BIOGEOGRAPHIC ANALYSIS OF THE MAMMAL COMMUNITIES IN THE VENEZUELAN ANDES

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The Andes of Venezuela represent a tectonic raising integrated by a set of reaches separated by faults, which act as geographical barriers, conditioning the geographic distribution of many plants and animals as well. This characteristic favours the allopatric speciation and high levels of endemism, which confer a great taxonomic, evolutionary and biogeographic interest to the Andean region (Cuatrecasas, 1986; Patton *et al.*, 1990; Reig, 1986).

As part of a high tropical mountain region, the Venezuelan Andes have a great landscape heterogeneity as a consequence of the geomorphological processes and local climatic peculiarities. This has allowed differentiation of vegetation communities or ecological units, associated to different substrates and/or macro and mesoclimes, often with alternance in the altitudinal gradients where a decrease of the richness, diversity, and species replacement occurs (Sarmiento *et al.*, 1971).

The environmental diversity found in the Venezuelan Andes can be divided into different landscape types or ecological units. It is in each case the result of the particular combination of different selective pressures, which operate indistinctively above all the biotic elements and configure their communities, each with their own composition and structure.

An altitudinal substitution of these units is often found; for instance in the wet basins the sequence is: submontane forest, seasonal forest, cloud forests and finally the paramos. The horizontal continuity of these units is reduced in direct relation to the altitude, as a consequence of the topographic characteristics, which confer an insularity to these units which increases with altitude. It is known that the species richness (biodiversity) decreases with altitude. In contrast, the frequency of endemic species should be expected to increase in direct relationship with the altitude, as a consequence of the processes of allopatric speciation.

The distribution patterns of mammals and the structure of their communities are strongly associated with the temporal and spatial heterogeneity of the habitat (Andrade, 1993). For the non-flying mammals, in spite of the controversies related to the systematic status of some groups, we have a good idea of their diversification in the Venezuelan Andes (Reig, 1986; Wilson and Reeder, 1993). However, their horizontal and vertical distribution patterns are not yet clear. The lists of bat species are still incomplete due to insufficient collecting

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more of which would be needed to provide knowledge of the diversity of this complex group in the Andean region of Venezuela. The information on the ecological units is far from complete by virtue of the almost total absence of systematized information. Current research is reduced to fragmentary lists and incomplete coverage at unit level (Handley, 1976; Aagaard, 1982; Péfaur and Díaz de Pascual, 1982; Soriano, 1983).

Therefore, we have found it necessary to elaborate a diagnosis that enables us: i) to update the list of the mammal diversity in the Andes of Venezuela and ii) to characterize the mammal communities associated with the main ecological units of the region. The resulting information will contribute to the knowledge of the mammal fauna which characterize the north of South American mountane environments, and represents a useful element for the measure and design of the protected natural areas.

STUDY AREA

Geographical location

The Venezuelan Andes constitute a prolongation of the "Cordillera Oriental" of the Andes of Colombia (Figure 1); which extend 425 km towards the northeast, from 7° 30' and 10° 10' N and from 69° 20' to 70° 50' W, to the "Depresión de Lara" (González, 1980, Vivas, 1992). This mountain chain represents 4% of the Venezuelan surface area (Schubert and Vivas, 1993) and two segments can be distinguished (Figure 1): the first from the Nudo de Pamplona to the "Macizo de El Tamá" (Districts Junín and Páez of the Táchira and Apure states, respectively), where a discontinuity called "Depression del Táchira" which separates it from the other segment called "Cordillera de Mérida"; this segment occupies part of Táchira, Mérida, Barinas, Trujillo, Portuguesa and Lara states, separating it from the "Lago de Maracaibo" basin and the "Llanos" region (Monasterio and Reyes, 1980).

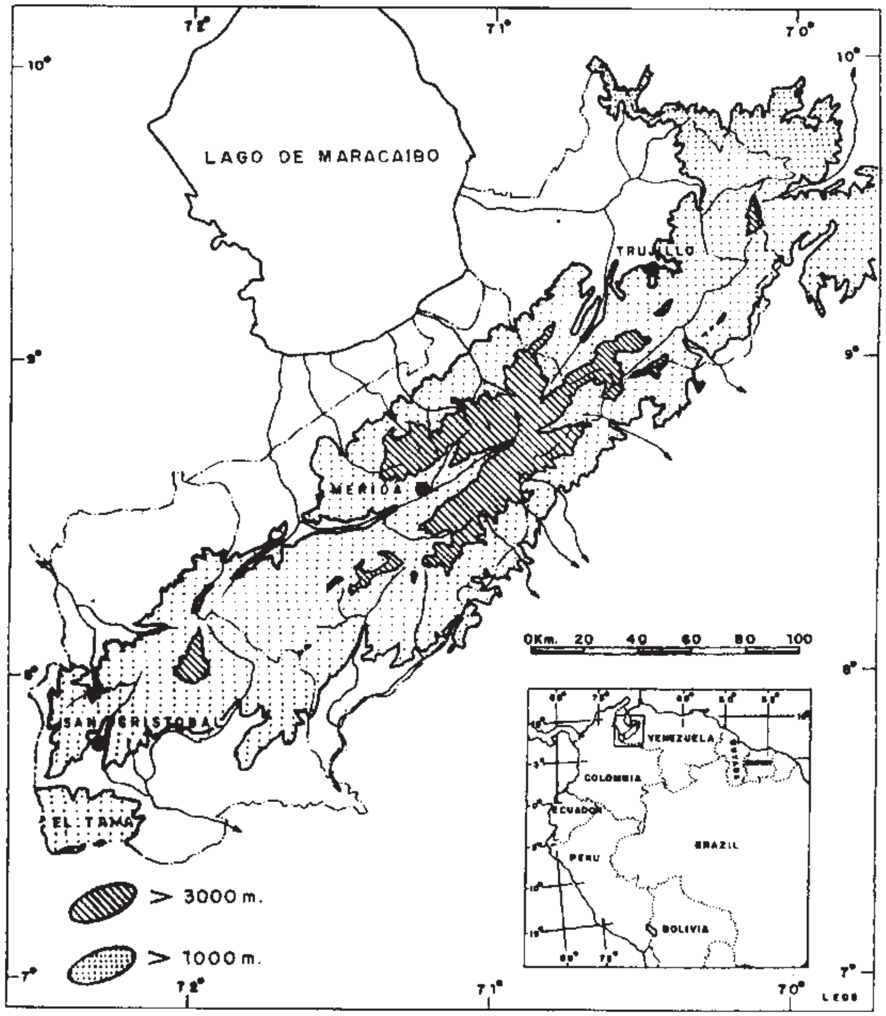

Fig. 1. Geographic location of the Venezuelan Andes. Continuous gross line represents the level of 1000 m elevation, that separates the Macizo de El Tamá from the Cordillera de Mérida.

Principal ecological units

In this study, we have focussed our attention on the five ecological units with greatest coverage above 800 m elevation. Also we will summarize the distinctive features of each one, following the criteria of Ataroff and Sarmiento (unpubl. data):

Seasonal Forests

This forest presents a canopy between 20 and 25 m, with emerging elements which can reach 30 m. In this stratum species of the genera *Spondias, Tabebuia, Cedrela, Ficus, Heliocarpus, Erythrina,* and *Inga* may be found as dominant. The intermediate stratum found between 12 and 20 m is characterized by species belonging to the genera *Vismia, Miconia, Cecropia, Piper, Solanum, Montrichardia* and *Urena*. In the herbaceous stratum Araceae and Ciclantaceae of the genera *Anthurium* and *Asplundia*, respectively are dominant. Many of the important species are deciduous and lianas and epiphytes are scarce. A relevant ecological characteristic of this unit is the presence of a dry season, which may vary between one and three months. The annual mean temperature varies, depending on the altitude, between 16 and 23°C.

In the wet basins this unit is found between 800 and 1700 m, a belt which is more or less continuous in the Lago de Maracaibo basin and the Llanos, while dry basins are restricted to gallery forests in the overflowing terraces of the rivers and to the permanent streams within the same altitudinal gradient.

This unit has been the object of intensive human activity since pre-Columbian times. Thus, in spite of its vast coverage, it is very difficult to find it in its original form since it has been modified or substituted by coffee cultivation, citrons tree plantations, sugar cane cultivation, cattle-raising or human settlements.

Cloud Forests

This denomination includes a complex variety of humid forests that constitute the superior belt of continuous forests in the Andes. They are forests 25 to 35 m high with several arboreal strata, irregular canopy and a richness of tree species that varies between 40 and 60 species by hectare, mainly evergreen, which support a great variety of epiphytes (Bromeliceae, Orquidiaceae, Araceae, Piperaceae and pteridophites). Among the most characteristic elements of the arboreal strata are the genera *Mauria, Cordia, Brunellia, Montanoa, Weinmannia, Clusia, Podocarpus, Decussocarpus, Heliocarpus, Trema* and *Vochysia*. The most characteristic feature of the shrubby and herbaceous strata is the presence of species of arborescent ferns from the Cyatheaceae family; in these strata species of the genera *Arthrostylidium, Chusquea, Canna, Gaultheria, Chamaedorea, Piper, Psychotria,* and *Renealmia* may also be found.

Under favourable climatic conditions these forests occupy the altitudinal belt between 1700 and 3000 m. The annual mean temperatures oscillate between 18 and 10°C, with day-night variations from 6 to 8°C. The annual rainfall varies from 1000 mm to 2600 mm. Other factors such as cloud and the daily mists are also associated with this unit, conferring high levels of relative humidity to the environment, reducing the daily variations of temperature and sunstroke as well.

Paramos

This unit may be divided into two main subtypes (Monasterio, 1980): Andean paramo, located between 2800 and 4000 m and the high-Andean paramo, corresponding to the belt between 4000 to 4800 m. In addition to their altitudinal location, these subtypes can be recognized by the floristic composition, plant coverage, mean monthly temperatures, maximum and minimal temperatures and frost frequency. In the present work we will characterize only the Andean paramo, since the mayority of information comes from this subtype.

The Andean paramos comprise a great variety of plant formations, where two strata may be distinguished: the upper one, shrubby and open, whose height varies between 0.5 and 4.0 m, according to the location, is dominated by species of Asteraceae of the Espeletini tribe ("frailejones"), belonging to the genera *Espeletia, Coespeletia, Espeletiopsis, Libanothamnus or Ruilopezia* and some shrubs such as *Hypericum, Chaetolepis, Pernettia, Hesperomeles* and *Arcytophyllum*. The lower stratum is herbaceous, with height variation between 0 and 40 cm, of variable coverage (between 2 and 80%) is dominated by cushion species of the genera *Aciachne* and *Arenaria*, rosettes such as: *Hypochoeris, Acaena, Calandrinia, Geranium*, grassy plants such as *Senecio, Sisyrinchium, Castilleja* and grasses of the genera *Agrostis, Poa, Calamagrostis* and *Bromus* (Monasterio, 1980).

TABLE I
NUMBER OF SPECIES BY ORDER AND ECOLOGICAL UNIT. ABREVIATION FOR ECOLOGICAL UNITS ARE: SF = SEASONAL FOREST, CF = CLOUD FOREST, PA = PARAMO, DEF = DRY EVERGREEN FOREST, AND TS = THORN FOREST.

ORDERS	Species	%	SF	CF	PA	DEF	TS
Didelphimorphia	14	9.0	13	7	1	1	3
Paucituberculata	1	0.6	-	1	1	-	-
Xenarthra	5	3.2	3	3	-	-	1
Insectivora	2	1.3	1	2	1	1	-
Chiroptera	74	46.8	54	32	2	9	30
Primates	2	1.3	2	1	-	-	-
Carnivora	14	9.0	11	11	6	3	2
Artiodactyla	4	2.6	3	1	1	1	-
Rodentia	40	25.6	30	21	7	6	3
Lagomorpha	1	0.6	-	-	1	-	-
TOTAL	157	100.0	117	79	20	21	39

The climatic aspects that characterize this environment are the large daily temperature fluctuations, often accompanied by nocturnal frosts and seasonal oscillations of the water balance throughout the year (Monasterio and Reyes, 1980). The annual mean temperature varies:between -4 and 10°C, depending on the altitude. The annual total rainfall oscillates between 650 and 1800 mm.

Evergreen Dry Forests

These forests of low stature may become open shrub in certain local conditions. The average forest has an arboreal upper stratum between 3 and 5 m, with open canopy which is dominated by species of the genera: *Clusia, Oyedaea, Psidium, Hesperomeles, Vaccinium, Weinmannia* and *Dodonaea*. The lower stratum is shrubby, much more dense, reaching 1.5 m and whose main species represent the genera: *Cavendishia, Myrsine, Symplocos, Mercetia, Stevia, Baccharis, Gnaphalium, Eugenia, Monochaetum, Epidendrum* and the fern *Pteridium aquilinum*.

This forest can be found between 1600 and 2700 m. In dry basins, the upper limit is the Andean paramo and the lower one is the thorn shrub, while in wet basins these limits are the cloud forest and the seasonal forest respectively. The annual rainfall oscillates between 500 and 1000 mm and, according to the altitude, the annual average temperature varies between 18 and 10°C. Relatively high temperatures and low precipitations, cause a hydric deficit from four to six months of the year.

Thorn Shrub

The intensive anthropical intervention to which the thorn shrubs have been submitted by action of the felling and caprine overgrazing, has led to selection of thorny species, which characterize these environments. They now appear as open forests where three strata may be distinguished: an arboreal one from 3 to 4 m average height, whose main species belong to the leguminous genera *Prosopis* and *Acacia* and, as emergents, the columnar cacti of the genera *Stenocereus, Subpilocereus* and *Pilosocereus*; a shrubby stratum from 0.5 to 2 m, of which the main genera are *Croton, Cordia, Jatropha*, and *Opuntia*; in the understorey (between 0 and 40 cm), the most conspicuous species are also cacti and the genera *Opuntia, Melocactus* and *Mammilaria*. Trees present some vascular epiphytes such as Peperomiceae, Bromeliaceae and Orchidiaceae.

The main climatic consequence is the hydric deficit for most of the year where total yearly rainfall varies between 450 and 550 mm, distributed according to a tetraseasonal pattern. The average annual temperature is 17.3°C in the highest locations and 25.5°C at lower altitude (Andressen and Ponte, 1975).

MATERIALS AND METHODS

This study was carried out in two stages: the first consisted of an exhaustive review of bibliography and national mammal collections, wherein Andean specimens are deposited, particularly the Colección de Vertebrados de la Universidad de Los Andes (CVULA), the Museo de Historia Natural La Salle (MHNLS), the Museo de la Estación Biológica de Rancho Grande (EBRG) and the Museo de Ciencias Naturales de Guanare (MCNG). For the bibliographical review the references of Aagaard (1982), Cabrera (1958, 1961), Díaz de Pascual (1988), Handley, (1976), Péfaur and Diaz de Pascual (1982), Muñoz (1996), Soriano *et al.* (1990) and Soriano and Ochoa (1997) were mainly used. The taxonomic nomenclature employed follows the criteria presented in the work edited by Wilson and Reeder (1993). When assigning a given species to a particular ecological unit the geographical location of the capture site and the altitude were taken into account. Thus a preliminary diagnosis concerning the community composition in each selected ecological unit was made and critical areas requiring additional sampling effort to complete the inventories were detected.

In the second phase a capture programme in the previously identified areas was formalized, to complement the available information. The ecological units sampled were the seasonal forests, cloud forests and paramos of the Táchira State. No or few disturbed areas were selected, where collections were effected using the Sherman, National and Victor traps, so covering most of the different terrestrial, aquatic and arboreal microhabitats. A global trapping and mist net effort of 15414 traps/night and 1560 hours/net was made. All collected material has been deposited at the CVULA in Mérida and EBRG in Maracay.

The lack of mammal lists from submontane forests corresponding to the Andean piedmont prevent us from analyzing the changes in the species richness related to the altitudinal gradient. Nevertheless, we have used the list for low elevation forests from the Venezuelan Guayana region (Ochoa *et al.*, 1993) to make comparisons, and although they will not correspond exactly with those of the Andean piedmont, at least they will permit us to appreciate the trends.

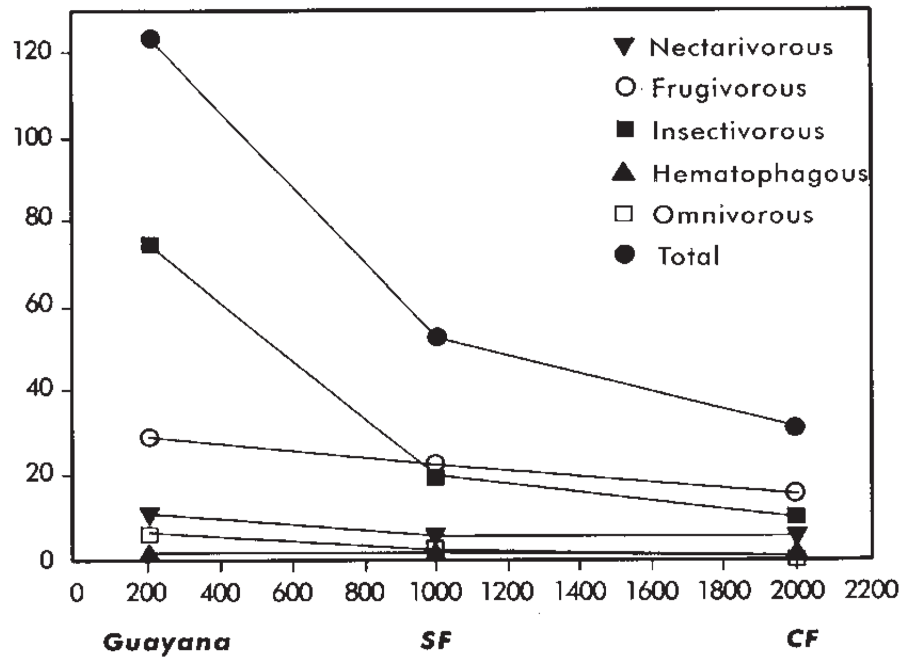

Fig. 2. Bat richness changes by guild along an elevational gradient. Including tropical rainforest (Guayana), montane seasonal forest (SF), and montane cloud forest (CF).

RESULTS AND DISCUSSION

Species richness and geographical distribution patterns

At least 157 mammal species, grouped in 10 orders and 29 families, inhabit the Andes of Venezuela (Appendix 1), and this represents 45.9 percent of the registered species in the country (Soriano and Ochoa, 1997). Bats constitute the most diversified taxon which is made up of 46.8 percent of the known mammals of the region. These relationships correspond with the trends found for the Chiroptera all over the country (Ochoa *et al.*, 1993; Soriano and Ochoa, 1997) and in the rest of tropical South America (Reig, 1986).

The capture and review of collections programme gave 29 new records for the Andean region above 800 m (distinguished with R in Appendix 1): Didelphimorphia (1), Xenarthra (4), Chiroptera (21), Primates (1), Carnivora (2) and Artiodactyla (1). The collection number and locality of some of the voucher specimens are referred to in Appendix 2. Although the Andes occupy only 4% of the country area the relationship species/area reaches values of 42.8 x 10^{-4} spp./km^2. This represents almost an order of magnitude higher (8.3 fold) than those corresponding to the Guayana region (Delta Amacuro, Bolivar and Amazonas States), which represent approximately 50% of the national territory and where 5.14x10^{-4} spp./km^2 have been recorded.

Thirty one species (indicated with asterisk in Appendix 1) exhibit an exclusively Andean geographical distribution, which represents almost one fifth (19.9%) of the listed species. Among them three distribution patterns can be distinguished: i) wide within the region (WD in Appendix 1), i.e., Cordillera de Mérida and at least part of the Colombian Cordillera Oriental, where *Monodelphis adusta* (Didelphimorphia), *Sturnira aratathomasi*, *S. bidens*, *S. bogotensis* (Chiroptera), *Tremarctos ornatus*, *Nassuella olivacea* (Carnivora), and *Aepeomys lugens*, *Agouti taczanowskii*, *Akodon bogotensis*, *Chilomys instans*, *Ichthyomys hydrobates*, *Melanomys caliginosus*, *Thomasomys laniger* (Rodentia) exemplify this pattern, ii) restricted or endemic to the Cordillera de Mérida (CM), that means all the mountains on the northeast of the Depresión del Táchira; this is the case of *Gracilinanus dryas* (Didelphimorphia), *Cryptotis meridensis* (Insectivora), *Anoura luismanueli* (Chiroptera), *Mazama bricenii* (Artiodactyla) and *Neusticomys mussoi*, *Oecomys flavicans*, *Oryzomys meridensis*, *Oryzomys* sp., *Thomasomys vestitus* and *Olallamys edax* (Rodentia). iii) restricted to the Cordillera Oriental (CO), including some species whose most easterly distribution ends in the Macizo de El Tamá: *Caenolestes obscurus* (Paucituberculata), *Cryptotis thomasi* (Insectivora), and *Chibchanomys trichotis*, *Oligoryzomys griseolus*, *Oryzomys albigularis*, *Rhipidomys fulviventer*, *Thomasomys aureus* and *T. hylophilus* (Rodentia) illustrate this situation. Special mention is made of mouse *Rhipidomys venustus*, whose distribution area encompasses the Cordillera of Mérida and extends to the Cordillera de la Costa in northern Venezuela (Handley, 1976; Wilson and Reeder, 1993), thus converting it in an endemic species of Venezuela, although not exclusive to the Andes.

Ecological distribution

Upon examining the species composition in the different ecological units evaluated (Table 1) a clear richness gradient may be appreciated, where the cloud and seasonal forests exhibit the greatest number of species (117 and 79, respectively), followed by the thorn shrubs (39), dry evergreen forests (21) and paramos (20). With the exception of this last unit, we consider that the capture efforts effected in each one of the ecological units, indicated in the methodology, have been sufficient to offer a reasonably complete idea of their composition; consequently, the taxonomic aspects that distinguish them are due to intrinsic differences among them. The decrease in the number of cloud forest species compared to those found in seasonal forests are clearly associated with the altitudinal gradient which imposes more severe thermal conditions on the inhabitants of the cloud forests, with a consequent reduction in species richness. In the paramos the structural simplicity of the environment combined with the prevailing extreme climatic conditions, causes the drastic reduction which is observed in the number of species.

Although species richness in the dry evergreen forests is expected to be less than in the cloud and seasonal forests, due to low humidity and reduced complexity, we consider that the numbers obtained (21 species) do not reflect the real diversity of this unit and are rather due to insufficient sampling. Evidence of this situation shown by the species *Sciurus granatensis*, which is undoubtedly found in this unit, but since its presence has not yet been confirmed we put a question mark in the corresponding space in Appendix 1.

As opposed to dry evergreen forests we expect thorn shrubs to show a smaller diversification of the mammal communities, since we consider that the inventories accomplished in this unit have been sufficiently representative of their temporary and spatial variability. The field data indicate the absence of typical rodents in this ecological unit (Soriano *et al.*, 1999). Similarly, most of the recorded taxonomic composition could be the consequence of the breakthrough of some species originating from the surrounding seasonal forests, through the galleries of the rivers and streams as is the case of the Didelphimorphia *Monodelphis brevicaudata*, the Chiroptera *Carollia perspicillata, Sturnira lilium, Platyrrhinus helleri, Artibeus hartii, Artibeus jamaicensis, Artibeus lituratus* and the Rodentia *Coendu prehensilis, Sigmodon hispidus* and *Thomasomys laniger*.

Taking into account these observations, and the fact that the seasonal forests, cloud forests and paramos constitute the ecological units with greatest coverage in the region, and represent a continuity in the altitudinal gradient whose inventories are considered relatively complete, the information gathered for these three units allows us to compare the altitudinal distribution patterns that the different mammal species recorded in the Venezuelan Andes exhibit.

Some lowlands (<800 m) taxa, particularly: *Marmosa robinsoni, Monodelphis brevicaudata, Cabassous centralis, Oligoryzomys fulvescens, Nectomys squamipes, Rhipidomys couesi, R. venezuelae, Sigmodon hispidus, Sigmodontomys alfari, Coendu prehensilis, Dinomys branickii, Dasyprocta leporina, Agouti paca, Proechimys* sp., *Cebus olivaceus, Panthera onca, Mazama americana* and many Phyllostominae bats widen their altitudinal distribution and surpass the inferior limit of the seasonal forests. However, they do not reach the corresponding levels in the cloud forests. The seasonal forests also share some species with the cloud forests, for example *Didelphis albiventris, Gracilinanus dryas, Cryptotis meridensis, Aepeomys lugens, Akodon urichi, Ichthyomys hydrobates, Oryzomys meridensis, Rhipidomys venustus, Thomasomys vestitus* and *Sphiggurus vestitus*.

Six species are considered typical elements of the cloud forests (the Chiroptera *Sturnira bidens, Sturnira bogotensis* and the Rodentia *Chilomys instans, Thomasomys aureus, Thomasomys hylophilus*, and *Olallamys edax*), while the rest of the mammals recorded in this unit may widen their ecological distributions toward other contiguous ecological units.

The 19 species which characterize the communities associated with the paramos except the subspecies *Odocoileus virginianus goudotii* (Artiodactyla) and *Silvilagus brasiliensis meridensis* (Lagomorpha), which appear to be exclusively associated with this ecological unit, none are exclusive or characteristic mammal species of the paramo. In the particular case of the rodents, our results are in agreement with the published data by Hershkovitz (1958), who indicated the absence of this taxon in the forests and distributions restricted to paramo environments. In the case of *Akodon bogotensis* its ecological preferences relate it more to open areas with grassy coverage (Aagaard, 1982; Díaz de Pascual, 1994). Similar results have been mentioned by López-Arévalo and Montenegro-Díaz (1993) and López-Arévalo *et al.*, (1993) in the reservation of Carpanta of the Cordillera Oriental, Colombia.

The only confirmed Primate species in the seasonal forests is *Cebus olivaceus*, although the presence of *Alouatta seniculus* is very probable (Appendix 1), since it is present in superior belts, such as the cloud forest. The fact that this species has not been registered may be an indication of the anthropic alteration that it has suffered in these wild environments, to which the primates are highly sensitive (Ochoa *et al.*, 1993).

Mammal communities of the seasonal and cloud forests possessing the greatest number of species, provide almost the whole species list of the region (Table I, Appendix 1). The seasonal forests house 117 species (74.4% of the regional total), of which 14 are restricted to the Andean region (Appendix 1). Also, in these forests nine of the ten endemic species of the Cordillera de Mérida (90%) are represented. The cloud forests possess 78 species (50% of the regional total), of which four are endemic (40%) and 24 are exclusive to the region; among the latter are, *Chilomys instans, Oligoryzomys griseolus, Chibchanomys trichotis, Akodon bogotensis* and *Olallamys edax* which are found solely in sites located above the lower limit of this unit.

In the ecological distribution context bats require special consideration; Figure 2 shows an important decline in the number of species when moving from the forests of the region of Guayana (123) to the seasonal (54) and cloud forests (31). Similar situations have been referred to by Graham (1983) for The Andes of Peru and for Venezuela by Fleming (1986) using the data of Handley (1976). These authors interpreted the observed altitudinal decline as the result of a reduction in the available resources. However, the same is not manifested proportionally, in the functional groups (trofic categories) or in all the taxa. Thus, we can appreciate in Figure 2, that the insectivorous guild seems to be directly responsible for the decline, showing a high correlation with the total of bats (Spearman correlation coefficient rs= 0.99; P= 0.05), while, on the contrary, the rest of the functional categories decline following other trends.

Diet has a great influence on the metabolic rate of bats and consequently in their thermoregulatory capacities (McNab, 1982). McNab shows that bats with diets based on proteins (insects) have lower metabolic rates than those whose diet is composed of carbohydrates (fruit and/or nectar). The few insectivorous bat species that occupy these high mountain environments belong exclusively to two families (Vespertilionidae and Molossidae). Vespertilionidae is the only bat family of extratropical origin that inhabit the neotropics, and Molossidae is the only tropical family of insectivore bats whose representatives reach temperate latitudes. This information leads us to think that the species decline with altitude is due to the inefficiency in the thermoregulatory function of the species of tropical origin that characterize the insectivorous guild (Soriano, 1983).

Taxonomic and biogeographic remarks

Given the geographical separation of the Cordillera de Mérida and the Venezuelan portion of the Cordillera Oriental (Macizo de El Tamá), in the present study we have followed the nomenclatural criteria in Wilson and Reeder (1993) and we recognize *Cryptotis thomasi* as a different species of *C. meridensis*. This is not the case for the deer of the genus *Mazama*, since although we expect the presence of *M. rufina* for Venezuela in the Macizo of El Tamá, we do not have vouchers from that locality, therefore we have only recognized *M. bricenii* as endemic to the Cordillera de Mérida.

Handley (1987) restricted the Venezuelan geographic range of *Artibeus cinereus* to the southern Orinoco river basin, but he did not specify which species inhabit in the Venezuelan Andes. Herein we recognized two forms occurring in the Venezuelan Andes: *A. glaucus* and *A. phaeotis* which are reported by the first time (Appendix 1 and 2).

The Depresión del Táchira does not seem to have operated as an effective barrier for bats, and there are no endemic species of bats in the Venezuelan Andes, except in the case of *Anoura luismanueli*, which has not been registered outside of the Cordillera de Mérida, but whose presence in the Cordillera Oriental is very probable (Molinari, 1994). However, the insularity exhibited by the arid enclaves that characterize the ecological unit of the thorn shrubs, means that it is necessary to examine the taxonomic status of at least, the Andean populations of the bats *Glossophaga longirostris* and *Rhogeessa minutilla*, since such isolated populations were not considered in the previous reviews of those species (Webster and Handley, 1986; LaVal, 1973).

In seasonal forests a high diversification of the genera *Oecomys* and *Rhipidomys* is observed, so that almost 50% of the species recorded in Venezuela are found represented in this unit; however, both taxa reach their maximum diversification in Guayana (Ochoa *et al*., 1993). The genus *Oecomys*, seems to be characteristic of the low and median elevation forests; in the seasonal forests it is represented by four species, of which *Oecomys flavicans* is endemic to the Andean region (Appendix 1). Similarly, the genus *Rhipidomys* is represented by three species in the seasonal forests, of which *Rhipidomys fulviventer* constitutes a new endemism and its ecological distribution reaches the cloud forests.

Within the Andean genus *Thomasomys* the inverse phenomenon is observed, their representatives are exclusively, restricted to seasonal forests, cloud forests and paramos, and with a maximum in the cloud forests (Soriano *et al*., 1999). Within this gradient there seem to be a substitution of the genus *Oecomys* by the genus *Thomasomys*, as seasonal forest changes to cloud forest; and it is interesting that both these taxa are found in the semiarboreal rodents guild. A similar distribution pattern was found for the *Thomasomys* species in the Peruvian Andes (Patton, *et al*., 1990).

The genus *Akodon* is represented in Venezuela by two species *A. urichi* and *A. bogotensis*, the first one with a wide distribution within the evaluated ecological gradient, while *A. bogotensis* is restricted to the cloud forests and paramos. It is convenient to examine the taxonomic identity of the populations of the latter, in the light of the parapatric or gradient speciation model, as has been referred to by Patton *et al*. (1990). Thus, given its high Andean distribution pattern, we expect that the morphotype of the Cordillera de Mérida, by virtue of its possible geographical isolation, could be distinguishable from the rest of the Andean populations. In the same way, we think that the identity of the Venezuelan populations of *T. laniger* and *Chilomys instans* would have to be examined.

The genus *Oryzomys* is represented by five species in Venezuela; of which only *O. meridensis* is recorded in the Andean region and constitutes a recognized complex of species (Aguilera *et al*., 1995); whose wide distribution extends from the seasonal forests to the cloud forests, including the dry evergreen forests. These different populations show morphological variations possibly associated with the altitudinal gradient (Rivas, 1993). Recent karyologic studies revealed that within the *O. albigularis* complex at least two forms may be distinguished in the Venezuelan Andes: one of them referable to *O. meridensis*, and is found in Lara, Trujillo and Mérida states, and the other not yet described, is located at the Uribante dam in the Táchira State (Aguilera *et al*. 1995) and will provide a new endemism for the Cordillera de Mérida. Attention and special effort should be put into the aquatic rodents collection of the genera *Chibchanomys*, *Ichthyomys* and *Neusticomys*, since these Ichthiominae seem to have their greatest adaptive radiation in the Andes (Voss, 1988; Ochoa and Soriano, 1991) and because in these taxa two important aspects are combined: i) an extremely low vagility, imposed by their high dependency on the existing resources in permanent water bodies and ii) the inherent difficulty when capturing them, resulting in their scarce representation in collections and museums.

Priorities for Conservation

The high richness and endemism indexes that characterize the Andean seasonal forests (Appendix 1) are seen to be threatened by a high habitat fragmentation and an intensive anthropic activity, product of the agricultural developments in this unit; this constitutes the called "coffee belt" where the principal human settlements and cities of the region are located. The situation is made more dramatic if it is taken into account that this unit lacks an adequate representation within the Venezuelan system of areas under special protection. It is a high priority to take measures to safeguard their integrity. The expansion of the agricultural frontier in the Andes of Venezuela has also affected the cloud forests, yet a large area in pristine conditions still exists which has been largely incorporated into National Parks and other protected areas.

Finally, it is necessary to emphasize the special attention that the dry evergreen forests and thorn shrubs require. The first of these units constitutes a priority in the future zoological inventories design, due to the scarce available information on the structure and composition of their animal communities. The second one must be considered in the short term within the strategies used for the conservation of natural environments that characterize the Venezuelan Andes, evaluating the acceleration in degradation rates and loss of this ecological unit in the wake of urbanistic processes associated with the towns of greatest importance such as Mérida city, La Grita, and Valera. Such strategies should combine the effort of all of those institutions interested in the protection and the management of the biodiversity that typifies the Andean region, taking into account the relevant commitments made by the regional governments.

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Appendix 1

List of the high-Andean mammals of Venezuela with their distribution by State and ecological unit.

Explication of simbology about distribution of each species: (*) restricted to Andean region; (WD) wide into the Andes; (CO) restricted to Cordillera Oriental (Colombia) and Macizo de El Tamá (Venezuela), (CM) endemic from the Cordillera de Mérida, (R) first record of the species for the Venezuelan Andes. Abreviation for the ecological units are: (SF) Seasonal Forest, (CF) Cloud Forest, (PA) Paramo, (DEF) Dry Evergreen Forest and (TS) Thorn Shrub. Records comming from: (a) field observations or signs; (b) bibliography; (c) colects and museums, (?) probable presence in the unit. Abreviations of the States: Ba = Barinas, La = Lara, Me = Mérida, Ta = Táchira, Tr = Trujillo. "sp." is used for two species of the genera *Oryzomys* and *Proechimys*, respectively, which have not yet specific epitet (Aguilera *et al.*, 1995).

	Andean	Ecological Units				
TAXA	States	SF	CF	PA	DEF	TS
DIDELPHIMORPHIA (14)						
Didelphidae						
Caluromys philander (R)	Me	c				
Caluromys lanatus	Me	b/c	c			
Chironectes minimus	Ta,Me	c	b			
Didelphis albiventris	Ba,Ta,Me,Tr	c	b/c	c	c	
Didelphis marsupialis	La,Ba,Ta,Me,Tr	b/c	b/c			c
* *Gracilinanus dryas* (CM)	Ta,Me,Tr	c	b/c			
Gracilinanus marica	Me		b			
Marmosa robinsoni	Ba,Me,Tr	b/c				c
Marmosops fuscatus	Ba,Me,Tr	b/c				
Marmosops impavidus	Ta		b			
Metachirus nudicaudatus	Ba,Me	b/c				
Micoureus demerarae	La,Ba,Me,Tr	b/c	b/c			
* *Monodelphis adusta* (WD)	Ta,Me	b/c				
Monodelphis brevicaudata	Ba,Ta,Me,Tr	b/c				c
PAUCITUBERCULATA (1)						
Caenolestidae						
* *Caenolestes obscurus* (CO)	Ta		b	b		
XENARTHRA (5)						
Myrmecophagidae						
Tamandua mexicana (R)	Ta,Me	?				c
Bradypodidae						
Bradypus variegatus	Tr	?	b			
Megalonychidae						
Choloepus hoffmanni (R)	Me	c	c			
Dasypodidae						
Cabassous centralis (R)	Tr	c				
Dasypus novemcinctus (R)	La,Me	c	c			
INSECTIVORA (2)						
Soricidae						
* *Cryptotis meridensis* (CM)	Ta,Me,Tr	c	b/c	b/c	c	
* *Cryptotis thomasi* (CO)	Ta		b			
CHIROPTERA (74)						
Emballonuridae						
Peropteryx kapleri	Ba,Ta	b				c
Noctilionidae						
Noctilio leporinus (R)	Me					c
Mormoopidae						
Mormoops megalophylla (R)	La,Me	c				c
Pteronotus parnelli	La,Ba	c/b				
Phyllostomidae						
Chrotopterus auritus (R)	La	c				
Lonchorhyna aurita	Ba	b				
Micronycteris hirsuta (R)	Me	c				
Micronycteris megalotis	Ba,Ta,Me	b				c
Micronycteris microtis (R)	Me		c			
Micronycteris minuta (R)	La	c				
Phyllostomus discolor (R)	Me	c				c
Phyllostomus hastatus	Ba	b				
Tonatia brasiliense	Ba	b				
Tonatia saurophila (R)	Me	c				
Glossophaga longirostris	Me					b/c
Glossophaga soricina	Ba,Ta,Me	b/c				c

Appendix 1 (Cont.)

	Andean	Ecological Units				
TAXA	States	SF	CF	PA	DEF	TS
Lonchophylla robusta	Ba,Me	b/c				
Anoura caudifera	Ba,Me,Tr	c	b			
Anoura cultrata	Me,Tr		b/c			
Anoura geoffroyi	Ba,Me,Tr	b/c	b/c			c
Anoura latidens	Ba,Me	b	c			
* *Anoura luismanueli* (CM)	Ba,Ta,Me,Tr	b/c	b/c		c	
Leptonycteris curasoae	Ta,Me,Tr					b/c
Carollia brevicauda	La,Ba,Ta,Me,Tr	b/c	b/c		c	
Carollia castanea (R)	Me	c				
Carollia perspicillata	La,Ba,Ta,Me,Tr	b/c				c
* *Sturnira aratathomasi* (WD)	Me		b/c			
* *Sturnira bidens* (WD)	Me,Tr		b/c			
* *Sturnira bogotensis* (WD)	Ta,Me		b/c		c	
Sturnira erythromos	La,Ba,Ta,Me,Tr	b/c	b/c		c	
Sturnira lilium	La,Ta,Me,Tr	b/c	c			c
Sturnira ludovici	La,Ba,Me,Tr	b/c	b/c			
Sturnira tildae	Ta	b				
Uroderma bilobatum	Ba,Ta,Me	b/c				c
Platyrrhynus umbratus	La,Ba,Ta,Me,Tr	b/c	b/c			c
Platyrrhynus vittatus	La,Ba,Me,Tr	b/c	c			
Platyrrhynus helleri	Ba,Me	b/c				c
Chiroderma salvini (R)	Me	c				
Chiroderma trinitatum	Me	b				
Chiroderma villosum (R)	Me	c				
Artibeus amplus	Ba,Me,Tr	c	b/c			
Artibeus glaucus (R)	La,Ba,Ta,Me	c	c			
Artibeus hartii	Ba,Ta,Me	c	b/c			c
Artibeus jamaicensis	Ba,Ta,Me	b/c				c
Artibeus lituratus	Ba,Ta,Me	b/c	b/c			c
Artibeus phaeotis (R)	Ba	c				
Vampyressa pusilla	Ba,Ta	b/c				
Sphaeronycteris toxophyllum	La,Me	c	b/c			
Ametrida centurio	Me		b			
Desmodus rotundus	La,Ta,Me,Tr	b	b			b/c
Diphylla ecaudata (R)	Ta	c				
Vespertilionidae						
Myotis albescens (R)	Me					c
Myotis oxyotus	Ta,Ba,Me,Tr	b/c	b/c			
Myotis keaysi	Ba,Me	b/c				c
Myotis riparius	Ba	b				
Eptesicus andinus	Ba	b				
Eptesicus brasiliensis	La,Ba,Ta,Me,Tr	c	b/c		c	
Eptesicus fuscus	Ta,Me		c	b/c		
Eptesicus montosus	Me		b/c			
Histiotus humboldti (R)	Ta,Me		c		c	b/c
Histiotus montanus	Me		b/c			
Lasiurus borealis	Ta, Me		b		c	c
Lasiurus cinereus	Me	c	b	b	c	c
Lasiurus ega	Me,Tr	c	b			
Rhogeessa minutilla	Me					b
Rhogeessa tumida (R)	Ta					c
Molossidae						
Tadarida brasiliensis	Ta,Me	c	b/c		c	
Eumops auripendulus (R)	Me					c
Eumops glaucinus	Ta,Me	b				b
Eumops perotis	Me					b
Promops centralis (R)	Me	c				
Molossus bondae (R)	Ta					c
Molossus molossus	Ba,La,Me	b/c				c
Nyctinomops macrotis	Me	b				
PRIMATES (2)						
Alouatta seniculus	Ta,Me	?	c			
Cebus olivaceus (R)	La	c				
CARNIVORA (14)						
Canidae						
Cerdocyon thous	La,Ta,Me	b/c	c			c
Urocyon cinereoargenteus (R)	Me				c	
Ursidae						
* *Tremarctos ornatus* (WD)	La,Ta,Me,Tr	c	b	b		
Procyonidae						
Nassua nassua	Ta,Me,Tr	b/c	b/c	c		

Appendix 1 (Cont.)

TAXA	Andean States	SF	CF	PA	DEF	TS
		Ecological Units				
* *Nassuella olivacea* (WD)	Ta,Me,Tr	?	b/c	c		
Potos flavus	Ta,Me,Tr	b	b/c		?	
Mustelidae						
Conepatus semistriatus	Me	b/c	c		?	
Eira barbara	La,Ta,Me	b	b		?	
Lontra longicaudis	Ta,Me	c	a	a	?	
Mustela frenata	Ta,Me,Tr	c	b/c	c	c	
Felidae						
Herpailurus yaguarondi (R)	Me					a
Leopardus tigrina	Me	b	b/c		?	
Panthera onca	Me	b				
Puma concolor	Ta,Me,Tr	a	b	b	a	
ARTIODACTYLA (4)						
Cervidae						
Mazama americana	La,Me	b/a				
* *Mazama bricenii* (CM)	Me,Tr	b/c	b/c	?	c	
Odocoileus virginianus	Me			b/c		
Tayasuidae						
Pecari tajacu (R)	La	a				
RODENTIA (40)						
Sciuridae						
Sciurus granatensis	Ba,Ta,Me,Tr	b/c	b/c		?	?
Heteromyidae						
Heteromys anomalus	La,Ba,Ta,Me,Tr	b/c	b/c			
Muridae						
* *Aepeomys lugens* (WD)	La,Ta,Me,Tr	c	b/c	b/c	c	
* *Akodon bogotensis* (WD)	Ta,Me,Tr		b/c	b/c	c	
Akodon urichi	La,Me		c	b/c	b/c	
* *Chibchanomys trichotis* (CO)	Ta		b			
Nectomys squamipes	Ba	b				
* *Chilomys instans* (WD)	Ta,Me		b/c			
* *Ichthyomys hydrobates* (WD)	Ta,Me	b/c	b/c		c	
* *Melanomys caliginosus* (WD)	Ba,Me,Ta	b/c				
Microryzomys minutus	Ba,Ta,Me,Tr	c	b/c	b/c	c	
Neacomys tenuipes	Ba,Ta,Tr	b/c				
* *Neusticomys mussoi* (CM)	Ta	b				
Oecomys bicolor	Ta	b				
Oecomys concolor	Ta	b				
* *Oecomys flavicans* (CM)	Me	b				
Oecomys cf. *trinitatis* (R)	Ba	c				
Oligoryzomys fulvescens	Ba,Ta,Me	b/c	b/c			
* *Oligorizomys griseolus* (CO)	Ta		b			
* *Oryzomys albigularis* (CO)	Ta		b			
* *Oryzomys meridensis* (CM)	La,Ba,Ta,Me,Tr	b/c	b/c		c	
* *Oryzomys sp* (CM)	Ta	b/c				
Rhipidomys couesi	Ba,Me	b/c				
Rhipidomys fulviventer	Ta		b			
Rhipidomys venezuelae	La,Tr,Me	b/c				
Rhipidomys venustus	La,Tr,Ta,Me	c	b/c			
Sigmodon hispidus	Ba,Tr	b				c
Sigmodontomys alfari	Me	b				
* *Thomasomys aureus* (CO)	Ta		b			
* *Thomasomys hylophilus* (CO)	Ta		b/c			
* *Thomasomys laniger* (WD)	Ta,Me,Tr	b/c	b/c	c	c	c
* *Thomasomys vestitus* (CM)	Me,Tr	b	b/c			
Erethizontidae						
Coendu prehensilis	Ta,Me	c				
Sphiggurus vestitus	Me	b/c	c			
Dinomyidae						
Dinomys branickii	Ta	b				
Dasyproctidae						
Dasyprocta leporina	La,Me	a				
Agoutidae						
Agouti paca	La,Ba	b				
* *Agouti taczanowskii* (WD)	Me,Ta		b/c	c		
Echimyidae						
Proechimys sp.	Ta	b				
* *Olallamys edax* (CM)	Me		b			
LAGOMORPHA (1)						
Leporidae						
Silvilagus brasiliensis	Me			b		

Appendix 2
New mammal records for the Venezuelan Andean Region.

The list includes ORDER, FAMILY, ***Species***, Andean State, locality, elevation and catalogue numbers of the voucher specimens at Colección de Vertebrados de la Universidad de los Andes, Mérida (CVULA) or Museo de la Estación Biológica de Rancho Grande, Maracay (EBRG).

DIDELPHIMORPHIA: DIDELPHIDAE: ***Caluromys philander:*** Mérida: Qda. La Campana, 9 km ENE Sto. Domingo 1500 m (CVULA-I-5652).
XENARTHRA: MYRMECOPHAGIDAE: ***Tamandua mexicana:*** Mérida: Caparú, 3 km SE San Juan de Lagunillas, 900 m (CVULA-I-5760); Táchira: La Quinta, 3 km E Seboruco, 1000 m (CVULA-I-5934, 5935).
MEGALONYCHIDAE: ***Choloepus hoffmanni:*** Táchira: Presa La Honda, 10 km SSE de Pregonero 1100 m (CVULA-I-2448). Mérida: La Chorrera, 3 km E Jají, 2000 m (CVULA-I-4403).
DASYPODIDAE: ***Cabassous centralis:*** Trujillo State: Agua Negra, near Sabaneta, 1357 m (CVULA-I-5765). ***Dasypus novemcinctus***: Mérida: Monte Zerpa 6 km N Mérida, 2000 m (CVULA-I-5635).
CHIROPTERA: NOCTILIONIDAE: ***Noctilio leporinus***: Mérida: La Variante 3 km SSE de Lagunillas, 970 m (CVULA-I-5819-5821).
MORMOOPIDAE: ***Mormoops megalophilla:*** Lara, El Blanquito, P.N. Yacambú, 9 km SE de Sanare, 1600 m (CVULA-I-2721); Mérida: Laguna de Caparú, 3 km SE de San Juan de Lagunillas, 900 m. (CVULA-I-3471).
PHYLLOSTOMIDAE: ***Chrotopterus auritus***: Lara: El Blanquito (P.N. Yacambú), 9 km SE Sanare, 1600 m (EBRG-4184). ***Micronycteris hirsuta:*** Mérida: Santa Cruz de Mora (CVULA-I-). ***Micronycteris microtis***: Mérida: Monterrey, 8 km NNE Mérida, 2400 m (CVULA-I-1351, 1445, 2486). ***Micronycteris minuta***: Lara, El Blanquito, P.N. Yacambú, 9 km SE de Sanare, 1600 m (CVULA-I-2715). ***Phyllostomus discolor:*** Mérida: Laguna de Caparú, 3 km SE de San Juan de Lagunillas, 900 m. (CVULA-I-3478); Carretera Zea-Tovar, 1.5 km SE Zea, 1150 m (CVULA-I-3031-3033). ***Tonatia saurophila***: Mérida: Mérida: El Paramito, 2 km SO Zea, 1000 m (CVULA-I-). ***Carollia castanea***: Mérida: 7.5 km WSW Mesa Bolívar, 800 m (CVULA-I-3396, 3398, 3399). ***Chiroderma salvini***: Mérida: 1.5 km SE Zea, 1150 m (CVULA-I-3171). ***Chiroderma villosum***: Mérida: (CVULA-I-). ***Artibeus glaucus***: Mérida: 1.5 km SE Zea, 1150 m (CVULA-I-3566, 33578, 3583); Trujillo: Finca La Nona, 5 km E Boconó, 2050 m (CVULA-I-3081). ***Artibeus phaeotis*** Mérida: 1.5 km SE Zea, 1150 m (CVULA-I-3561). ***Diphylla ecaudata***: Táchira: Cueva de La Honda, 12 km S Pregonero, 1100 m (CVULA-I-2017).
VESPERTILIONIDAE: ***Myotis albescens***: Mérida: La Variante, 3 km SSE Lagunillas, 970 m (CVULA-I-5818). ***Rhogeessa tumida***: Táchira: La Quinta, 6 km E Seboruco (CVULA-I-5772-5775). MOLOSSIDAE: ***Eumops auripendulus***: Mérida: Laguna de Caparú, 3 km SE San Juan de Lagunillas, 900 m. (CVULA-I-3419). ***Promops centralis***: Mérida: La Pedregosa, Mérida, 1500 m (CVULA-I-3440). ***Molossus bondae***: Táchira: El Haticó, 4 km E Seboruco, 1300 m (CVULA-I-5721, 5722).
PRIMATES: CEBIDAE: ***Cebus olivaceus***: Lara, El Blanquito, P.N. Yacambú, 9 km SE de Sanare, 1700 m (EBRG-15724).
CARNIVORA: CANIDAE: ***Urocyon cinereoargenteus***: Mérida: 1 km W de Mucuchies, 2800 m (CVULA-I-5634). FELIDAE: ***Herpailurus yaguarondi***: Mérida: highway Mérida-Estanques 800 m (CVULA-I-5901).
ARTIODACTYLA: TAYASUIDAE: ***Pecari tajacu***: Lara: Cumbre las Trojas 25 km S Cabudare (EBRG-2281).
RODENTIA: MURIDAE: ***Oecomys* cf. *trinitatis***: Mérida: Cerro Alto, 3 km N La Soledad, 1600 m (CVULA-I-905).