A FUNCTIONAL COMPARISON BETWEEN BAT ASSEMBLAGES OF ANDEAN ARID ENCLAVES

UNA COMPARACIÓN FUNCIONAL ENTRE LOS ENSAMBLAJES DE MURCIÉLAGOS DE LOS ENCLAVES ÁRIDOS ANDINOS

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ABSTRACT

Climatic characteristics and low environmental complexity of tropical xerophitic ecosystems determine the functional structure of bat assemblages, which may be mainly affected by lack of food and shelter in relation to wet environments. Several xerophitic enclaves with similar physiognomy occur along the Andes of northern South America. These similarities suggest that differences in bat composition are due to biogeographic effect, while similarities in functional structure are due to equivalent selective pressures. Data on bat assemblages of these environments is scarce and fragmented. The goal of this work was to gather complete lists of bat species for five inter-Andean xerophitic enclaves and compare both composition and functional structure between them. The five arid Andean enclaves are located along the Cordillera Oriental (Colombia) and Cordillera de Mérida (Venezuela). For comparisons, we also used data from literature for seven additional lists from other continental and insular arid locations of northern Venezuela and the Caribbean. In each location, we caught bats by mist netting monthly or bimonthly during a year to get the composition of each bat assemblage. We used rarefaction curves to determine when species accumulation reached a plateau and the Chao2 and Jackknife2 index to estimate the species richness. For taxonomic and functional comparisons we used clustering analysis of the different arid environments considered and a wet lowland rainforest as an external group, using the distance of dissimilarity of Bray-Curtis and group average linkage method. Although results of both taxonomic and functional analysis were similar showing two main groups of assemblages which can be distinguished by their differences in the importance of nectarivores, frugivores and hematophages guilds, however, functional analysis was much more reliable than taxonomic. Additionally, we detected that when a xerophitic site was in contact with wet environments, "alien species" were included in the assemblage, affecting the taxonomic and functional structures. Thus, when these alien species are not taken into account, the essential assemblage of a tropical xeric environment is composed by insectivorous and nectarivorous bat species.

Keywords: Andes, arid zones, bat assemblages, Neotropics, Colombia, Venezuela.

RESUMEN

Las características climáticas y la baja complejidad ambiental de los ecosistemas xerofíticos neotropicales determinan la estructura funcional de los ensamblajes de murciélagos, los cuales pueden ser principalmente afectados por la carencia de alimento y/o refugio en comparación con los ambientes húmedos. A lo largo de los Andes del Norte de Suramérica se encuentran algunos enclaves áridos, cuya similar fisonomía sugiere que los efectos biogeográficos pueden explicar las diferencias en la composición de sus ensamblajes de murciélagos; igualmente, las equivalentes presiones ambientales podrían explicar sus semejantes estructuras funcionales. Los datos sobre ensamblajes de murciélagos en estos ecosistemas son escasos y fragmentarios, por lo que el propósito de este trabajo fue completar los listados de especies de cinco enclaves áridos inter-andinos y compararlos en cuanto a su composición y estructura funcional. También usamos los listados publicados de siete sitios adicionales del Norte de Venezuela y del Caribe. En cada sitio, realizamos capturas mensuales o bimensuales durante un año, utilizando redes de neblina hasta completar la composición de especies de cada uno de los ensamblajes. Construimos curvas de rarefacción para determinar el plateau de la curva de acumulación de especies y los índices de Chao2 y Jackknife2 para estimar la riqueza de especies. Empleamos el análisis de grupos, con la distancia de Bray-Curtis y el método de unión promedio para las comparaciones taxonómicas y funcionales entre los diferentes sitios considerados, utilizando como grupo externo una localidad de selva húmeda neotropical. Los resultados de los análisis taxonómicos y funcionales fueron similares, al separar dos grupos principales de ensamblajes, por sus diferencias en la importancia de los gremios de nectarívoros, frugívoros y hematófagos. Sin embargo, el análisis funcional fue más preciso que el taxonómico. Adicionalmente, detectamos que cuando un ambiente

xerofítico está en contacto con otro húmedo aparecen especies alóctonas que distorsionan sus estructuras taxonómicas y funcionales. Así, cuando estas especies no son tenidas en cuenta, encontramos que el ensamblaje esencial de un ambiente árido neotropical está compuesto por especies insectívoras y nectarívoras.

Palabras clave: Andes, zonas áridas, murciélagos, ensamblajes, Neotrópico, Colombia, Venezuela.

INTRODUCTION

In the last forty years there has been an increased use of functional groups and guilds to analyze and compare bat assemblages from different tropical localities, which has showed to be a very useful tool in ecological studies (Bonaccorso 1979, Findley 1976, Fleming 1986, Fleming *et al.* 1972, Giannini and Kalko 2004, Graham 1983, Humphrey *et al.* 1983, Kalko 1998, McNab 1971, Smith and Genoways 1974, Soriano 2000, Tamsitt 1967, Willig *et al.* 1993, Wilson 1973). However, the majority of these studies were carried out in forested environments, and the knowledge we have on other less humid environments is very poor. In consequence, much work most be done to complete the information for dry environments.

We think that the structure of bat assemblages is the result of environmental pressures, and it is possible to determine certain common structural features in assemblages being subjected to similar environmental pressures (Soriano 2000). Therefore, climatic characteristics and low environmental complexity of the tropical xerophitic ecosystems determine the functional structure of bat assemblages, which may be mainly affected by lack of food and shelter in relation to wetter environments (Kelt *et al.* 1996). Along the Andes of northern South America several xerophitic enclaves occur, which are geographically isolated, and show similar physiognomy (Ruiz *et al.* 2002, Sarmiento 1976, Soriano and Ruiz 2003). Previous studies carried out in some of them showed very close functional similarities between their bat assemblages (Cadena *et al.* 1998, Ruiz 1995, Sosa 1991). These similarities allow us to postulate that differences in bat composition might be due to historic and biogeographic effects, while similarities in functional structure are due to equivalent selective pressures (Soriano 2000).

Although data on bat composition of tropical arid environments is still scarce and fragmented, especially in the inter-Andean xerophitic enclaves, the goal of this work was to gather complete list of bat species for these environments, compare their composition and functional structure in order to test the hypotheses above. Likewise, for these functional comparisons, we will contrast the approach proposed by Soriano (2000) with that carried out by Smith and Genoways (1974).

METHODS

Study areas

Fieldwork was carried out in three Andean enclaves of Venezuela and Colombia (Figure 1): i) La Puerta, restricted to the mountain hillsides of the middle Motatán river basin between Trujillo and Mérida state, Venezuela (1000-1800 m); ii) La Quinta, located between the confluence of the La Grita and Del Valle rivers, near the town of Seboruco, Táchira state, Venezuela (800-1300 m); and iii) Cúcuta-Ureña, shared by both countries in Norte de Santander department (Colombia) and Táchira state (Venezuela), respectively (400-1000 m). Additionally, we took into account available data from other two Andean enclaves (Ruiz 1995, Sosa 1991): iv) Lagunillas, located at the middle of the Chama river basin, and higher Nuestra Señora river basin, in Mérida state, Venezuela (500-1800 m); and v) La Tatacoa, at the high Magdalena river valley, between Tolima and Huila departments of Colombia (500-1000 m).

Vegetation in these arid enclaves changes due to a moisture gradient, and different community sub-types occur along this gradient, from very arid to wetter zones (premontane thorn shrub and tropical dry forest, respectively, *sensu* Holdridge (Espinal and Montenegro 1977, Ewel *et al.* 1976). This has also been described as part of the ecological unit called "thorn scrub", in which the main common arboreal species belong to Mimosaceae and Cactaceae (*Prosopis*, *Acacia*, and *Pilosocereus*, *Stenocereus* and *Cereus* (= *Subpilocereus*), respectively; Ataroff and Sarmiento 2003, 2004, Rico *et al.* 1996, Ruiz *et al.* 2002). Most of these enclaves show signs of anthropic disturbance, such as extensive sugar cane cultivation and grazing by cows and goats. Average annual precipitation of these Andean arid enclaves oscillates between 400
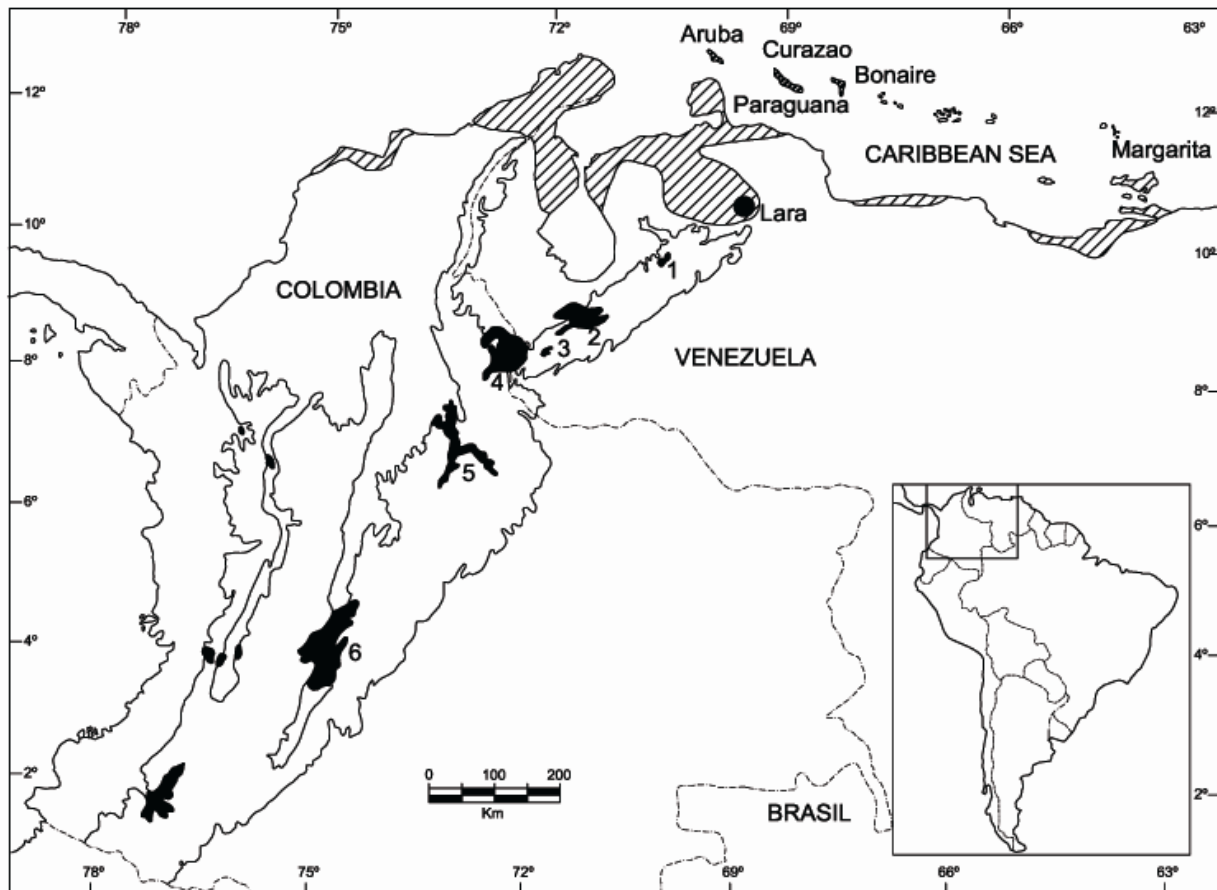
Figure 1. Geographic distribution of xerophitic enclaves along the Andes of Northern South America. Numbers indicate the Andean sites considered in this study: 1 = La Puerta, 2 = Lagunillas, 3 = La Quinta, 4 = Cúcuta-Ureña, 5 = Chicamocha and 6 = La Tatacoa.

and 800 mm, distributed in a bimodal pattern. Depending on elevation of locality, annual average temperatures ranged between 23-30°C, showing an isothermal pattern (Ataroff and Sarmiento 2003, 2004).

Fieldwork

During one year, we carried out a monthly capture program at Lagunillas (1990-1991) and Tatacoa (1993-1994); and a bimonthly capture program at La Quinta (1998-1999), Cúcuta-Ureña (1998-1999) and La Puerta (2004-2005). On each occasion, four to six mist nets were set up between 0.5 and 3 m high on dark nights, from 1800 to 0100 h, in all sites. Mist nests were placed near the ground in the thorn shrub vegetation, and checked every 20-30 min. Total capture efforts for locality ranged between 270-1159 net-hours. All captured

bats were identified and released. We also took some voucher specimens of all species captured from each location and housed them at Colección de Vertebrados de la Universidad de Los Andes, Mérida-Venezuela (CVULA) or Instituto de Ciencias de la Universidad Nacional, Bogotá-Colombia (ICN).

Species richness

For each locality we assumed that species lists were complete once the curves of cumulative number of species as a function of effort (night of mist-netting) reached a plateau. We then computed the expected rarefaction curve and its standard deviation from species presence-absence data (sampling without replacement using the EstimateS 7.5 program; Colwell 2005). We also calculated the expected species richness using non-parametric

estimates such as Chao2 and Jackknife2 (Colwell and Coddington 1994). Data from museum records and literature were used to complete the definitive list of each locality.

Taxonomical and functional comparisons

In order to compare our data with those from other Andean and non-Andean arid localities, the following procedure was carried out: 1) We selected the most complete species lists available, published by different authors from eight additional arid locations in northern South America and close islands (Bisbal 1983, 1990, Cadena *et al.* 1998, Husson 1960, Smith and Rivero 1991). 2) We unified the taxonomic nomenclature according to that used by Simmons (2005) and recent literature. 3) We determined the functional structure of each assemblage following the criteria used by Soriano (2000): *i*) assigning a *Trophic Value* (*TV*) to each species, as a fraction of the unity, according to values used by Wilson (1973), the information of diet synthesized by Gardner (1977), and our personal observations for different trophic habits (see Appendix 1; in Table 2 these data are summarized); *ii*) *Trophic Equivalents* (*TE*) values were calculated for the different categories in each assemblage, as the sum of *TV* in each functional category. 4) Two similarity analyses were carried out: *i*) Taxonomic similarity between each pair of localities was calculated using the Sørensen qualitative coefficient (Magurran 1988): $Cs = 2j / (a+b)$, where *j* is the number of species shared by both local assemblages, *a* is the number of species at the locality A, and *b* is the number of species at the locality B. *ii*) Functional similarity was calculated using the quantitative coefficient of Sørensen: $Cpq = 2jN /(a+b)$, where *jN* is the sum of the lowest value of trophic equivalents (*TE*) by functional category between both local assemblages and *a* and *b* are the number of species for each local assemblage. With the aim of determining both taxonomic and functional affinities among selected dry localities, we carried out a cluster analysis using, respectively, the taxonomic and functional distance matrix (Bray-Curtis) data by means of group average linkage, included in the program PC-ORD, version 4.0 (McCune and Mefford 1999). In the cluster analysis of functional data we used data for the humid locality of Imataca as an external group (Soriano 2000). We also analyzed our data using the methodology employed by Smith and Genoways (1974), in which the

Importance Value as a percentage of the species number of each functional category is taken into account.

RESULTS

Species richness

In all selected localities both curves of cumulative number of species as a function of effort, as well as expected rarefaction curves, reached a plateau (Figure 2), whereas sampling efforts were different between localities (Table 1). Number of species ranged between 12 and 23 according to locality (Table 1, Appendix 1). Although the predicted values of mean Jackknife2 and Chao2 estimators ranged above our data; in all cases except in Lagunillas, our empirical data were placed in the lower limit of the confidence intervals (Table 1). In the case of Lagunillas, eight additional species were captured outside the study, and when these were taken into account the species list reached the predicted value of both estimators. In Cúcuta-Ureña, variation coefficient (CV) was >0.5; therefore we employed the Incidence-based Coverage Estimate (ICE; Lee and Chao 1994) as an additional estimator, which was above our empirical value. Data of total number of species and abundance are summarized in Appendix 1. Localities can be divided into three richness categories: i) Lagunillas and La Tatacoa, which shown to be the richest (27 and 23 species, respectively; see Appendix 1), ii) Margarita, Lara, La Puerta, La Quinta, and Cúcuta-Ureña (ranging between 17-12 spp.); and iii) Curazao, Paraguaná, Bonaire and Aruba are the poorest (ranging between 8-4 spp.). The bat assemblages in each locality considered were composed of representatives of the families Emballonuridae, Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Vespertilionidae and Molossidae; with representatives of 52 species, of which 48 were present in our captures (Appendix 1). Representatives of the Furipteridae and Thyropteridae families were absent from these environments.

Functional structure

Assemblage of species showed that in these arid environments trophic structure was mainly composed of insectivorous, frugivorous, and nectarivorous bats (Table 2). In contrast with the wet site (Imataca), these arid localities showed: i) an almost total absence of carnivores and
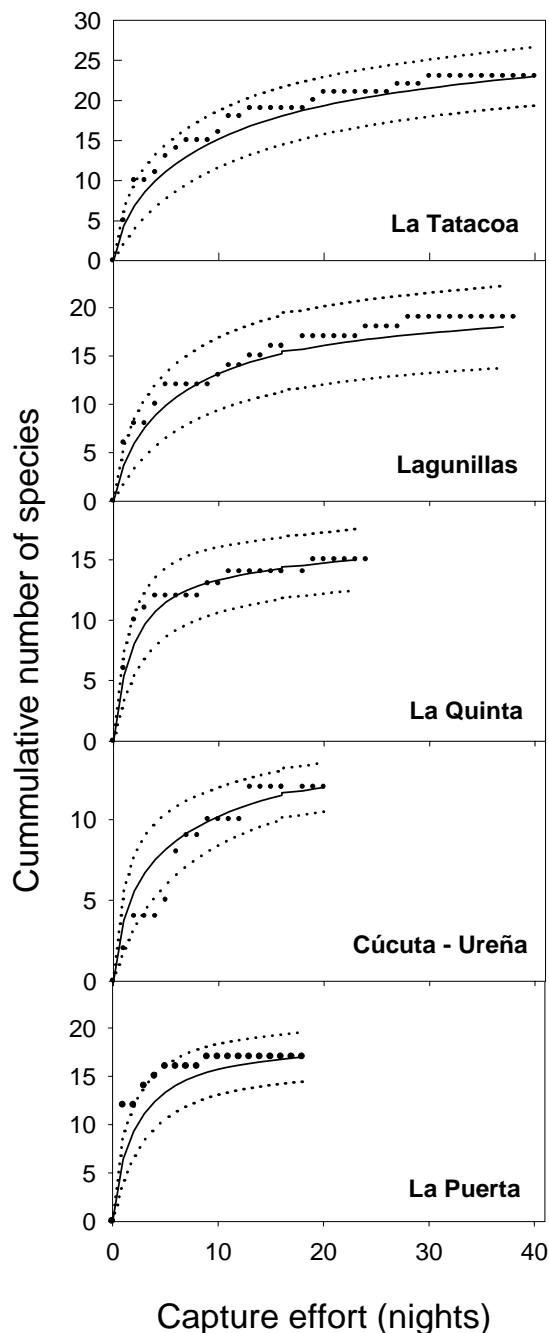
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Figure 2. Species accumulation curves describing the number of species for a given capture effort in the five arid Andean enclaves studied. Solid lines represent the mean of species for 100 randomizations of the sample pooling order. Dotted lines represent 95 % confidence intervals. The empirical species richness in each assemblage was not significantly different than Chao2 and Jackknife2 estimators (Table 1).

piscivores; likewise, it can be observed that vampires are absent in Paraguaná and the Antillean islands (Aruba, Curazao and Bonaire), and iii) an important reduction in the frugivore, insectivore and nectarivore component. However, if we consider the importance value (IV, *sensu* Smith and Genoways 1974) of functional categories for each locality, these can be divided into three groups (Figure 3). The first group composed of the most simple functional structures, in which the insectivore component acquires the higher relative values (up 75%; Figure 3a); followed by four localities in which frugivory reach the highest of IV (Figure 3b). Finally, a group as in the wet locality, which has representatives in almost all functional categories, reflected in the most equitable distribution of the IV values (Figure 3c).

Taxonomic and functional clustering

The taxonomic cluster analysis showed that the first dichotomy was the one separating the group of Aruba, Curazao, Bonaire and Paraguaná, from the other conformed of all the Andean enclaves, including Margarita, Lara and the external group (Figure 4a). If we consider the last cluster defined at 50% similarity, three subgroups appear: i) Imataca (external group), followed by ii) La Puerta, La Quinta, Lagunillas, Chicamocha, Margarita island, La Tatacoa, and iii) Cúcuta-Ureña and Lara.

In the functional cluster analysis the first dichotomy separates the external group (Imataca) from all the arid localities. Among these two main clusters were defined at 50% similarity: one composed of Aruba, Curazao, Bonaire and Paraguaná, and the other including Margarita, Lara and all the Andean enclaves (Figure 4b).

DISCUSSION

Species richness and taxonomic comparison

One general feature in all these arid environments is the lower species richness compared to wet localities (Appendix 1). This decrease in bat species richness can be understood as the consequence of the concomitant effect of both insularity and restrictive climatic conditions. However, all the localities considered did not behave in the same way; we observed that this effect seemed to be less strong in Andean enclaves than on Caribbean islands such as Aruba, Curazao and Bonaire, which showed the poorest species list (Appendix 1). We obtained contradictory results

Table 1. Empirical data and predicted values of species richness in the selected localities

Localities	Total effort (net per nights)	Observed species (S_{obs})	Captures N° ind	Chao2	Jackknife2	ICE
La Puerta	18	17	366	17.5 (17.0-24.8)	19.83	
Lagunillas	38	19 (+8)	566	21.92 (19.4-40.0)	25.76	
La Quinta	24	15	438	15.48 (15.0-22.9)	17.87	
Cucuta-Ureña	20	12	161	12.67 (12.1-19.8)	13.14	13.65
La Tatacoa	40	23	518	25.44 (23.4-38.6)	29.9	

for the Paraguaná peninsula, whose species list is as short and similar in composition as any Caribbean island considered (Appendix 1). For this reason Paraguaná appears classified with these islands in the same cluster of the taxonomic analysis linked with 80% of similarity (Figure 4a). In contrast, Margarita Island showed a longer bat species list, and therefore it was classified with other continental localities, such as Lara and Andean enclaves, in the taxonomic cluster analysis (Figure 4a).

If we consider the non-connectivity among Andean, Caribbean, and continental arid localities as a criterion of insularity, we could expect that species richness was a function of the surface of each locality (MacArthur and Wilson 1967).

However, these richness patterns were not correlated with the size of each arid zone (r^2 = 0.003; $p > 0.05$; $n = 12$). The surface of the Paraguaná peninsula is almost eight times larger than Curazao (the largest of the Caribbean islands considered), but they have similar species richness; while Margarita Island is almost three times smaller than Paraguaná, and its species richness is three times higher, which is very similar to Lara and some Andean enclaves (Appendix 1). The Paraguaná peninsula is joined to the continent by a very narrow (~1km) 40 km long sandy isthmus (Figure 1) whose vegetation is almost absent, and environmental conditions are very hard; therefore, this peninsula could be considered as an island in practice (Soriano
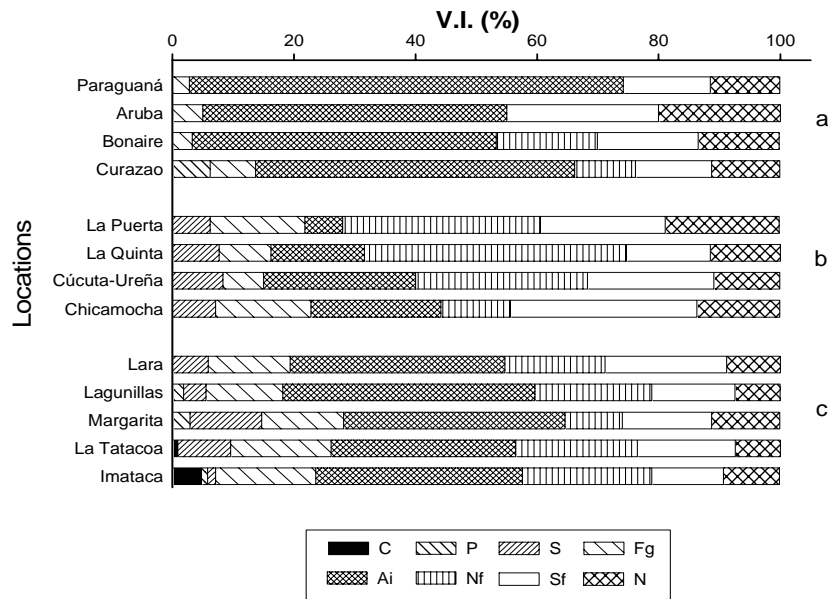

Figure 3. Importance Values (IV) in percentage for each site considered, using trophic values (*sensu* Smith and Genoways 1974). Abbreviations: C = Carnivores, P = Piscivores, S = Sanguivores, Fg = Foliage gleaners insectivores, Ai = Aerial insectivores, Nf = Nomadics frugivores, Sf = Sedentaries frugivores, N = Nectarivores.

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Table 2. Trophic Equivalents by functional category of bat assemblages in arid environments from Colombia, Venezuela and some neighboring Caribbean islands.

Locations	C	P	S	Fg	Ai	Nf	Sf	N	No. spp.
La Tatacoa [a]	0.2	0.0	2.0	3.8	7.0	4.6	3.7	1.7	23
Chicamocha [b]	0.0	0.0	1.0	2.2	3.0	1.6	4.3	1.9	14
Cúcuta-Ureña [c]	0.0	0.0	1.0	0.8	3.0	3.4	2.5	1.3	12
La Quinta [c]	0.0	0.0	1.0	1.4	2.0	7.2	2.2	2.2	16
Lagunillas [d]	0.0	0.5	1.0	3.4	11.2	5.2	3.7	2.0	27
La Puerta [c]	0.0	0.0	1.0	2.5	2.0	5.2	3.3	3.0	17
Lara [e]	0.0	0.0	1.0	2.3	6.0	2.8	3.4	1.5	17
Paraguaná [f]	0.0	0.0	0.0	0.2	5.0	0.0	1.0	0.8	7
Aruba [g]	0.0	0.0	0.0	0.2	2.0	0.0	1.0	0.8	4
Curazao [g]	0.0	0.5	0.0	0.6	4.2	0.8	1.0	0.9	8
Bonaire [g]	0.0	0.0	0.0	0.2	3.0	1.0	1.0	0.8	6
Margarita [h]	0.0	0.5	2.0	2.3	6.2	1.6	2.5	1.9	17
Imataca [i]	3.8	0.8	1.0	12.9	26.5	16.6	9.2	7.2	78

Abbreviations: C = Carnivores, P = Piscivores, S = Sanguivores, Fg = Foliage gleaners insectivores, Ai = Aerial insectivores, Nf = Nomadics frugivores, Sf = Sedentaries frugivores, N = Nectarivores.
The original list come from: [a] Ruiz (1995), [b] Cadena *et al*. (1998), [c] this study, [d] Sosa (1991), [e] Smith and Rivero (1991), [f] Bisbal (1990), [g] Husson (1960), [h] Bisbal (1983), [i] Soriano (2000).

and Ruiz 2003). In addition, Paraguaná shares the same kind of vegetation as Aruba, Curazao and Bonaire composed of an extended thorn shrub, without riparian or humid formations, because there are no permanent fresh water bodies (Husson 1960). This similar habitat complexity could be the explanation of the lowest species richness showed by these localities.

In contrast, cluster analysis showed that Andean and some continental sites have higher species richness and a greater similarity with wet environments (Imataca) than with Caribbean islands and Paraguaná (Figure 4a). We think that this is due to the proximity of humid forest which surrounds these arid sites, with representatives of the genera *Anoura, Carollia, Sturnira, Uroderma*, *Platyrrhinus, Artibeus,* and *Desmodus* amongst others, which are resident species in wet environments. These can occasionally use the food resources in these arid environments (Cadena *et al.* 1998, Ruiz *et al.* 1997, Sosa and Soriano 1993, Soriano *et al*. 2000), but their roosting sites are in the wet environments; and therefore have been

detected in the inventories as shared species in both humid and arid sites (Similarity = 23%).

Trophic structure and functional comparisons

All arid localities analyzed are structured by assemblages in which insectivores, nectarivores and frugivores seem to be the only shared guilds (Figure 3). By contrast in wet environments the absence or strong reduction of functional categories such as carnivores, piscivores, hematophages, foliage insectivores and frugivores seems to be a general feature of these arid sites (Table 2, Figure 3). Such trophic simplification could be the result of a combination of several factors such as environmental constraints, lack of roosting sites and lack of feeding resources. However, we suggest that values recorded for the aerial insectivore category could be greater if we considered that representatives of the family Molossidae could be under-recorded due to bias of the capture techniques employed. Likewise, we consider that for Lara and Andean localities, the contribution to the frugivorous guild made by

representatives of the subfamily Stenoderminae could be over-recorded due to the proximity of riparian forests that connect an arid locality with more humid environments. In addition, the sanguivore guild is absent from Paraguaná and all Caribbean islands except Margarita island. In Lara and Andean enclaves the presence of goats seems to favors large populations of vampire bats (PJS pers. obs.); however in Paraguaná and the Caribbean islands vampires are absents, even when this feeding resource is very abundant. Therefore, we think that such absence could be the consequence of more restrictive environmental conditions in these arid localities.

In contrast with taxonomic cluster, in our results from the functional cluster analysis (Figure 4b) Imataca was separated as an external group, as expected, and this allowed us to recognize two main groups of assemblages from arid environments, which can be distinguished by their differences in the importance of nectarivore frugivore and hematophage guilds (Figure 3, Table 2). We consider it to be very important that in the Caribbean islands and Paraguaná the frugivorous guild is mainly conformed of the Glossophaginae bats *Glossophaga longirostris* and *Leptonycteris curasoae*, which also belong to the nectarivorous guild, and therefore, each one partially contributes to the frugivorous guild (Appendix 1). When there are no humid formations near arid environments strict frugivores seem to be absent or their presence to be very rare (e.g. Curazao). Although the results of taxonomic and functional approaches were very similar (Figure 4), functional analysis seems to show a better resolution in the clustering than in the taxonomic analysis. We think that in this particular case the proximity of the Caribbean islands to each other may explain that similarity among species lists was also very high. Likewise, historic factors such the Pleistocene joins between Andean enclaves with the northern coastal of Colombia and Venezuela (Hernández *et al.* 1992) allow us to explain the taxonomic similarities.

If these arid environments are so similar in vegetal structure, plant composition, and climatic characteristics, the following question arises: what are the causes of functional structure differences among these bat assemblages? We also saw that the presence of some species in the arid localities could be the result of proximity of humid environments; however, how can we distinguish between alien and true native species? We could probably answer these questions
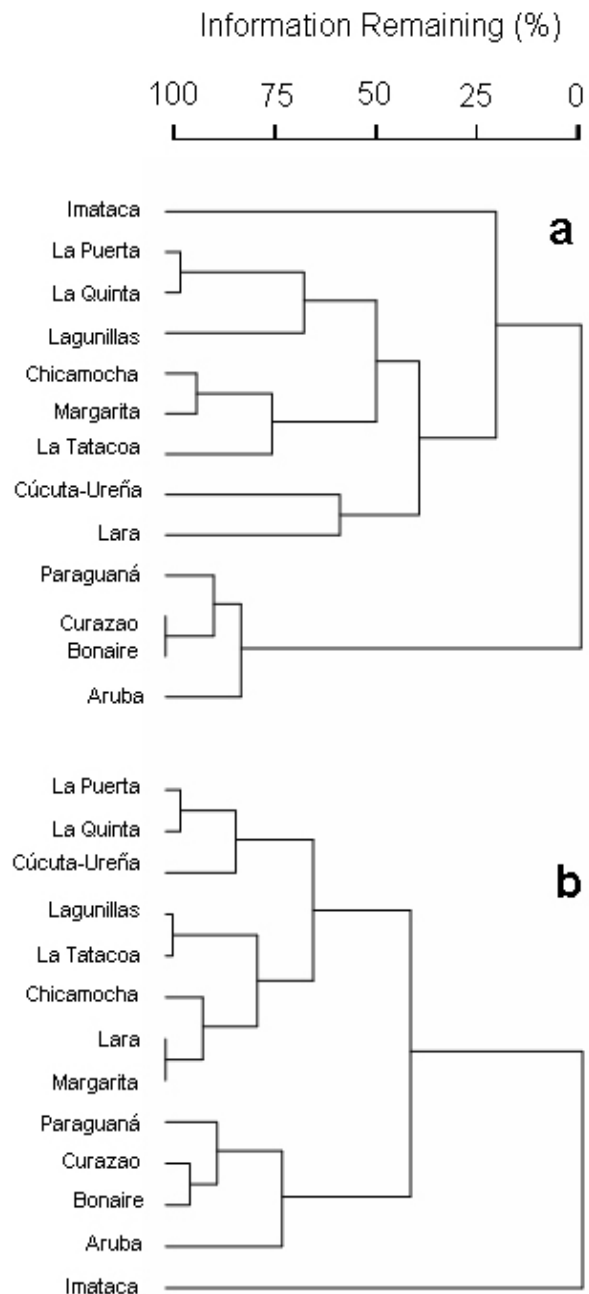

Figure 4. Clustering analysis of different arid environments and a wet lowland rainforest as an external group (Distance of dissimilarity of Bray-Curtis and Group average Linkage method): a) Taxonomic comparison and b) Functional comparison.

if we knew: which is the basic or elemental trophic structure of a bat assemblage from a given tropical xerophitic environment.

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When the locality of Paraguaná (Venezuela) is used as a typical representative of an arid environment isolated from wet sites, it can be seen that the bat assemblage is composed mainly of insectivorous and nectarivorous species, and the frugivorous category does not have strict frugivores (i.e. species with trophic value = 1), which means that it is composed of species belonging mainly to the nectarivorous category (subfamily Glossophaginae). Thus, in Paraguaná and the Caribbean islands representatives of the frugivorous guild are mainly nectarivore species which also include fruits in their diet, such as the species *Glossophaga longirostris* and *Leptonycteris curasoae* (Martino *et al.* 2002, Petit 1997, Ruiz *et al.* 1997, Sosa and Soriano 1993, Soriano *et al.* 1991). By contrast, in Andean enclaves and some continental arid zones, such as La Tatacoa, Chicamocha, Cúcuta-Ureña, La Quinta, Lagunillas, La Puerta, Lara and Margarita island, in addition to these species these areas occupied or visited by "alien species" from the neighboring wet habitats. These may include strict frugivores (such as representatives of the genera *Sturnira*, *Artibeus*, *Carollia*, *Uroderma*, amongst others) and representatives of the other functional categories, (e.g. *Micronycteris, Tonatia, Phyllostomus,* and *Anour*a) which are typical of wet environments, as is shown by a locality found in the Amazon region (at Imataca, Venezuela) in Figure 3b. Therefore, our results support the hypotheses proposed by Soriano (2000) and also suggest that in comparison to wet environments, the basic or essential structure of a tropical arid environment bat assemblage has the following distinctive features: i) a relatively larges component of insectivorous species, ii) a relatively depleted frugivore component, and iii) a higher relative importance of nectarivorous species, which incidentally, are the most important fruit consumers due to their mutualistic relationships with the columnar cacti.

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LITERATURE CITED

ATAROFF, M. and L. SARMIENTO 2003. Diversidad en Los Andes de Venezuela. 1. Mapa de unidades ecológicas del estado Mérida. Instituto de Ciencias Ambientales y Ecológicas (ICAE), Universidad de Los Andes, Mérida, Venezuela.

ATAROFF, M. and L. SARMIENTO. 2004. Las Unidades Ecológicas de los Andes de Venezuela. Pp. 9-26, *in* E. La Marca and P.J. Soriano (eds): Reptiles de los Andes de Venezuela. Fundación Polar, Conservación Internacional, CODEPRE-ULA, Fundacite Mérida, BIOGEOS, Mérida, Venezuela.

BISBAL, F.J. 1983. Inventario preliminar de fauna de la Isla de Margarita. Ministerio del Ambiente y de los Recursos Naturales Renovables Serie Informe Técnico DGSIIA/IT/138.

BISBAL, F.J. 1990. Inventario preliminar de la fauna del Cerro Santa Ana, Península de Paraguaná, Estado Falcón, Venezuela. Acta Científica Venezolana 41:177-185.

BONACCORSO, F.J. 1979. Foraging and reproductive ecology in a Panamanian bat community. Bulletin of the Florida State Museum, Biological Sciences 24:359-408.

CADENA, A., J. ALVAREZ, F. SÁNCHEZ, C. ARIZA and A. ALBESIANO. 1998. Dieta de los murciélagos frugívoros en la zona árida del río Chicamocha (Santander, Colombia). Boletín de la Sociedad Biológica de Concepción, Chile 69:47-53.

COLWELL, R.K. 2005. EstimateS. Statistical estimation of species richness and shared species from samples. University of Connecticut, Storrs, USA.

COLWELL, R.K. and J.A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophic Transactions of the Royal Society of London, B Biological Sciences 345:101-118.

ESPINAL, L.S. and F. MONTENEGRO. 1977. Zonas de vida o formaciones vegetales de Colombia. Memoria explicativa sobre el mapa ecológico. Zonas de vida o formaciones vegetales de Colombia. Memoria explicativa sobre el mapa ecológico. Instituto Geográfico Agustín Codazzi, IGAC, Bogotá, Colombia.

EWEL, J.J., A. MADRIZ and J. TOSI. 1976. Zonas de vida de Venezuela. Memoria explicativa sobre el mapa ecológico. Zonas de vida de Venezuela. Memoria explicativa sobre el mapa ecológico. 2nd. MAC-FONAIAP, Caracas-Venezuela.

FINDLEY, J.S. 1976. The structure of bat communities. The American Naturalist 110:129-139.

FLEMING, T.H. 1986. The structure of Neotropical bat communities: a preliminary analysis. Revista Chilena

de Historia Natural 59:135-150.

FLEMING, T.H., E.T. HOOPER AND D.E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles, and movements. Ecology 53:555-569.

GARDNER, A.L. 1977. Feeding habits. Pp. 293-350, *in* R.J. Baker, J.K. Jones y D.C. Carter (eds.): Biology of bats of the new world family phyllostomatidae. Part II. Special publications the Museum Texas Tech University. No 13, Texas.

GRAHAM, G.L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. Journal of Mammalogy 64:559-571.

HERNÁNDEZ, J., T. WALSCHBURGER, R. ORTIZ and A. HURTADO. 1992. Origen y distribución de la biota suramericana y colombiana. Pp. 55-104, *in* G. Halffter (ed.): La diversidad biológica de Iberoamérica. Volumen especial de Acta Zoológica Mexicana, CYTED-D, Xalapa.

HUMPHREY, S.R., F.J. BONACCORSO and T.L. ZINN. 1983. Guild structure of surface-gleaning bats in Panama. Ecology 64:284-294.

HUSSON, A.M. 1960. De zoolgdieren van de Nederlandse Antillen. De zoolgdieren van de Nederlandse Antillen. Natuurwetenschappelijke Werkgroep Nederlandse Antillen., Curaçao.

KALKO, E.K.V. 1998. Organization and diversity of tropical bat communities through space and time. Zoology 101:281-297.

KELT, D.A., J.H. BROWN, E.J. HESKE, P.A. MARQUET, S.R. MORTON, J.R.W. REID, K.A. ROGOVIN and G. SHENBROT. 1996. Community structure of desert small mammals: comparisons accross four continents. Ecology 77:746-761.

LEE, S.M. and A. CHAO. 1994. Estimating population size via sample coverage for closed capture-recapture models. Biometrics 50:88-97.

MACARTHUR, R.H. and E.O. WILSON. 1967. The theory of island biogeography. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

MAGURRAN, A.E. 1988. Ecological diversity and its measurement. Ecological diversity and its measurement. Cambridge University Press, Cambridge, Great Britain.

MARTINO, A.M.G., J.O. ARANGUREN and A. ARENDS. 2002. Feeding habits of *Leptonycteris curasoae* in northern venezuela. The South Western Naturalist 47:78-85.

MCCUNE, B. and M.J. MEFFORD 1999. PC-ORD. Multivariate analysis of ecological data. Version 4, Gleneden Beach: MjM Software Design.

MCNAB, B.K. 1971. The structure of tropical bat faunas. Ecology 52:352-358.

PETIT, S. 1997. The diet and reproductive schedules of *Leptonycteris curasoae* and *Glassophaga longirostris elongata* (Chiroptera: Glossophaginae) on Curaçao. Biotropica 29:214-223.

RICO, R., L.E. RODRÍGUEZ, R. PÉREZ and A. VALERO. 1996. Mapa y análisis de la vegetación xerófila de las lagunas de Caparú, cuenca media del río Chama, Estado Mérida. Plantula 1(1):83-94.

RUIZ, A. 1995. Ecología del murciélago *Glossophaga longirostris* (Phyllostomidae) y su interrelación con las cactáceas columnares en la zona árida de La Tatacoa, Huila. Thesis Licenciado en Biología. Facultad de Ciencias, Universidad de Los Andes, Bogotá D.C.

RUIZ, A., J. CAVELIER, M. SANTOS and P.J. SORIANO. 2002. Cacti in the dry formations of Colombia. Pp. 324-341, *in* T.H. Fleming and A. Valiente-Banuet (eds.): Columnar cacti and their mutualists: evolution, ecology, and conservation. Arizona University Press, Tucson.

RUIZ, A., M. SANTOS, P. SORIANO, J. CAVELIER and A. CADENA. 1997. Relaciones mutualísticas entre el murciélago *Glossophaga longirostris* y las cactáceas columnares en la zona árida de La Tatacoa, Colombia. Biotropica 29:469-479.

SARMIENTO, G. 1976. Evolution of arid vegetation in Tropical America. Pp. 65-99, *in* D.W. Goodall (ed.): Evolution of Desert Biota. Univ. of Texas Press, Austin.

SIMMONS, N.B. 2005. Order Chiroptera. Pp: 312-529, *in*: Wilson D.E., Reeder D.M. (eds) Mammals Species of the World: A taxonomic and geographic reference, 3ra edn. Johns Hopkins University Press, Baltimore, Maryland, USA.

SMITH, J.D. and H.H. GENOWAYS. 1974. Bats of Margarita Island, Venezuela, with zoogeographic comments. Bulletin of the Southern California Academy of Sciences 73:64-79.

SMITH, R.F. and A. RIVERO. 1991. Los recursos ecológicos de la zona árida de los alrededores de Barquisimeto. Pp. 69-119, *in* R.F. Smith, A. Rivero, F. Ortega and J.A. Catalá (eds.): Ecología del Estado Lara. Biollania, Edición Especial No. 1, Guanare, Edo. Portuguesa, Venezuela.

SORIANO, P.J. 2000. Functional structure of bat communities in tropical rainforest and andean cloud forest. Ecotrópicos 13:1-20.

SORIANO, P.J. and A. RUIZ. 2003. Arbustales Xertofíticos. Pp. 696-715, *in* M. Aguilera, A. Azócar and E. González-Giménez (eds.): Biodiversidad en Venezuela. Fundación Polar, Ministerio de Ciencia y Tecnología, Fondo Nacional de Ciencia y Tecnología (FONACIT), Caracas.

SORIANO, P., A. RUIZ and J.M. NASSAR. 2000. Notas sobre la distribución e importancia ecológica de los murciélagos *Leptonycteris curasoae* y *Glossophaga longirostris* en zonas áridas andinas. Ecotrópicos 13(2):91-95.

SORIANO, P.J., M. SOSA and O. ROSSELL. 1991. Hábitos alimentarios de *Glossophaga longirostris* Miller (Chiroptera: Phyllostomidae) en una zona árida de los Andes venezolanos. Revista de Biología Tropical 39:267-272.

SOSA, M. 1991. Relaciones ecológicas entre el murciélago *Glossophaga longirostris* y las cactáceas columnares en el bolsón árido de Lagunillas, Mérida, Venezuela. Thesis Licenciado en Biología, Universidad de Los Andes, Mérida.

SOSA, M.and P. SORIANO. 1993. Solapamiento de dieta entre *Leptonycteris curasoae* y *Glossophaga longirostris* (Mammalia: Chiroptera). Revista de Biología Tropical 41:529-532.

TAMSITT, J.R. 1967. Niche and species diversity in neotropical bats. Nature 213:784-786.

WILLIG, M.R., G.R. CAMILO and S.J. NOBLE. 1993. Dietary overlap in frugivorous and insectivorous bats from edaphic cerrado habitats of Brazil. Journal of Mammalogy 74:117-128.

WILSON, D.E. 1973. Bats faunas: a trophic comparison. Systematic Zoology 22:14-29.

APPENDIX 1. Bat species that integrated all list used in the analysis. Numbers in columns represent the trophic values (TV) of each species by guild: C = Carnivores, P = Piscivores, S = Sanguivores, Fg = Foliage gleaners insectivores, Ai = Aerial insectivores, Nf = Nomadics frugivores, Sf = Sedentaries frugivores, N = Nectarivores. Locations represented by number a: 1 = La Puerta, Venezuela; 2 = Lagunillas, Venezuela; 3 = La Quinta, Venezuela; 4 = Cúcuta-Ureña, Colombia and Venezuela; 5 = Chicamocha, Colombia; 6 = La Tatacoa, Colombia; 7 = Lara, Venezuela; 8 = Paraguaná, Venezuela; 9 = Aruba, Netherlands; 10 = Curazao, Netherlands; 11 = Bonaire, Netherlands; 12 = Margarita, Venezuela.

Species by Family	Guilds								Locations											
	C	P	S	Fg	Ai	Nf	Sf	N	1	2	3	4	5	6	7	8	9	10	11	12
Enballonuridae																				
Saccopteryx bilineata					1									X						
Saccopteryx leptura					1															X
Peropterix macrotis					1								X			X				X
Noctilionidae																				
Noctilio leporinus		0.5		0.3	0.2					X								X		X
Mormoopidae																				
Pteronotus parnelli					1									X		X				X
Pteronotus davyi					1										X	X				
Pteronotus gymnonotus					1								X							
Mormoops megalophylla					1					X						X	X	X	X	X
Phyllostomidae																				
Micronycteris megalotis				0.8			0.2			X			X	X						X
Micronycteris microtis				0.8			0.2								X					
Micronycteris schmidtorum				0.8			0.2								X					
Tonatia saurophila				0.8			0.2							X						
Lophostoma silvicolum				0.8			0.2							X						
Phyllostomus discolor				0.4			0.3	0.3	X	X	X		X	X						X
Phyllostomus hastatus	0.2			0.3			0.3	0.2						X						
Glossophaga longirostris				0.1			0.5	0.4		X			X	X	X	X	X	X	X	X
Glossophaga soricina				0.2			0.2	0.6	X		X	X	X	X	X					X
Anoura geoffroyi				0.1			0.4	0.5	X	X	X									
Choeroniscus goodmani				0.1			0.1	0.8	X											
Leptonycteris curasoae				0.1			0.5	0.4	X	X	X	X	X		X	X	X	X	X	X
Carollia brevicauda				0.2			0.8						X							
Carollia perspicillata				0.2			0.8		X	X	X	X	X	X	X					X
Sturnira lilium							1		X	X		X	X	X	X					
Uroderma bilobatum						1				X	X			X	X					
Uroderma magnirostrum						1			X			X		X						
Platyrrhinus helleri						1				X	X									

APPENDIX 1. Continued.

Species by Family	C	P	S	Fg	Ai	Nf	Sf	N	1	2	3	4	5	6	7	8	9	10	11	12
Platyrrhinus umbratus						1			X											
Platyrrhinus vittatus						1				X										
Vampyressa melissa						1								X						
Mesophilla macconnelli						1				X										
Artibeus amplus				0.1		0.8		0.1				X								
Artibeus hartii				0.1		0.8		0.1	X	X	X									
Artibeus jamaicensis				0.1		0.8		0.1	X	X	X	X	X		X			X		X
Artibeus lituratus				0.1		0.8		0.1	X	X	X	X	X	X						X
Artibeus glaucus				0.1		0.8		0.1	X	X	X			X						
Ametrida centurio						1													X	
Sphaeronycteris toxophillum						1									X					
Desmodus rotundus			1						X	X	X	X	X	X	X					X
Desmodus youngi			1											X						X
Natalidae																				
Natalus tumidirostris					1										X	X		X		
Vespertilionidae																				
Histiotus montanus			1						X	X										
Lasiurus blossevillii					1					X			X							
Lasiurus cinereus					1					X										
Rhogeessa io					1				X		X		X	X						
Rhogeessa minutilla					1					X					X					X
Eptesicus furinalis					1									X						
Eptesicus fuscus					1				X											
Myotis albescens					1					X										
Myotis keaysi					1					X										
Myotis nesopolus					1										X			X	X	
Myotis nigricans					1					X				X						
Myotis sp.					1							X								
Molossidae																				
Molossops temminckii					1									X						
Eumops auripendulus					1					X										
Eumops glaucinus					1					X					X					
Eumops perotis					1					X										
Molossus currentium					1						X									
Molossus molossus					1					X		X		X	X	X		X	X	X
Total number of species by locations									17	27	16	12	14	23	17	7	4	8	6	17