spider Monkey**

The main distribution in Venezuela is south of the Orinoco and the Maracaibo Basin. Mondolfi and Eisenberg (1979) discussed distributions in northern Venezuela. Isolated populations still persist in Guatopo and Cupira. The ecology has not been studied in the north, but Castellanos and Chanin (1996) have studied this species in Bolivar. Mature forest with continuous canopy seems to be the preferred habitat. It can occupy semi-deciduous tropical forest but evergreen forest seems to be optimal.

ORDER CARNIVORA

Bisbal (1989) has reviewed the distribution and the status of the Carnivora of Venezuela.

FAMILY CANIDAE

Urocyon cinereoargenteus

Gray Fox

Apparently this species is confined to north-central Venezuela. There it prefers tropical dry forest at elevations of 100-700 m (Bisbal, 1982). Vouchered records from Cojedes come from the southern limits of the coast range. Mondolfi and Bisbal (1985) analyzed the diet.

Cerdocyon thous

Crab-eating Fox

The most widespread canid in Venezuela, it is tolerant of a range of habitats but is most abundant in dry deciduous forest, particularly along savanna/forest ecotones. Brady (1979), Montgomery and Lubin (1978a), and Sunquist et al. (1989) studied its behavior and ecology at Hato Masaguaral. Adult foxes live in monogamous pairs and defend a home range of 45-100 ha. A crude density of 2.5/km² was estimated for Masaguaral.

Speothos venaticus

Bush Dog

This species is still noted south of the Orinoco. Bisbal (1989) plotted specimens from Carabobo, and Linares (1968) discussed the former presence of specimens from northern Venezuela. Strahl et al. (1992) summarized previous records, added accounts from south of the Orinoco, and discussed hunter's observations in northern Venezuela in the vicinity of Parque Nacionales San Esteban and Guatopo. This species is vulnerable to infection by canine distemper and may be wiped out by contact with domestic dogs. Its status is unclear in North-Central Venezuela.

FAMILY PROCYONIDAE

Procyon cancrivorus

Crab-eating Raccoon

This species is common throughout Venezuela. It is associated with both humid forest and seasonally wet forest. It has usually been taken at elevations below 500 m and generally near water.

Potos flavus

Kinkajou

In north-central Venezuela this species is found in tropical humid forest and premontane humid forest. It is absent over much of the llanos.

FAMILY MUSTELIDAE*Mustela frenata*

Long-tailed Weasel

In northern Venezuela it is confined to the north coastal ranges and is absent from the llanos. It is abundant in the Andean states of Tachira and Merida.

Eira barbara

Tayra

In northern Venezuela it is strongly associated with tropical humid forest but extends into the llanos in gallery forests. Sunquist et al. (1989) studied the species at Masaguaral and confirmed its dependency on forest cover. One female had a home range of 9 km² during the dry season.

Galictis vittata

Grison

This species is widely distributed in north-central Venezuela. It prefers tropical dry forest at modest elevations. Sunquist et al. (1989) studied this species at Masaguaral and found a female used a minimum area of 4.15 km². The species is mainly carnivorous (Bisbal, 1986).

Conepatus semistriatus

Hog-nosed Skunk

In Venezuela the species does not occur south of the Orinoco River. It is strongly tied to dry deciduous forest but may also be found in moist forest. It was studied by Sunquist et al. (1989) at Masaguaral, where one female had a home range of 53 ha in the dry season. Density estimates for Masaguaral were 6-12/km².

Lontra longicaudis

Otter

The species is found in rivers of the north coast range, but records are sparse. The status is unknown for north-central Venezuela (Bisbal, 1989).

Pteronura brasiliensis

Giant Otter

Although the species occurs in the Orinoco River and Territorio Amazonas, it has been exterminated over much of its range. There is one vouchered specimen from southern Guarico (Bisbal, 1989).

FAMILY FELIDAE

The biology of the smaller cats is reviewed by Mondolfi (1986).

Leopardus pardalis

Ocelot

The ocelot is found in all the life zones of Venezuela at lower elevations. It prefers forested habitats, but makes use of forest edge. Extending into the llanos via gallery forests, it is common in all semi-deciduous forest types there. It was studied by Sunquist and Ludlow at Masaguaral (Ludlow, 1986; Ludlow and Sunquist, 1987; Sunquist et al., 1989) and at Hato Piñero by Farrell (1998). Adult males defend a territory that includes the territories of from one to three adult females. Male home ranges of 6.2-9.4 km² during the wet and dry seasons contrast with female ranges of 1.4-2.6 km². Densities of 0.25 individuals/km² can be achieved in gallery forest habitat.

Leopardus wiedii

Margay Cat

In north-central Venezuela this cat has been taken in the north coastal ranges. It is strongly tied to humid, closed canopy forests, no doubt reflecting its strong arboreal tendencies (Bisbal, 1989).

Leopardus tigrinus

Little Spotted Cat

Very few specimen records exist for this cat in Venezuela. It is known from the premontane forests of Aragua, Miranda, and the Distrito Federal. (See also Bisbal, 1989.)

Herpailurus yagouaroundi

Jaguarundi

A frequently seen cat due to its diurnal habits, it is strongly associated with tropical dry forest and is commonly encountered at the interface of grasslands and

forests. Although most abundant in the lowlands, it can occur up to 900 m elevation. The jaguarundi is rarely found south of the Orinoco (Bisbal, 1989).

Puma concolor

Puma

Records from north-central Venezuela are scattered. This cat has suffered greatly from persecution by humans, but is still found in virtually all national parks and better protected larger cattle ranches in North-Central Venezuela. It has been taken in Guatopo, and is an occasional visitor at Masaguaral. Pumas used nearly all habitat types in Hato Piñero, Cojedes, slightly overlapping the habitats preferred by jaguars. Capybara (*Hydrochaeris hydrochaeris*), white-tailed deer (*Odocoileus virginianus*), and collared peccary (*Tayassu tajacu*) were among the top prey items (Farrell, 1999).

Panthera onca

Jaguar

The status of the jaguar in Venezuela has been discussed by Mondolfi and Hoogesteijn (1986) ; Hoogesteijn and Mondolfi (1993); and Hoogesteijn, Hoogesteijn, and Mondolfi (1993). The jaguar was widespread in Venezuela, but persecution has confined it to the larger national parks or large tracts of ranch lands. We found jaguar in Guatopo and recorded occasional visits at Masaguaral. Jaguars occur at low densities in most of the national parks in the northern states. More suitable habitat and greater numbers occur in los llanos altos, where large connected patches of semi-deciduous forest and gallery forest create suitable areas for residency that typically include several cattle ranches. This was species was the subject of an intensive study at Hato Piñero, where abundant habitat remains and persecution is rare (Farrell, 1999). Piñero is connected to other ranches containing intact habitat and adequate natural prey. It is this network of connected forests that maintain jaguars in los llanos altos. Both species of peccaries, capybaras, and spectacled caiman (*Caiman crocodilus*) are among the most important prey items. Though clearly fond of forest cover, when secure from hunting, jaguars will use savanna edges, small savannas, and dirt roads.

ORDER PERISSODACTYLA

Tapirus terrestris

Once widely distributed in northern Venezuela, this species has become locally extinct in many areas through hunting and land development. In north-central Venezuela it still occurs in the larger national parks and some of the larger cattle ranches. Tapirs occurred at a crude density of 0.6/km² in Guatopo. Though

associated with tropical evergreen forests in much of its range, in the llanos it uses gallery forest and semi-deciduous forest. During the dry season, it may reside in quite dry habitats, but will travel regularly to water holes. Food habits and preferred habitat use patterns were studied by Salas (1996) and Salas and Fuller (1996) in southern Venezuela.

ORDER ARTIODACTYLA

FAMILY TAYASSUIDAE

Tayassu pecari

White-lipped Peccary

Although widely distributed south of the Orinoco River and present in western Apure, this species is rarer north of the Orinoco. Groups occur along the more heavily forested parts of the coastal range. Hernandez et al. (1995) described behaviors and Barreto et al. (1997) described diet in Hato Piñero (Barreto and Hernandez, 1988). Hato Piñero is part of the range of two large groups (60 and 115 individuals) and there are reliable reports from other parts of Cojedes and extreme western Guarico. More tied to deep forest than *Tayassu tajacu*, *T. pecari* persists in los llanos altos where long strips of relatively moist forest along active waterways or old river beds, combine with large patches of semi-deciduous forest. Despite a clear preference for forest and a strong tie to water in the dry season, these groups will use savanna edges and small savannas, particularly when the introduced mango fruits (*Mangifera indica*) are in season. Predictable visitation sites at water during the dry season, combined with a fearlessness maladaptive for the age of firearms, makes this species very vulnerable to overhunting.

Tayassu tajacu

Collared Peccary

Grubb (1993) recommended the generic name *Pecari* for this species. It was found over much of lowland Venezuela, has been locally extirpated in many areas, yet is more resilient than its larger cousin *T. pecari*, due to: 1) smaller, more widely dispersed groups that occupy a larger variety of habitats; and 2) its greater caution in response to humans, and fragmentation of groups when in flight. Robinson and Eisenberg (1985) discussed seasonal variation in group size, and Castellanos (1983) analyzed the ecology of the species with the use of radiotelemetry. In Guatopo populations had a crude density of 1.9/km². In the dry, deciduous forests of the llanos at the Hato Masaguaral densities of 8.5/km² were estimated. Food habits were studied at Hato Piñero by Barreto et al. (1997). A greater proportion of *Pithecellobium saman* (a moisture loving tree) seeds were found in the *T. pecari* diet. Forest edge seeds were slightly more common in *T. tajacu* stomachs, forest interior seeds more common in *T. pecari* stomachs (Barreto

et al., 1997). Still on a preliminary basis, with a small sample, this resource partitioning on a dietary basis was equivocal. Responses to human hunting pressure now affect these ecological relationships and *T. pecari* may in part be where it is now because it can persist there. Although *T. pecari* groups are larger, and on a year-round basis make use of a larger net area, *T. tajacu* groups are more generalists, taking advantage of more habitat types, and specifically, more dry ecotones than their larger cousins. Although groups as large as 30-40 may occur, observers at Hato Piñero more frequently encountered groups of 11-15 animals. *T. tajacu* is a preferred prey of both pumas and jaguars.

FAMILY CERVIDAE

Mazama americana

Red Brocket

Present over much of lowland Venezuela, absent over most of the llanos, penetrating only the western llanos altos in wide gallery forests. It seems to prefer moist evergreen forest and is seldom found far from permanent water. Bisbal (1991) reviewed the distribution. It is a browser, but feeds seasonally on fruit (Bisbal, 1994). The species is abundant in Guatopo and Avila.

Mazama gouazoubira

Brown Brocket

This species has a disjunct distribution in northern Venezuela (Bisbal, 1991). It is more tolerant of drier sites and deciduous forests than is *M. americana*. It has been collected in deciduous forests in the northern coastal range in Estados Aragua and Carabobo, and occupies thorn forests in Falcon and Yaracuy.

Odocoileus virginianus

White-tailed Deer

This species is found over much of lowland Venezuela and is tolerant of a wide range of habitat types. Highest densities occur in the forested savannas found over much of the llanos. It will use the fringes of tropical evergreen forest where it can co-occur with *M. americana*. Densities of 2/km² are an average value for much of the llanos. Brokx (1972a, b, 1984) and Brokx and Anderssen (1970) pioneered the study of *O. virginianus* in northern Venezuela. Stüwe (1985) compared the biology of Venezuelan and Virginian (U.S.) populations. *O. virginianus* is both important to pumas as a prey item, and over-hunted virtually everywhere it is not rigorously protected.

ORDER RODENTIA
SUBORDER SCIUROGNATHI
FAMILY SCIURIDAE
Squirrels

Sciurus granatensis
Neotropical Red Squirrel

This species is abundant in north-central Venezuela but is confined to forested tracts. It is able to exploit dry, deciduous forest and thereby extends into the llanos. O'Connell (1981, 1982) has studied the species at Masaguaral and Guatopo; Heaney and Thorington (1978) studied it in Panama. Nitikiman (1985) reviewed the species.

FAMILY HETEROMYIDAE

Heteromys anomalus
Forest Spiny Pocket Mouse

This mouse is widely distributed in northern Venezuela but is most abundant in moist evergreen forests, although it extends into dry zone forests near permanent water. O'Connell (1981) studied the species at Masaguaral and Guatopo and Rood (1963) and Valdez et al. (1984) at Rancho Grande.

FAMILY MURIDAE
Rats and Mice

SUBFAMILY SIGMODONTINAE
New World Rats and Mice

Note: The names *Oryzomys capito*, *O. bicolor*, and *O. concolor* were employed by Handley (1976), Eisenberg, O'Connell, and August (1979), O'Connell (1981, 1982), and August (1981, 1983, 1984). The taxonomic revisions by Musser and Williams (1985) and Musser, Carleton, Brothers, and Gardner (1998) supplemented by Aguilera et al. (1995) and Perez-Zapata et al. (1986) have led to the usage of new binomials throughout the following discussions of the species.

TRIBE ORYZOMYINI
GENUS OECOMYS
Arboreal Rice Rats

This group was raised from the level of subgenus to full genus (see Musser and Carleton, 1993).

Oecomys bicolor

Handley (1976) employed *bicolor* as the species name for the second smaller species of *Oecomys* found in northern Venezuela, the name *O. speciosus* is now recognized for the lowland dry deciduous forest forms (see below).

Oecomys concolor

Handley (1976) used this name for the larger species of *Oecomys* found in northern Venezuela. The elevation of *O. trinitatus* to a full species suggests this name be applied to the northern Venezuelan forms (see below), while *O. concolor* be retained for forms south of the Orinoco (Linares, 1998).

Oecomys flavicans

Linares (1998) lists this species as a shorter-tailed form that, in a macro-habitat sense, may co-occur with *O. trinitatis*. Its relationship with *trinitatis* and *O. concolor* remains to be determined.

Oecomys speciosus

This arboreal rice rat is found in the palm and open woodlands of northern Venezuela (Musser and Carleton, 1993). O'Connell (1981) studied it at Masaguaral.

Oecomys trinitatus

This arboreal rice rat is found in the evergreen forest habitats of northern Venezuela. O'Connell (1981, 1989) studied it at Guatopo.

GENUS ORYZOMYS*Oryzomys albigularis*

Nominal forms of *O. albigularis* were studied by Aguilera, Perez-Zapata, and Matino (1995) in northern Venezuela. A diploid number ($2n$) of 66 was recorded for all samples, but the number of autosomal arms (FN) varied: 90,92,104. They postulated the variations represent an allospecies. *O. caracolus* Thomas, 1914, ($2n=66$, FN=90) is assigned to populations from the north coastal range of Venezuela.

Oryzomys capito

Handley (1976) employed *capito* as the species name for the terrestrial rice rats inhabiting the lower altitudes in northern Venezuela. At the time *O. capito* included many subspecies following Hershkovitz (1944). Current thinking has resulted in the break-up of *capito* into some full species. Redefinitions of species initiated by Musser and Williams (1984) established that *O. talamancae* be recognized in northern Venezuela and was reinforced by Perez-Zapata et al. (1986). *Oryzomys yunganensis* may be the more appropriate name for the non-*talamancae* forms in northern Venezuela and south of the Orinoco, but more research is necessary.

Musser et al. (1998) have revised *O. capito* and suggest *O. megacephalus* be employed as the senior name for the remaining forms previously included in *O. capito*.

Oryzomys talamancae

Perez-Zapata et al. (1986) investigated the *O. capito*-like complex in northern Venezuela. The low chromosome numbered form ($2n=34$) was provisionally assigned to *O. talamancae*. O'Connell (1981, 1989) studied it at Guatopo.

GENUS MICRORYZOMYS*Microryzomys minutus*

Pygmy Rice Rat

This species occurs in high montane areas of northern Venezuela at elevations of 1150-3810 m; it is essentially terrestrial in the cloud forests. Handley (1976) has taken specimens at Parque de Avila. Aagaard (1982) studied the species at Merida.

GENUS OLIGORYZOMYS*Oligoryzomys fulvescens*

This species is widespread in north-central Venezuela, ranging to 2000 m elevation but most abundant at < 1500 m. It is tolerant of disturbed habitats and is found in agricultural areas. Moist sites are preferred but it also is found in evergreen and dry, deciduous forests.

GENUS *NEACOMYS**Neacomys tenuipes*

Spiny Mouse

The spiny mouse is abundant in the mountains of north-central Venezuela from 404 m to 1655 m elevation. It is associated strongly with moist forest. O'Connell (1981, 1989) studied the species in Guatopo.

TRIBE THOMASOMYINI**GENUS *RHIPIDOMYS***

Climbing Rats

Handley (1976) recognized seven species from Venezuela. Pending a revision of the genus his designations are followed.

Rhipidomys couesi

Linares (1998) records this species from the north coastal range, although it is associated strongly with the Andes.

Rhipidomys venezulae

The common arboreal rat is found in the lowlands. The species is reasonably abundant below 1500 m and occupies evergreen and deciduous tropical forests. O'Connell (1981, 1989) studied it at Masaguaral and Guatopo.

Rhipidomys venustus

This higher altitude species is taken from 1160 m to 3160 m (Handley, 1976). In north-central Venezuela it occurred in cloud forest and tropical evergreen forests in the extreme northern ranges of Distrito Federal and Miranda.

TRIBE PHYLLOTINI*Calomys hummelincki*

Although noted in the Falcon arid zone and scattered locations in Venezuela (Eisenberg, 1989), Linares (1998) records two specimens from the state of Guarico.

TRIBE ICTHYOMYINI*Ichthyomys pittieri*

Fishing Rat

The fishing rat was described by Handley and Mondolfi (1963) from Aragua and subsequently studied by Voss, Siva, and Valdes (1982). This is a high altitude form found near streams.

TRIBE AKODONTINI*Akodon urichi*

The only species of *Akodon* in north-central Venezuela, it is found in moist sites usually in tropical evergreen forests above 500 m (Handley, 1976). It also is found in north and south coastal ranges. O'Connell (1981, 1989) studied it at Guatopo.

TRIBE ZYOGDONTOMYINI*Zygodontomys brevicauda*

Cane Rat

This common lowland, terrestrial rat is found in the grasslands of Venezuela, usually near streams or moist areas. Density can reach very high numbers during the breeding season. Numbers can fluctuate from 260 to 7400/km². O'Connell (1981, 1989) and Vivas (1986) studied it at Masaguaral. Aguilera (1985) studied growth and reproduction in captivity. *Zygodontomys microtinus* is a frequently used synonym.

TRIBE SIGMODONTINI*Sigmodon hispidus*

Cotton Rat

The cotton rat occurs in northwestern Venezuela and is associated with moist grassy sites in the lowlands. It is tolerant of human activities. It invades agricultural fields and pastures. *S. alstoni* replaces it in the llanos.

Sigmodon (Sigmomys) alstoni

This rat is found in grassland sites, subject to seasonal inundation. Tolerant of human activities, it occupies pasture and agricultural fields. O'Connell (1981, 1989) and Vivas (1986) studied it at Masaguaral and vicinity.

Holochilus sciureus

Marsh Rat

The name *sciureus* is usually applied to the central Venezuelan forms (Musser and Carleton, 1993), but Handley (1976) employed *H. brasiliensis*. Aguilera et al. (1993) separate populations of *Holochilus* from northern Venezuela with a $2n$ chromosome number of 46 as *H. venezuelae*. They contrast this value with samples they assigned to *H. brasiliensis* from the Amazon area. The problem needs to be resolved. Marsh rats, as the name implies, are associated with lowland wet sites. They can become a serious agricultural pest.

SUBORDER HISTRICOGNATHI

FAMILY ERETHIZONTIDAE

Porcupines

GENUS *COENDOU*

Prehensile-tailed Porcupines

The hairy dwarf porcupines were separated in their own genus *Sphiggurus* by Husson (1978; Woods, 1993). Other authors include them in *Coendou* (Emmons and Feer, 1997).

Coendou prehensilis

The common lowland, prehensile-tailed porcupine is usually found in tropical evergreen forest below 1000 m. It can extend to lowland dry forest in the vicinity of permanent water. Montgomery and Lubin (1978) studied it at Masaguaral. Roberts, Brand, and Maliniak (1985) recorded reproduction and growth of this species in captivity.

Sphiggurus vestitus pruinosus

Woods (1993) included *pruinosus* as a subspecies of *vestitus*. Handley (1976) treated *priunosus* as a full species.

Concepción and Molinari (1991) examined a small, long-haired porcupine from 3.5 km southwest of Zea in the state of Merida. The chromosome numbers

were $2n=42$ and $FN=76$. These numbers are identical with *Erethizon* but different from *Coendou rothschildi*. They advocate the separation of the genus *Sphiggurus* from *Coendou*, a view opposed by Handley and Pine (1992).

I (JFE) examined a specimen at CEBRG with the following data on the label: 1 male caught at Rancho Grande, Aragua; Venezuela. Measurements 490-210-51-23 wt 900 g. The tail is very short (42% of HB); the dorsal hair is long with the underlying spines evident on the lower back; the spines are white-tipped.

This taxon is rare in collections and appears to be confined to montane evergreen forests.

FAMILY CAVIIDAE

Cavies

Cavia aperea

Guinea Pig

Handley (1976) listed the forms from Venezuela as *C. porcellus*. This name is usually applied to feral domestic or domestic forms (Woods, 1993). Ojasti (1964) reviewed the problem of the origins of guinea pigs in Venezuela. Whether they are escaped domestics or represent relictual populations remains to be determined. The distribution is fragmented. Handley (1976) took specimens from Carabobo.

FAMILY HYDROCHAERIDAE

Capybara

Hydrochaeris hydrochaeris

This species is potentially abundant throughout the lowland tropics but is always associated with wet sites. Its highest abundance is reached in the wet llanos (llanos bajos). Ojasti (1973) demonstrated that it can be harvested as a renewable resource. Its behavior has been studied by Ojasti (1986) and Azacarate (1980). The current distribution of capybara is not only dictated by suitable mixes of water, forage, and cover, but also by the exceptionally intense hunting pressure it receives annually for semana santa. Though large groups occur on a number of well-defended and managed private ranches, the situation "outside" is more grim. An important prey item for both jaguar and puma.

FAMILY DASYPROCTIDAE**Agouti***Dasyprocta aguti* (*D. leporina*)

The specific name for agoutis in north-central Venezuela remains in dispute; *D. leporina* is frequently used. Ojasti (1964) made an attempt at a preliminary revision. Woods (1993) offers the latest thinking on the problem. Emmons and Feer (1997) have attempted to standardize the nomenclature.

This species is associated with moist areas in lowland forests and can extend into dry, deciduous forests. It is an important small game species but can become locally extinct through hunting. Smythe (1978) has offered the most thorough study of ecology and behavior of the closely related *D. punctata* in Panama.

FAMILY AGOUTIDAE*Agouti paca***Paca**

This species can be common in tropical evergreen forests near permanent water. It extends into the llanos via gallery forests. Hunted for its meat, which is the most prized in the neotropics, it has been driven to local extinction in many areas. Smythe (1995) and associates have pioneered in the study of the domestication process for this species as a means of supplying meat to the specialty food markets.

FAMILY ECHIMYIDAE*Echimys semivillosus***Arboreal Spiny Rat**

Makalata didelphoides (*Echimys armatus*) has been described from Trinidad and the adjacent coast of Venezuela. *Echimys semivillosus* is known from the gallery forests of llanos in north-central Venezuela, but specimens of *Echimys* from the coastal ranges need to be checked for their species identity. *Echimys* are present in Guatopo but were not collected. *Echimys semivillosus* were studied by August (1981b) at Masaguaral; they were taken in gallery forest. Sunquist et al. (1989) found *Echimys* was preyed upon by *Eira barbara*. The whole group is being revised by Emmons (pers. comm.).

Proechimys guairae

Handley (1976) listed the northern Venezuelan specimens as *P. semispinosus*, but see Gardner (1989). Reig et al. (1976, 1980) examined the karyotypic diversity of spiny rats and proposed a revision of the group. Aguilera and Conti (1994) discussed the chromosomal speciation exhibited by *Proechimys* in northern Venezuela. Within the area discussed in this report the name *P. guairae*, a super species, is applied. The $2n$ number varies: 44, 46, 48, 50, 52 with an FN ranging from 72 to 74. This species is abundant in lowland to mid-elevation evergreen forests and gallery forests. O'Connell (1981, 1989) studied it at Guatopo. Linares (1998) lists this form as *P. trinitatis*. Its common occurrence in ocelot scats in Hato Piñero attest to its residency in the large tracts of semi-deciduous forest there.

ORDER LAGOMORPHA**FAMILY LEPORIDAE**

Hares and Rabbits

GENUS SYLVILAGUS

Cottontail Rabbits and Allies

Sylvilagus brasiliensis

Brazilian Cottontail

The Brazilian cottontail has a fragmented distribution in north-central Venezuela. It prefers moist habitats, usually in clearings or on the edge of evergreen tropical forests. It can range to elevations of 1500 m. The species is present in Guatopo.

Sylvilagus floridanus

Cottontail

This species is common in lowland habitats, often quite dry such as thorn forests, savannas, and range lands. It replaces *S. brasiliensis* in the llanos. It is abundant at Hato Masaguaral and Hato Piñero. Ojeda-Castillo and Keith (1982) present data on the breeding biology of this species from Guarico. Though widespread in Hato Piñero, frequencies were highest in well-drained dry habitats.

ORDER CHIROPTERA

Numerous taxonomic and distribution studies of bats have been carried out in Venezuela. Handley (1976) offered excellent data on habitat preferences and altitudinal distributions. Eisenberg (1989, pp. 424-425) analyzed some trends in

Table 2. Species of Chiroptera with records in north-central Venezuela according to Linares (1987, 1998).

Emballonuridae (8)

Rhynchonycteris naso
Saccopteryx bilineata
S. leptura
S. canescens
Peropteryx macrotis
P. kappleri
P. trinitatus
Diclidurus albus

Noctilionidae (2)

Noctilio albiventris
N. leporinus

Mormoopidae (5)

Mormoops megalophylla
Pteronotus davyi
P. gymnotus
P. parnellii
P. personatus

Phyllostomidae (56)**Phyllostominae (21)**

Micronycteris brachyotis
M. hirsuta
M. megalotis
M. microtis
M. minuta
M. nicefori
M. schmidtorum
M. sylvestris
Tonatia bidens (T. saurophila)
T. brasiliense (T. venezuelae)
T. silvicola
Lonchorhina aurita
Macrophyllum macrophyllum
Mimon crenulatum
Trachops cirrhosus
Phyllostomus discolor
P. elongatus
P. hastatus
Phylloderma stenops
Chrotopterus auritus
Vampyrus spectrum

Glossophaginae (8)

Glossophaga soricina
G. longirostris
Leptoncycteris curasoae
Anoura caudifer
A. culturata

A. geoffroyi

A. latidens

Choeroniscus godmani

Carollinae (2)

Carollia brevicauda
C. perspicillata

Sturnirinae (3)

Sturnira lucovici
S. lilium
S. erythromos

Stenodermatinae (19)

Uroderma bilobatum
U. magnirostrum
Platyrrhinus (Vampyrops) dorsalis
P. helleri
P. umbratus
P. vittatus
Vampyrodes caraccioli
Vampyressa pusilla
Chiroderma salvini
C. trinitatum
C. villosum
Artibeus harti
A. cinereus
A. lituratus
A. jamaicensis
Ametrida centurio
Sphaeroncycteris toxophyllum
Centurio senex

Desmodontinae (3)

Desmolus rotundus
Diphylla ecaudata
Diaemus youngi

Natalidae (1)

Natalus stramineus

Thyropteridae (1)

Thyroptera discifera

Vespertilionidae (15)

Histiotus humboldti
Lasiurus cinereus
L. blossevilli (borealis)
L. ega
Rhogoessa tumida

Table 2 Continued.

<i>R. minutilla</i>	<i>Eumops auripendulus</i>
<i>Myotis albescens</i>	<i>E. bonariensis</i>
<i>M. nigricans</i>	<i>E. dabbenei</i>
<i>M. oxyotus</i>	<i>E. glaucinus</i>
<i>M. keaysi</i>	<i>E. hansae</i>
<i>Eptesicus brasiliensis</i>	<i>E. perotis</i>
<i>E. diminutus</i>	<i>Nyctinomops aurispinosa</i>
<i>E. furinalis</i>	<i>N. laticaudata</i>
<i>E. fuscus</i>	<i>Molossus ater</i>
<i>E. montosus (E. andinus)</i>	<i>M. bondae</i>
	<i>M. coibensis</i>
Molossidae (20)	<i>M. molossus</i>
<i>Molossops greenhalli</i>	<i>M. pretiosus</i>
<i>M. parvus</i>	<i>M. sinaloae</i>
<i>M. planirostris</i>	<i>Promops centralis</i>
<i>M. temmincki</i>	<i>Tadarida brasiliensis</i>

A total of 108 species.

altitudinal distributions and concluded that the highest species richness for bats lies below 700 m elevation. Some species are adapted for higher elevations, including *Lasiurus cinereus*, *Histiotus montanus*, and *Eptesicus fuscus* among others. Some species of *Sturnira* are also well adapted to moderate elevations. Ochoa-G. (1980) provided a useful analysis of bat altitudinal distributions by means of a transect over the north coastal range passing from the Valencia depression through Rancho Grande to the Caribbean coast.

Linares (1987, 1998) provided a fine summary of the distribution and ecology of Venezuelan bats. Ibañez (1981) offers a comprehensive monograph on the ecology and biology of bat communities in the llanos of Apure.

During our work in Guatopo and at Masaguaral, August (1979, 1981, 1985) pursued research on *Artibeus jamaicensis*, and August and Baker (1982) made important collections resulting in a paper on reproductive ecology for some key species.

Table 2 offers a possible list of bat species that could occur in north-central Venezuela deriving from the range maps of Linares (1987, 1998). This list can be compared with our vouchered records in Table 1. Table 3 lists the subset of bats with restricted ranges within north-central Venezuela.

DISCUSSION

Taxonomic studies of mammals have helped to clarify the species composition within the ecological communities to be found in northern Venezuela. The bibliography concluding the volume prepared by Aguilera (1985) summarizes those efforts, while Linares (1998) provides a recent synthesis. Work on the mammals during the last forty years involved the efforts of investigators not only within Venezuela but also from the United States, Canada, Spain, Colombia, and many other nationalities. Ecological studies take a great deal of time and, in a manner of speaking, are still in their infancy. Studies of small mammal ecology in the Cordillera Oriental in the Andes have important implications for understanding the fauna of the north coastal ranges for Venezuela. Only a handful of studies have been performed, but are well worth noting (Aagaard, 1982; Pafaur and Pasqual, 1985; Lopez-Arevalo, Montenegro-Diaz, and Cadena, 1993). The ecological studies within the six state areas of this paper are amply cited within the text, but O'Connell (1979, 1983, 1989), Ibañez (1981), August (1983, 1984), and Vivas (1986) deserve special mention as community studies. The efforts of Broxk (1972b, 1984) with deer and Ojasti (1973) with capybara focus on species of great economic importance.

Considering the six state areas (plus the Distrito Federal) of north-central Venezuela, several patterns of mammalian distributions are noteworthy. Endemic species of the llanos (*Monodelphis orinoci* and *Dasyus sabanicola*) are rare, perhaps attesting to its recent configuration. Western Apure contains many Amazonian elements and the Falcon Peninsula with a long history of aridity contains some endemics (*Marmosa xerophila*). The Maracaibo Basin shows affinities with northern Colombia and Central America (Eisenberg and Redford, 1979). At the present time, the north coastal ranges of Venezuela contain species that are also broadly distributed in the Andes Mountains of Colombia to the west and beyond. These include, among the marsupials, *Gracilinanus marica* and *Marmosops fuscatus*. Among the Chiroptera, *Eptesicus fuscus*, *Lasiurus cinereus*, and *Histiotus humboldti* are typical of the higher elevations. *Microryzomys minutus*, *Ichthyomys pittieri*, *Oryzomys talamancae*, *O. albigularis*, and *Sphiggurus vestitus* represent the montane rodents. As an "island" of tropical evergreen forest the coastal ranges support *Bradypus infuscatus*, *Ateles belzebuth*, *Felis (Leopardus) tigrina*, and *Potos flavus*.

Certain wide ranging genera of mammals found in the northern Neotropics are conspicuously absent from north-central Venezuela. These include: Primates--*Aotus*, *Saimiri*, and *Saguinus*; Carnivora--*Nasua* and *Bassaricyon*; Marsupials--*Philander* and *Metachirus*. The vast expanses of the llanos and the Andes to the west must serve as a filter barrier (Eisenberg and Redford, 1979).

Haffer (1974) first proposed that the north coastal ranges of Venezuela might serve as a refugial area for birds; Morton (1979) reinforced his ideas. In short,

Table 3. Species of Chiroptera having restricted ranges in north-central Venezuela (Linares, 1998).

I. Confined to the arid coastal strip	<i>Platyrrhinus helleri</i>
Glossophaginae	<i>P. dorsalis</i> (N)
<i>Leptonycteris curasoae</i>	<i>P. vittata</i> (N)
<i>Choeronycteris godmani</i>	<i>Vampyrodes caraccioli</i>
	<i>Vampyressa pusilla</i>
	<i>Chiroderma tinitatum</i> (N)
II. Confined to the coastal mountains or foothills	<i>Diphylla ecaudata</i>
Emballonuridae	Thyropteridae
<i>Pteropteryx kappleri</i>	<i>Thyroptera discifera</i> (N)
<i>Diclidurus albus</i> (N)	Vespertilionidae
<i>Mormoops megalophylla</i>	<i>Histiotis humboldti</i> (N)
<i>Pteronotus gymnotus</i> (S)	<i>Lasiurus cinereus</i> (N)
	<i>Eptesicus fuscus</i> (N)
	<i>E. montosus</i>
Phyllostomidae	Molossidae
<i>Micronycteris hirsuta</i> (N)	<i>Nyctinomops aurispinosa</i> (N)
<i>M. microtis</i> (N)	<i>N. laticaudata</i> (N)
<i>M. schmidtorum</i>	<i>Tadarida brasiliensis</i>
<i>Tonatia bidens</i>	<i>Molossus bondae</i>
<i>Lonchirhina aurita</i>	<i>M. pretiosus</i>
<i>Chrotopterus aurita</i>	<i>M. sinaloae</i>
<i>Anoura geoffroyi</i> (N)	
<i>A. caudifer</i>	
<i>Sturnira erythrimos</i>	

* N = found in the north coastal (front) ranges.

S = found in the southern (back) ranges.

No symbol = found in both forested ranges.

with respect to the avifauna, the north coastal ranges exhibit characteristics of an island. Taxa typical of the Andes are represented and basal taxa of Amazonas are also present. To some extent Eisenberg and Redford (1979) have discussed this problem with respect to the mammals. Clearly the students of the avifauna were in advance.

The term "llanos" is broadly applied to the woodland savannas and grasslands of central Venezuela and adjacent Colombia. The area exhibits great heterogeneity. Under appropriate conditions permanent water courses support multistratal tropical forest and have an associated but often depauperate forest fauna. Morton (1979) has analyzed the problem for the avifauna. August (1981) demonstrated the role of the gallery forests in supporting complex mammal communities. Almost all the llanos fauna is derived from the adjacent forest fauna although there are a few species endemic to the open grasslands. Mares and his

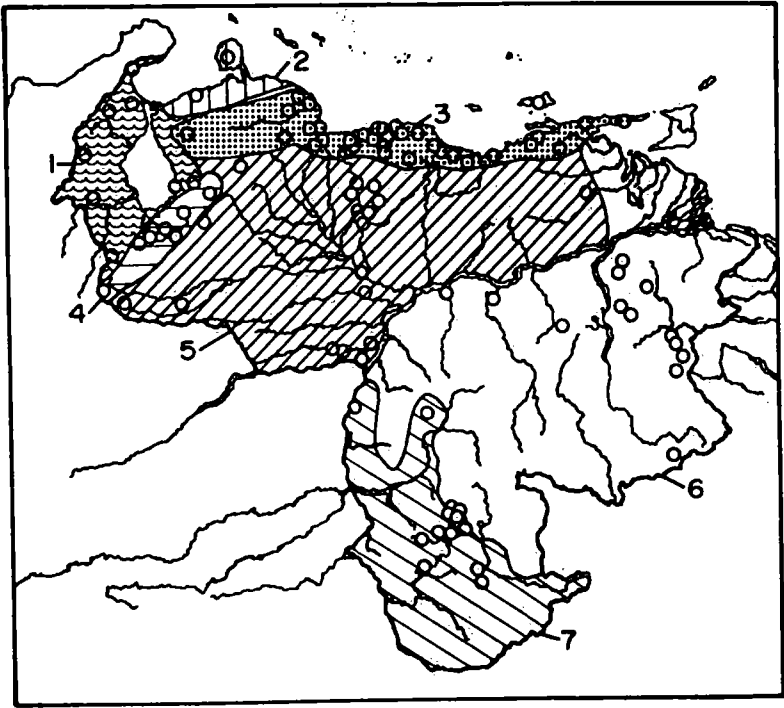


Figure 3. Biogeographic regions of Venezuela. Circles refer to collection stations as given in the publication by Handley (1976). 1 = Maracaibo Basin; 2 = Falcon arid zone; 3 = North coast range; 4 = Andean region; 5 = Llanos; 6 = Guyana Highlands; 7 = Amazon Lowlands. Boundaries of the regions are approximate, future research may define zone of intergradation. The region of the delta is excluded from consideration as is Isla Margarita and Trinidad. From Eisenberg and Redford (1979).

associates (Lacher, Mares, and Alho, 1989) have described an analogous phenomenon for the seasonally dry forests of Caatinga and Cerrado of Brazil.

The seasonally dry llanos and dry forests surround the north coastal ranges and to the west the dry forest band joins the arid Falcon Peninsula and the arid areas at the north end of the Maracaibo Basin. The eastern range of the Andes blocks simple emigration of the terrestrial fauna to north-central Venezuela from the Maracaibo region. At the present time the largest block of lowland, moist forest north of the Orinoco River and east of the Andes is in southwestern Apure.

Some species of mammals known to have occurred in northern Venezuela have been reduced to the point of local extinctions. *Speothos venaticus*, *Pteronura brasiliensis*, and *Priodontes maximus* may well be gone. *Ateles belzebuth*, *Tayussa pecari*, *Puma concolor*, and *Panthera onca* are threatened.

The national parks of north-central Venezuela are illustrated in Figure 2. El Avila, Henri Pittier (Rancho Grande), and San Esteban protect parts of the north coastal ranges. Macarao, Guatopo, Yurubi and Tirgua protect the interior ranges. La Laguna de Tacarigua protects a piece of coastal habitat in Estado Miranda. Aguaro-Guaraquito is a large park (4,000 km²) covering primarily private land in the llanos of Guarico. Of the 113,430 km² study area, a total of 9,282 km² (8.2%) lies within National Park Boundaries. However, the area covered by parks that effectively protects larger fauna may be less. If we subtract an area of 4,200 km² in which we suspect that parks currently may not effectively protect all fauna, and add 1,500 km² of private ranches where wildlife is protected, we arrive at a rough estimate that 6,582 km², or 5.8% of the total surface area of North-Central Venezuela that functions as wildlife refuges.

North-central Venezuela has much to be proud about in terms of mammalian conservation. Large natural areas about modern urban areas. Large ranches protect and manage fauna responsibly. There is a rich literature. However, at the time of this publication, there exists cause for concern. The noteworthy parks near Venezuela's largest cities (El Avila/Caracas; Henry Pittier/Maracay; San Esteban/Puerto Cabello & Valencia) are already partly compromised by their proximity to human developments. These parks face a future of increasing isolation due to human expansion unless a conscious and specific effort is made to prevent that. There will always be some problems of poaching of "game" species (Silva and Strahl, 1996) in the parks. A very active, well-funded, and continuous combined program of education and enforcement can keep that in check. Large-bodied species (jaguars, white-lipped peccaries, pumas) are native to the lower elevations of the coast range, but are presumed eliminated from many areas and scarce in others. They may yet completely disappear, unless their habitats are aggressively defended. Large cattle ranches can and do play a role in the preservation of wildlife (Hoogesteijn and Chapman, 1998). The public service that enlightened ranch management provides should not go unrecognized, nor, perhaps, in some cases, unrewarded. Effective conservation requires serious commitment. The long-term maintenance of the fauna described here will require

nothing less than a coordinated commitment, at the national level, and at every other level of Venezuelan society, even in the face of economic unpredictability and hardship. Once lost, these mammalian communities will be difficult to recover.

CONCLUDING REMARKS

The six-state area plus the Federal District may be considered a mega-landscape. The north coastal ranges (both front range and south range) have served as an island of forested habitat surrounded by lower elevational species that wax and wane in terms of forest cover. The extreme north range exhibits Andean connections. Voss and Emmons (1996) urge us to continue collecting until complete lists of organisms can be compiled. A worthy aim, but the area we have defined is a habitat mosaic with a long history of non-human disturbance. If the effects of *Homo sapiens* beginning about 10-15 thousand years ago are added in, the situation becomes even more complex. European agronomy was introduced in the 16th and 17th centuries, and human influences together with their agronomy led to profound changes. The deforestation of the last 50 years (Hamilton et al, 1976) has been dramatic.

We have tried to characterize the mammalian fauna of north-central Venezuela, recognizing that the sampling has occurred on fragments that are increasingly fragmented. What is the mammal list for Parque Nacional Guatopo? It depends. Handley (1976) published data from a survey of the southern portion. Eisenberg, O'Connell, and August (1979) published a list that derived from a longer, more intensive effort, yet with little collecting of Chiroptera. Only by analyzing multiple data sets do we approach a true evaluation of biological diversity. Yet some species (e.g. *Panthera onca*, *Puma concolor*) were better studied at alternative sites. We are left with comments in the introduction; combined lists suggest at least 95 species of mammals are to be found in Guatopo. The inventories for Parque Nacional Henri Pittier (Rancho Grande), El Avila, Hato Masaguaral, Hato El Piñero also remain open-ended.

With increasing habitat fragmentation in most parts of the globe, it is all too likely that most parks will lose more species than they gain, thus it may be more useful to characterize a bio-region than to restrict to an "insular" survey area of 15 km², 30 km², etc. in hopes that one straggler will be caught, vouchered for, and catalogued. With this said, we hope the list for the six states serves as some sort of benchmark for 1999.

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