ACKNOWLEDGMENTS

Foremost, I thank my major professor, Dr. Michael Willig, for his continual support, encouragement, criticism, and enthusiasm. Mike provided many and varied opportunities for me to grow as a researcher, thinker, educator, and person; hopefully those opportunities were not wasted. Under his guidance I have become a well-rounded scientist, critical thinker, proficient writer, and capable statistician.

I am indebted to my committee, Drs. Don Gettinger, Mark McGinley, Daryl Moorhead, Robert Owen, and Richard Strauss. Each has contributed significantly to my growth as a scientist and this dissertation would be lacking if not for their collective guidance. I also thank many faculty members of Texas Tech University, who have provided guidance and enriched my doctoral experience, including Drs. Ray Jackson, Kent Rylander, Michael San Francisco, Charlie Werth, Gene Wilde, and John Zak. I thank Dr. Michael Dini for helping to develop my skills as an instructor.

Many fellow graduate students made my time at Texas Tech enjoyable and productive. Stephen Cox was influential in my early development as a doctoral student; we had many discussions over a well-packed bowl that broadened my outlook of the world and biology. Christopher Bloch has been an invaluable office mate during the course of the analysis and writing of my dissertation, being a patient listener and sounding board for my ideas. In addition, I am indebted to Richard Stevens, Celia López-González, Carl Dick, Joel Brant, Chris Higgins, P. Marcos Gorreson, Ed Sobek, Michael Cramer, Kate Lyons, Michelle Secrest, Diane Hall, Brian Croyle, Javier Alvarez, Jeff Roberts, Don Yee, Carla Guthrie, and Kelly Johnson for their friendship, guidance, and support during various epochs of my doctoral studies. I am indebted to Jacy Lewis for her love, support, and encouragement during a critical time when I had abandoned my studies and may not have returned if not for her insistence; thank you.

This research generously was supported by grants from the National Science Foundation (NSF) to R. D. Owen and M. R. Willig entitled “Paraguayan Mammals and Their Ectoparasites: an Intensive Survey in a Temperate-Subtropical Interface” (DEB-

9400926, DEB-9741543, DEB-9741134). The Office of the Vice-President for Research and Graduate Studies and Office of Research Services at Texas Tech University (D. Schmidly and R. Sweazy) provided substantial financial support during the course of the project. Additional support was provided by the Texas Tech University Graduate School (Summer Research Awards), Department of Biological Sciences (Summer Research Awards and teaching assistantships), and the American Association of Mammalogists (Grant-in-Aid of Research Awards). The Ministério de Agricultura y Ganadería provided significant financial and logistic support. Personnel of the Museo National de Historia Natural del Paraguay and the Convention for International Trade of Endangered Species of Paraguay provided continual encouragement, support, and cooperation, especially noteworthy was the diversity of support that was graciously provided by A. L. Aquino. The Dirección de Parques Nacionales y Vida Silvestre also contributed significantly to the success of the project. The Department of Biological Sciences (J. Burns, M. San Francisco) and the Museum (R. Baker, R. Monk) of Texas Tech University, the Fundación Moises Bertoni (R. Gauto, A. Van Humbeeck), and the Universidad Católica Nuestra Señora de la Asunción (J. Usher) also provided assistance. For access to their land and provision of accommodations while in the field, I especially thank the many owners and administrators of estancias that we visited, personnel of Yaguareté Forests (P. Mueller) and Refugio Faunístico Atingy (M. Cubas), and especially the Fuerzas Armadas de la Republica del Paraguay. For assistance in the field or with logistic arrangements, I thank Heidi Amarilla, Sylvia Frutos, Steven Mezik, Margarita Mieres, and Guillermo Terol. For their dedication to the project and conscientious efforts in the field, I am extremely grateful to Ismael “Pajarito” Mora and Francisco “Mbaracayá” Pintos. I also owe a very large debt of gratitude to Lucy Aquino and her family for making my time in Paraguay as enriching and rewarding personally as it was professionally.

Lastly, I need to thank my family for their love, patience and understanding during the seemingly interminable time required to finish “my paper.” In particular, I thank my mother and father for their sacrifice and insistence that I go to college; hopefully, they feel their sacrifice was rewarded sufficiently.

TABLE OF CONTENTS

APPENDICES

LIST OF TABLES

LIST OF FIGURES

CHAPTER I
INTRODUCTION

Community ecology fundamentally addresses two interrelated questions: (1) what determines the number of species in a community, and (2) what processes are responsible for the identity of those species (Strong et al. 1984). Community may be defined broadly as "a collection of species occurring in the same place at the same time" (Fauth et al. 1996). Accordingly, assemblages are "phylogenetically related groups within a community" (Fauth et al. 1996). Ecological and evolutionary determinants (e.g., competition, productivity) and the availability of species (i.e., species pool) combine to determine the number, identity, and relative abundances of species that occur in a community or assemblage. Collectively, these characteristics define community structure. Indeed, structure implies that patterns of species coexistence depart from patterns derived from stochastic processes, such as those produced by null models (Poulin 1997). However, mechanisms that structure communities may operate at several scales of time and space. In addition, patterns at one scale may be a result of mechanisms operating at a different scale (Pickett et al. 1994). Therefore, it is often necessary to look for patterns at local and regional scales, as well as in ecological and evolutionary time, to understand which mechanisms determine community structure.

Systematics, ecology, and paleontology must be integrated in biogeographic studies that endeavor to define patterns and identify causal mechanisms at regional, continental, or global scales. Biogeographic processes per se may not exist; however, large scale geoclimatic (e.g., tectonic plate movements, changes in sea level, climate, and oceanic circulation), evolutionary (e.g., adaptation, speciation, extinction), and ecological (e.g., predation, competition) processes operate in concert to produce biogeographic patterns. Indeed, dispersal, the geographic translocation of individuals, may be the only truly biogeographic process (Myers and Giller 1988).

The equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) is a mechanistic theory which provides a framework within which ecological

processes, biogeographical patterns, and paleontological data are merged in a synthetic manner (Myers and Giller 1988). Islands possess many tractable qualities that make them attractive research foci. An island is less complex than a continent or ocean, and is visibly discreet so that resident populations may be distinguished more easily. In addition, by their abundance, as well as variation in shape, size, degree of isolation, and ecology, islands provide the replication necessary to conduct natural or non-manipulative experiments. The equilibrium theory of island biogeography (ETIB) predicts that larger islands maintain greater species richness than do smaller islands, and that islands more distant from a source area support fewer species than do islands closer to a source area (MacArthur and Wilson 1963, 1967). Distance affects richness primarily by molding immigration rates, whereas area affects richness primarily by molding extinction rates.

The ETIB makes predictions about species richness and turnover, but predicts nothing about relative species abundances. Nonetheless, qualitative predictions about species compositions on islands are possible based on evolutionary theory. Low primary diversity on islands (i.e., species diversity due to immigration) promotes in situ diversification, with more isolated islands evincing larger adaptive radiations. Whether intra-island or inter-island speciation is more important depends on dispersal ability of taxa and opportunities for isolation from parent populations (Paulay 1994). Compared to continents, small areas and increased isolation of islands result in relatively small populations, which make island species especially vulnerable to local extinction. Consequently, islands provide biotas with opportunities for larger radiations and more frequent in situ diversification than occur on mainlands, while simultaneously exposing island species to greater risk of extinction. Understanding of patterns of species richness has benefited from application of ETIB to island systems including habitat patches, lakes, caves, mountaintops, and host-parasite systems. The application of ETIB to host-ectoparasite systems seemed natural it ectoparasitologists because two of the primary factors that determine ectoparasite diversity are host body size and distance to a source of infestation, which are analogous to island size and distance to a source population (Dritschilo et al. 1975, Kuris et al. 1980).

Arthropod ectoparasites infest most vertebrate species. Because each host individual harbors an assemblage of ectoparasites, these systems provide opportunities to use non-manipulative experiments to study factors that structure assemblages (or communities). Hosts are habitat patches (i.e., islands) to their ectoparasites. In addition host individuals differ in size and age, and are members of populations and communities that vary in density, behavior, social organization, and phylogenetic affinity. Because variation in host traits are analogous to that observed on islands or across landscapes, ectoparasite assemblages provide opportunities to understand phenomena that are difficult to study at larger scales.

Host phylogeny, body size, and morphology interact to determine patterns of coexistence as well as the geographic distributions of arthropod ectoparasites (Freeland 1983, Gettinger and Ernest 1995). The close association of arthropod ectoparasites, most of which are obligate parasites, with their mammalian hosts often leads to specialization and host specificity. Host-specific adaptations often prevent ectoparasite species from successfully infesting alternate host species. In addition, chiropteran biology provides mechanisms that allow bats to serve as isolated evolutionary units (i.e., islands), such that their ectoparasite assemblages follow distinct evolutionary trajectories.

A multi-faceted approach is required to understand comprehensively factors that contribute to the structure of arthropod ectoparasite assemblages on bats. Therefore, I investigated assemblages at multiple taxonomic levels from the perspective of both host and ectoparasite species. First, I quantitatively describe the arthropod assemblages on bats of Paraguay, present patterns of host specificity, and investigate resource partitioning and species abundance distributions of ectoparasite assemblages for common species of bats (Chapter II). Second, I assess the importance of host body size on ectoparasite biodiversity (e.g. abundance, richness, and diversity) within the context of ETIB (Chapter III). Third, I assess the effect of host abundance on ectoparasite biodiversity within the context of ETIB (Chapter IV). I conclude with a synthesis concerning the effect of host traits on ectoparasite assemblages, and discuss ramifications for studies of biogeography and landscape ecology.

Literature Cited

Dritschilo, W., H. Cornell, D. Nafus, and B. O'Connor. 1975. Of mice and mites. Science 190:467-469.

Fauth, J. E., J. Bernardo, M. Camara, W. J. Resetarits, Jr., J. Van Buskirk, and S. A. McCollum. 1996. Simplifying the jargon of community ecology: a conceptual approach. The American Naturalist 147:282-286.

Freeland, W. J. 1983. Parasites and the coexistence of animal host species. The American Naturalist 121:223-236.

Gettinger, D., and K. A. Ernest. 1995. Small-mammal community structure and the specificity of ectoparasite associations in central Brazil. Revista Brasiliera de Biologia 55:331-341.

Kuris, A. M., A. R. Blaustein, and J. J. Alió. 1980. Hosts as islands. The American Naturalist 116:570-586.

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

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

Myers, A. A., and P. S. Giller. 1988. Process, pattern and scale in biogeography. Pp 3-21, in Analytical biogeography: an integrated approach to the study of animal and plant distributions (A. A. Myers and P. S. Giller eds.). Chapman and Hall, New York, New York.

Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. American Zoologist 34:134-144.

Pickett, S. T. A., J. Kolasa, and C. G. Jones. 1994. Integration in ecology. Pp. 3-25, in Ecological understanding: the nature of theory and the theory of nature. Academic Press, New York, New York.

Poulin, R. 1997. Species richness of parasite assemblages: evolution and patterns. Annual Review of Ecology and Systematics 28:341-358.

Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.). 1984. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, New York.

CHAPTER II
NATURAL HISTORY OF ARTHROPODS ECTOPARASITIC ON THE BATS OF PARAGUAY

Introduction

Bats and Their Ectoparasites as Model Systems

Assemblages of arthropod ectoparasites on bats provide an exemplary system for assessing the effects of ecological and evolutionary mechanisms on patterns of species richness, community structure, and diversity. Host phylogeny, body size, and morphology interact to determine patterns of coexistence as well as the geographic distributions of arthropod ectoparasites (Freeland 1983, Gettinger and Ernest 1995). Ectoparasites evince different levels of host specificity, the tendency of parasites to be restricted to particular host species (Margolis et al. 1982), and may be monoxenous (inhabit a single host species), oligoxenous (inhabit $\geq$ 2 host species of the same genus), pleioxenous (inhabit $\geq$ 2 genera in the same subfamily), or polyxenous (inhabit hosts from different subfamilies). Specificity may be related to ecological factors associated with host individuals (e.g., physical isolation, climatic restriction, host predation), evolutionary factors associated with host lineages (e.g., morphological or physiological adaptations), or interspecific competition among ectoparasites. The degree to which these factors influence host specificity is affected by the life history characteristics of ectoparasites (i.e., ectoparasites that rarely leave the host are more susceptible to factors leading to specificity; Wenzel and Tipton 1966*b*).

When species of a host assemblage (e.g., a bat assemblage) evince little niche overlap, opportunities for exchange of ectoparasites among host species are rare, predisposing host-specific ectoparasitic assemblages. In contrast, the opportunity for ectoparasite exchange is greater in species-rich host communities that comprise species that share resources and microhabitats, especially those associated with roosts. This selects against species-specific ectoparasitic assemblages (Gettinger and Ernest 1995). In

addition, high host species richness and likely elevated numbers of host individuals may result in a more species-rich ectoparasite assemblage because of an increase in resources.

Four generalizations can be made about ectoparasites that infest communities of similar host species (Freeland 1983). First, most parasite species successfully parasitize relatively few of the potential host species. Second, the more common parasites of one host species are usually not the more common parasites of other host species. Third, different host species do not harbor the same sets of parasite species. Finally, species of parasites that are shared by different host species usually do not infest them at similar frequencies.

Differences in body size, morphology, and feeding behavior among coexisting host species may be responsible for determining which of the available parasites a host is likely to acquire in nature (Freeland 1983). Although, closely related hosts may be susceptible to invasion by similar parasites, only host species that are adapted to cope with parasitic infestation survive. Therefore, when alternate host species invade a community, they may be infested and killed by parasites contracted from established hosts that serve as transmission vectors but are not affected as negatively by the parasites. Thus, parasite assemblages may structure host communities by precluding syntopy (Freeland 1983, Gaston 1996). In addition, observational data on ectoparasites of New World molossids (i.e., host species with polyctenids harbor no nycteribiids or streblids, and nycteribiids and streblids do not occur on the same host individual) suggest that competition may structure ectoparasite communities (Marshall 1982*a*, Wenzel and Tipton 1966*b*). Many catalogs and taxonomic works exist concerning New World bat ectoparasites, especially for the family Streblidae (e.g., Guerrero 1993, 1994*a*, 1994*b*, 1995*a*, 1995*b*, 1996, 1997, Wenzel 1976, Wenzel and Tipton 1966*b*). However, ecological aspects of these communities largely have been ignored, in part because most studies of ectoparasites are born of opportunity and not of design. Generally, biologists make ectoparasite collections as an ancillary consequence of studying a vertebrate host. This results in haphazard collections of ectoparasites from already dead specimens, increasing the chance of contamination and inaccurate assignment of host-parasite

associations. Such ectoparasite collections may be biased and are far from comprehensive (Marshall 1982, Wenzel and Tipton 1966*a*).

Study Area and Bat Fauna

Paraguay is a small country (406,752 km^2), approximately the size of the state of California, located in the heart of South America, where it is transected by the Tropic of Capricorn (Figure 2.1). It occurs at an interface of temperate and subtropical climates, and comprises a diverse suite of biomes, ranging from mesic (e.g., Atlantic Rainforest, Pantanal) to xeric (e.g., Chaco) habitats. Topography is relatively flat and low-lying, especially in the west (Bertoni and Gorham 1973, Fariña Sanchez 1973, Gorham 1973). Based on floral and geographic features, the country includes seven phytogeographic regions or biomes (Table 2.1): Matogrosense, Alto Chaco, Bajo Chaco, Ñeembucú, Campos Cerrados, Central Paraguay, and Alto Paraná (Hayes 1995, Willig et al. 2000). Much of the country, especially areas to the east of the Río Paraguay, has experienced extensive deforestation and fragmentation (Unruh 1973, Gorresen and Willig 2004), especially in the last two decades, and is dominated by agricultural landscapes (Gorresen and Willig 2004, Universidad Nacional de Asunción 1994).

Vegetative Setting. Three biomes compose the Chaco of western Paraguay (Figure 2.1). The Matogrosense biome is characterized by medium height (10 - 20 m) trees and sub-humid forests with dense undergrowth (e.g., bromeliads). It often is inundated, not only as a result of local rainfall, but more generally as a consequence of rains in the Brazilian Pantanal, which drain into the Río Paraguay. The Alto Chaco biome constitutes more than half of western Paraguay and despite its flat topography, is seldom inundated because rainfall is low and edaphic features facilitate water percolation. It is semi-arid and dominated by relatively short (5 - 10 m), dense, xerophytic thorn-scrub forest with a well-developed understory (terrestrial bromeliads and arborescent cacti). The Bajo Chaco biome comprises extensive palm savannas interdigitating with medium height (8 - 15 m), xerophytic, scrub forest on slightly elevated terrain. Corridors of taller (10 - 20 m), sub-humid, riparian forest parallel a series of meandering rivers and

intermittent streams that flow slowly eastward to the Río Paraguay. Extensive marshlands dominate areas adjacent to the riparian zones and the entire area is inundated seasonally for many months.

Eastern Paraguay comprises four biomes (Figure 2.1) that are the most topographically heterogeneous and humid regions of the country. The Campos Cerrados biome is a savanna formation characterized by a mosaic of dense forests, xerophytic woodlands (8 - 20 m), and grasslands. The topography is gently rolling, with the highlands supporting sub-humid forests (20 - 50m), and areas to the west containing patches of xerophytic forest, sub-humid forest, and palm savanna reminiscent of adjacent Chaco formations. The Central Paraguay biome is ecologically the most heterogeneous biome in Paraguay. In the west, along the Río Paraguay, it contains marshes, palm savannas, and patches of low humid deciduous forest, with more hilly terrain to the east supporting taller humid forests that are now fragmented as a consequence of timber management practices. Rivers in this biome are sluggish, bordered by marshes, and drain to the Río Paraguay. The Alto Paraná biome is characterized by rolling hills that are deeply cut by fast-flowing tributaries of the Río Paraná. Although historically dominated by tall (> 25 m), humid, deciduous forests, the region has been subject to severe deforestation and extensive flooding as a result of large and permanent impoundments (e.g., Represa de Itaipú). Nonetheless, several areas (e.g., Parque Nacional San Rafael, Estancia Rivas, Estancia Golondrina – Figure 1, Table A.1) have been protected and are relatively undisturbed. The Ñeembucú biome is dominated by extensive, seasonally inundated, wetlands associated with the confluence of the Río Paraguay and Río Paraná, and grasslands in flat, low terrain with slow moving rivers. Palm savannas typical of the Chaco and patches of low (8 - 15 m), sub-humid, Chaco-like forest are interspersed with formations more typical of eastern Paraguay. This biome represents a transition between the Chaco to the west and the taller humid forests of the eastern biomes (Hueck 1972).

Host Assemblage. Fifty-four species of bat are known from Paraguay (López-González 1998, 2005, Willig et al. 2000) representing six families and a diverse suite of feeding guilds including frugivores, insectivores, nectarivores, piscivores, and

sanguinivores (Table 2.2). This diversity of foraging strategies, combined with specific roost requirements of many species, effectively isolates many host species from each other, ostensibly facilitating host-specific ectoparasite assemblages. In addition, bats belonging to different guilds may be isolated geographically; insectivores are dominant in xeric regions and frugivores in mesic regions (Willig et al. 2000).

Ectoparasite Assemblage. In the New World, five families of insects are ectoparasitic on bats (Marshall 1982*a*), and most (four) are exclusively associated with bats (Table 2.3). Similarly, ten of 13 families of mites found on New World bats are exclusive to bats (Webb and Loomis 1977). Despite the cosmopolitan nature of many ectoparasite families, most species occur on a single host species or genus (Kim 1985, Marshall 1982*a*, Wenzel and Tipton 1966*a*).

The evolution of phylogenetically old and morphologically well-adapted groups of permanent ectoparasites occurred in parallel with that of their host (Dusbábek 1969*a*). Although these evolutionary processes (e.g., speciation, extinction, natural selection) should produce distinctive patterns of organization in parasite communities on mammals (Kim 1985), most work on ectoparasites remains focused on the description of species, taxonomy, and systematics, nearly always focusing on the ectoparasites themselves while referring to hosts only briefly. Recently, investigators have begun to examine patterns of ectoparasite assemblages on rodents (Gettinger and Ernest 1995) or bats (Gannon and Willig 1995) in attempts to investigate the role of host species and environmental factors in structuring these assemblages. The high diversity of bats and their ectoparasites in Paraguay, where tropical and temperate species reach their southern and northern termini, respectively, make this an ideal system to study ecological and evolutionary effects of isolation on ectoparasite assemblages.

Ectoparasite Natural History – Insecta

Insects ectoparasitic on bats spend their entire lives on the bodies or in the roosts of their hosts (Marshall 1982*a*). Because most bat species are tropical, most bat ectoparasites live in relatively amenable environments. These ectoparasitic insects range

in size from 1 - 27 mm and are flattened, either laterally or dorso-ventrally, so they can move easily through dense pelage or press themselves close to the body of their hosts. In addition, they are equipped with numerous setae and powerful claws that reduce abrasive damage, aid in locomotion, and help to maintain a firm grip on hosts (Marshall 1982*a*). Moreover, ectoparasites have behavioral adaptations that reduce the chance of dislodgement and ensure that they pass most of their lives in sites with low risk of mortality. All stages of insects that are parasitic on bats feed solely on host blood, with the exception of larval fleas that live in host guano. Survivorship without a meal for adult flies is < 30 hours and for larva is < 7 hours. Adult fleas can survive up to four days without food. Reproduction may occur year-round in all insects with reduced rates on hibernating hosts in temperate regions. Host grooming activity is a major cause of mortality in permanent ectoparasitic insects (Marshall 1982*a*). If hosts are ineffective at grooming due to poor health or deformities, ectoparasite populations can increase quickly (Marshall 1982*a*). Such high populations rarely cause poor host health, but are consequences of it (Marshall 1982*a*).

Streblidae and Nycteribiidae. Streblids and nycteribiids have three nymphal instars within the adult female, pupae are deposited in the roost, and adults live almost entirely on the host (Marshall 1982*a*). Bat flies undergo adrenotrophic vivaparity (i.e., the complete larval life cycle occurs within the female uterus). Females leave the host to deposit the 3rd instar, in the roost away from the immediate vicinity of the host so as to protect it from host-induced mortality (Marshall 1982*a*). Increases in ambient temperature, which typically occur during the day, likely trigger instar deposition. Streblid reproductive rates are thought to be lower than those of nycteribiids, which produce an offspring every nine days with a maximum of 16 per female. Adults feed as soon as they find a host and thereafter every few hours. Newly emerged adults live up to three days without a first meal, but flies that already have fed usually die in < 1 day. These flies move well by walking, jumping, or flying short distances, and thus do not require direct body contact for host transfer. Their life cycle is about one month in duration, allowing up to 12 generations per year, as these insects are largely tropical.

Adult nycteribiids range in size from 1.5 – 5.0 mm in length. Generally, streblids infest phyllostomids or noctilionids, whereas nycteribiids infest vespertilionids (Marshall 1982*a*).

Polyctenidae. These bat bugs are viviparous with three nymphal instars; adults always reside on the host. Reproductive rates are thought to be considerably lower than those of nycteribiids. Polyctenids may reach sexual maturity and mate before molting to the adult stage (Hagan 1951). They require blood meals every few hours, only inhabit colonial hosts that roost in caves or tree holes, and require body contact to transfer from host to host. In addition, polyctenids never have been found off the host body and appear incapable of locomotion elsewhere (Marshall 1971, 1982*a*, 1982*b*). In the New World, polyctenids are restricted to molossids and emballonurids (Marshall 1982*a*).

Ischnopsyllidae. Fleas are oviparous with three larval instars; pupae live in the roost and adults reside on the host (Marshall 1982*a*). Unlike other oviparous insects parasitic on bats, which deposit eggs in the host's roost, fleas deposit eggs haphazardly, most falling to the ground where they hatch and larvae develop. Ischnopsyllid reproductive rates are not available; however, based on the biology of other fleas, they probably lay many eggs per day and hundreds in a lifetime. Adults take a blood meal as soon as they find a host and then once every few hours. Whereas 94% of the 2000 plus species of known fleas parasitize mammals, only 5% of these are known from bats. Moreover, bat fleas are seldom common or abundant on host individuals. The reliance of immature flea stages on a stable host home (e.g., rodent or bird nests) may account for their relatively low rates of occurrence on bats, which may change roost location more frequently than do other hosts. Generally, fleas are found on molossids and vespertilionids (Marshall 1982*a*).

Ectoparasite Natural History – Acarina

Arachnids (i.e., mites and ticks) ectoparasitic on bats may spend their entire lives on the bodies of their hosts, as in the Spinturnicidae (Rudnick 1960) and Macronyssidae (Radovsky 1966), or may feed once and drop off of the host, as in the Argasidae (Oliver

1989), with the potential to spend each stage of their life cycle on a different host species. Unlike ectoparasitic insects, which are all obligate parasites throughout their life cycle and are highly host-specific, arachnids may be parasitic during only a single stage in their life cycle (e.g., Trombiculidae) or a single individual may parasitize animals of different classes (e.g., Argasidae). Ectoparasitic arachnids that occur on bats range in size from 150 microns to over 3 mm, and are usually dorso-ventrally flattened so they can move easily through dense pelage, adhere to patagia, or press themselves close to the host's body. In addition, they are equipped with numerous setae and powerful claws that reduce abrasive damage, aid in locomotion, and help maintain a firm grip on the host. Some mites die within a couple of days of removal from the host, whereas ticks may survive over four years without feeding.

Spinturnicidae. Spinturnicids are exclusively parasitic on bats and inhabit the wing and tail membranes (Rudnick 1960). These mites have strong legs with immovable coxae and are dorso-ventrally flattened to facilitate adherence to smooth hairless patagia. In addition, they adhere to and move over wing and tail membranes equally well, whether their dorsal or ventral side is against the host. They locomote poorly when not on patagia and die within two days of removal from the host. The life cycle of spinturnicids is reduced greatly, with the egg and larval stages occurring within an adult female, which gives birth directly to the protonymph. All independent life stages (protonymph, deutonymph, and adult) feed on blood and possibly lymphatic fluids. Mormoopids, phyllostomids, and vespertilionids are the primary hosts for New World spinturnicids (Rudnick 1960, Herrin and Tipton 1975).

Macronyssidae. Macronyssids parasitize bats, marsupials, rodents, and birds, and are known vectors of murine typhus, rickettsial pox, equine encephalitis, and coxsackie virus disease, which they may transmit to humans (Saunders 1975). The Macronyssidae likely evolved from the Laelapidae, which commonly parasitize rodents and birds, and have been documented on Old World bats (Radovsky 1966). Macronyssids have undergone a number of adaptive radiations, including the early times of Neotropical bat diversification. This likely led to several endemic genera on the Phyllostomoidea (e.g.,

Parichoronyssus, *Radfordiella*, *Macronyssoides* – Saunders 1975). A second radiation involved the invasion of the ornithonyssines from the north and gave rise to *Chiroptonyssus*, which infest molossids.

Engorged females produce single unembryonated eggs and lay them in the host's roost (Radovsky 1967). Larvae hatch and molt into protonymphs without feeding. Protonymphs must find a host and obtain a blood meal. After engorging, they leave the host, pass through a quiescent period, and molt into deutonymphs, which are inactive and do not feed before molting into adults (Radovsky 1967). Adults may mate soon after the last molt; females engorge greatly, whereas males take smaller meals and change little in size. Non-engorged adults are 500 - 600 microns; engorged females reach up to 1,200 microns. In addition to several families of bats (e.g., Emballonuridae, Nycteridae, Noctilionidae, Phyllostomidae, Vespertilionidae, Molossidae), in the New World macronyssids occur on reptiles, birds, marsupials, and rodents (Radovsky 1967, Saunders 1975).

Argasidae. Argasids (soft ticks) comprise about 170 species belonging to four genera, with *Ornithodoros* (100 species) and *Argas* (56 species) being most common (Crampton et al. 1996, Oliver 1989). The general argasid life cycle includes egg, larva, 2 - 8 (usually 3 - 4) nymphal instars, and the adult male and female.

Like all ticks, argasids are obligate sanguinivores. Individuals of each developmental stage usually ingest a single blood meal before molting. Adults feed several times and produce a group of eggs or sperm after each feeding. Nymphal and adult argasids feed rapidly, usually requiring only 30 minutes to a few hours, whereas larvae may require as long as ten days to engorge (Oliver 1989). Among the species that have slow feeding larvae are those ticks that infest birds and bats. The same individual may serve as host for successive developmental stages, but this probably occurs rarely. In general, ticks are opportunistic and a single species can feed on hosts belonging to different classes. Nonetheless, ticks show rhythms of feeding and drop-off that coincide with periods of rest or sleep in the host (Oliver 1989). In laboratory colonies, 70-80% of *Ornithodoros concanensis* survived four years without a meal (Oliver 1989). After

feeding, argasids typically do not use all of the blood meal for gamete production, but rather store some as a reserve. This facilitates survival for great lengths of time (i.e., many years). In addition, such behavior permits argasids to act as reservoirs of infectious diseases (Hoskins 1991). In nature, most argasid species produce one generation per year. Argasids do not mate on the host.

Many argasids are habitat specialists, living in protected areas such as caves, rock crevices, burrows, or hollow trees. Consequently, they feed on animals that rest in those locales. Indeed, 55 species of soft ticks are classified as strict bat parasites (Oliver 1989). These ticks are strongly and negatively phototactic and geotrophic, with the exception of females during oviposition periods, which last from a few days to several weeks, depending on species and environmental conditions, especially temperature. Argasids do not produce thousands of eggs as do most ixodid ticks; rather, they produce fewer, larger eggs. In addition, some argasids make considerable parental investments. For example, some argasids that parasitize bats brood eggs. Moreover, *Argas boueti* transport newly hatched larvae to roosting bats for feeding (Hoogstrall 1985). Argasids express a more "k-selective strategy" (*sensu* Pianka 1970) than do ixodid ticks, perhaps in part because they infest hosts that are more difficult for immature stages of ticks to locate.

Trombiculidae. Chiggers are a diverse group with the larvae of over 3000 species described between 1929 and 1977 (Brennan and Goff 1977). Only 10% of these larvae have been associated with adult stages. The larval stage of trombiculids is the only parasitic stage of chiggers, infesting many groups of vertebrates; post larval stages are free-living sediment dwellers (Baker et al. 1956). Developmental stages include egg, deutovum, larva, nymphochrysalis, nymph, imagochrysalis, and adult. Larvae, which are 150 - 300 microns long, crawl on the soil until they find a suitable host, to which they attach and feed on lymph and skin tissues. Blood is not important to trombiculids. Larvae feed once; engorgement takes three days. When a larva is replete, it detaches, enters the soil, becomes quiescent, and forms a nymphochrysalis (Baker et al. 1956). A 600 - 1,000 micron nymph emerges and preys on eggs and instars of other arthropods. When fully fed, the nymph become quiescent and forms an imagochrysalis. An adult

mite emerges, which resembles the nymph but is much larger, sexually mature and more hirsute. Adults have diets similar to those of nymphs. The entire life cycle takes 2 - 12 months, with 1 - 3 generations per year in temperate zones and up to six generations in tropical areas. Trombiculids are opportunistic parasites infesting reptiles, birds, and mammals (Reed and Brennan 1975).

Chirodiscidae. Most of the chirodiscids only infest bats and belong to the subfamily Labidocarpinae, which contains at least 15 genera and 70 species (Fain 1982*a*, 1982*b*; McDaniel 1970). Little has been published about chirodiscid biology; therefore most of the details about their life history remain uncertain. Chirodiscids have a nymphal reproductive form with rudimentary legs, which is fertilized by an adult male (Pinichpongse 1963*a*). This fertilized individual molts into an 8-legged unchitinized female, which must molt 1 - 2 more times to achieve maturity. A larval stage passes within mature females, which give birth to 6-legged larvae that molt into either 8-legged chitinized females or males (McDaniel 1970). These larvae mature after 1 more molt. The origin of the copulatory nymphal female is unknown. These mites have limited locomotion because their 1st and 2nd pairs of legs are modified for grasping and maintain firm holds at the base of host hair, where chirodiscids feed on sebaceous secretions (Pinichpongse 1963*a*).

Myobiidae. Twenty-two genera of myobiids comprise hundreds of species that infest bats (Dusbábek 1969*b*, Uchikawa 1988). Females attach eggs to the pelage of the host, however larvae and adults attach to the skin of the host (Lukoschus et al. 1981). Myobiids have two larval stages, each with three pairs of legs; a protonymph, with a rudimentary 4^{th} pair of legs; a deutonymph, with four pairs of legs; and the adult stage, which has genitalia. Myobiids feed on blood of the host, and transfer of individuals from one host to another probably requires direct body contact (Baker et al. 1956). With few exceptions, each genus of myobiid mite is restricted to a single family or subfamily of host (Uchikawa1988). Myobiids infest the Marsupialia, Insectivora, Rodentia, and Chiroptera. Among New World bats, myobiids occur on emballonurids, mormoopids, phyllostomids, and vespertilionids (Dusbábek 1960, 1969).

Materials and Methods

Field Methods

Mammals and their associated ectoparasites were collected from July 1995 to June 1997, and again from July to August in 1998, as part of an investigation entitled "Paraguayan Mammals and Their Ectoparasites: an Intensive Survey in a Temperate-Subtropical Interface." Bats were surveyed at 28 sites (Table A.1), representing all major biomes, including many protected areas, and spanning gradients of moisture and temperature in Paraguay (Figure 2.1). Because of the potential importance of the Río Paraguay as a biogeographic barrier (Myers 1982), approximately one-half of the sites were on each side (east or west) of the river. In general, mist nets were erected in all habitats at a site and were monitored for captures from dusk until 0100 h. Much of the time, nets were monitored until dawn. Rates of capture for bats in the field depend on a variety of factors including net characteristics (e.g., mesh size, length, condition, placement, configuration), temporal factors (e.g., length of time, particular hours of the night, period in the lunar cycle – Gannon and Willig 1997), local weather conditions (especially with respect to temperature and precipitation), and history (i.e., number of consecutive nights at a site – Simmons and Voss 1998). Captured bats were sacrificed and prepared as standard museum specimens. Specific bat identification was initiated in the field but verified by C. López-González after comparison with systematic reference materials (López-González 1998, 2005). The systematic recommendations of López-González (1998, 2005) were followed for bat taxa in Paraguay. Ectoparasites were collected from most host specimens. However, if more than 50 individuals of a host species were collected at a site, nearly all subsequent individuals were released without examination for ectoparasites. Half of the bat collection was deposited at the Museum of Texas Tech University (TTU) and half at the Museo Nacional de Historia Natural del Paraguay (MNHNP).

Most studies of ectoparasites are of limited value because specimens are collected haphazardly or from already dead host specimens, increasing opportunities for

contamination that result in inaccurate host associations. Because of the emphasis on ectoparasites during this study, all mammal specimens were collected live, maintained in separate containers, anesthetized, and brushed for ectoparasites before further processing. Hosts that died before processing were not inspected for ectoparasites. Upon anesthetization, mammalian hosts were brushed and inspected visually for ectoparasites. Ectoparasites from each host were then placed in labeled vials containing 70% ethanol. After collecting ectoparasites from each host, the brush, collection chamber, and all objects that serve as vectors of cross-host contamination during processing, were washed thoroughly. In addition, hosts were processed in taxonomic blocks (i.e., all *Artibeus lituratus* were processed, followed by *Artibeus fimbriatus*) to reduce the likelihood of contamination among host taxa. Indeed, all aspects of the protocol for mammal collection, specimen processing and preparation, and ectoparasite collection were designed to reduce the possibility of significant horizontal contamination (i.e., assignment of ectoparasites to the wrong host species).

Laboratory Work

Before specific identification of ectoparasites was undertaken, each ectoparasite sample was sorted into families and counted; each family of parasite from each host individual was placed in a separate vial. Samples containing no ectoparasites were recorded as negative. Subsequently, members of each family of ectoparasites were identified using the most recent, comprehensive information about South American representatives for each family including Wenzel (1976) and Wenzel et al. (1966) for the Streblidae; Guimarães (1966, 1972) for the Nycteribiidae; Ueshima (1972), Ferris and Usinger (1939, 1945), and Ronderos (1959, 1962) for the Polyctenidae; Rudnick (1960), Machado-Allison (1965), and Herrin and Tipton (1975) for the Spinturnicidae; Radovsky (1967) and Saunders (1975) for the Macronyssidae; Dusbábek (1969*b*, 1969*c*) and Fain (1978) for the Myobiidae; Jones et al. (1972) and Fairchild et al. (1966) for the Ixodidae and Argasidae; Reed and Brennan (1975), Brennan and Reed (1974, 1975), Brennan and Yunker (1966), and Brennan and Goff (1977) for the Trombiculidae; McDaniel (1970,

1973), Pinichpongse (1963a, 1963b, 1963c, 1963d), de la Cruz (1969) and Dusbábek and de la Cruz (1966) for the Chirodiscidae. Other publications were used as required for more recently described taxa of many of these families (i.e., Brennan 1958, 1970, Loomis and Wrenn 1984, Matheson 1935, 1941).

Streblid identifications were confirmed during collaborative work between Carl Dick (Texas Tech University) and the personnel of the University of Illinois, Chicago (R. L. Wenzel and M. Dean). All fleas (Siphonaptera) were identified by Robert E. Lewis (Iowa State University). Polyctenids were identified by Donald Gettinger (University of Central Arkansas) and Carl Dick. All other taxa were identified preliminarily by the author. Subsequently, identifications of macronyssid and spinturnicid mites were reviewed by Donald Gettinger.

The insects (e.g., Streblidae, Nycteribiidae, Polyctenidae, Siphonaptera) were identified using a dissecting scope. Slides were made of a representative collection of individuals (Wenzel et al. 1966). Mites (e.g., Macronyssidae, Spinturnicidae, Trombiculidae, Chirodiscidae, Myobiidae) and ticks (e.g., Argasidae, Ixodidae) have diagnostic characters too small to view reliably with a dissecting scope. Therefore, these specimens were cleared in either potassium hydroxide or a lactic acid-phenol mixture to allow closer inspection of the ectoskeleton (Krantz 1970). Each specimen was prepared in PVA Mounting Medium, Hoyer's Solution, or Canada Balsam under a round cover slip and dried on a drying plate (Wenzel et al. 1966, Krantz 1970). Specimens were examined under a phase-contrast light microscope. Slides were rung using insulating varnish to prevent re-hydration of the mounting medium. Each slide was labeled with host identification number, ectoparasite family, and slide number. All mounted and fluid preserved specimens are stored at the University of Central Arkansas under the care of Donald Gettinger.

The taxonomy and systematics of insects ectoparasitic on neotropical bats are well known (e.g., Guerrero 1993, 1994*a*, 1994*b*, 1995*a*, 1995*b*, 1996, 1997, Ueshima 1972, Wenzel 1976, Wenzel et al. 1966). As a result, identification to the species level was possible in most cases. The exception is the Nycteribiidae, which is represented by a

single genus (*Basilia*) in South America. However, male specimens of different species of *Basilia* are indistinguishable using phenotypic characters. In addition, taxonomic work on nycteribiids is confounded by numerous synonomies associated with some species (Guimarães 1966, 1972). In general, the taxonomy of this group is not well established. Consequently, I only described females as morphospecies. Males from the same host individual as females were assumed to belong to the same species as the females. No more than one species of *Basilia* was ever found on a host individual based on consideration of females. Male *Basilia* on host individuals with no female *Basilia* were simply identified as *Basilia* spp.

Mite taxa with larger individuals (e.g., Macronyssidae, Spinturnicidae) were identified to species. Those taxa with small ($\leq$ 450 microns) individuals (e.g., Trombiculidae, Myobiidae, Chirodiscidae) often were difficult to resolve to the specific level. Nonetheless, most individuals in these taxa were identified successfully to species. Where individuals could be identified to genus and possessed sufficient diagnostic characters to be distinguished from other members of the genus, species were given numeric designations (e.g., *Basilia* sp. 4). Three species of polyctenid that fit these criteria appear to be undescribed and were designated as "new species" (e.g., *Hesperoctenes* n. sp. 1). Where individuals could be identified to genus but no species-diagnostic characters were discernable, no specific designation was applied (e.g., *Labidocarpus* sp.). A number of mites and ticks could be identified only to family; these individuals were given "unknown" status (e.g., unknown spinturnicid). New taxa that closely resemble known species may have been assigned to known designations in current keys. One such case has been discovered already; streblids originally assigned to *Metelasmus paucisetus* were assigned to a new species, *M. wenzeli* (Graciolli and Dick 2004). This represents a simple name change and does not affect infestation metrics or indices of biodiversity. The effect of the use of morphospecies in ecological studies was investigated for terrestrial invertebrates (Oliver and Beattie 1996, Pik et al. 1999). Estimates of richness and diversity differed little between data sets classified to morphospecies (i.e., arthropods identified by non-specialists) and those based on well

documented species inventories (i.e., arthropods identified by specialists). Moreover, ranking of diversity for habitats was identical using both identification methods.

Three host-parasite parameters (Gettinger and Earnest 1995, Gannon and Willig 1995) were estimated separately for each ectoparasite species on each host species. Incidence is the percent of inspected host individuals that were infested by a particular ectoparasite species. Prevalence is the mean number of ectoparasites per inspected host. Density is the mean number of ectoparasites per infested host. In addition, a specificity index (SI) was calculated for each host-ectoparasite association. SI ranges from 0 (i.e., no individuals of an ectoparasite species occur on a particular host species) to 1.0 (all individuals of an ectoparasite species occur on a particular host species). For each ectoparasite species, SI is the proportion of the total number of individuals of the ectoparasite species that occurred on a particular host species. For example, if an ectoparasite is monoxenous it has an SI of 1.0 on the primary host species because 100% of the individuals of that ectoparasite species occur on the same host species. Alternatively, an ectoparasite species for which 10 individuals were collected from each of 10 host species for a total of 100 individuals, has an SI of 0.1 on each of those host species.

Host specificity was assigned to ectoparasite species in two fashions. First, specificity was defined in the most general sense, which included all observed associations regardless of probable contamination or the apparent transient nature of the association. Second, specificity was defined in a strict sense ignoring associations that were likely due to contamination or transitory relationships (i.e., all associations with an incidence of < 0.05). These were defined as primary associations, with hosts and parasites of these associations referred to as primary hosts and primary ectoparasites, respectively. An exception to this rule was made for small mite taxa (e.g., Myobiidae, Chirodiscidae, Trombiculidae) that were rare on all host species. The host on which these parasites most often were found was considered to be the primary association.

Species that comprise a small portion of a host's ectoparasite fauna may not represent contamination or transient associations, but instead may be naturally rare. A

common definition (e.g. Chalcraft et al. 2004, Stevens and Willig 2000, Willig et al. 2003) considers a species to be rare if its abundance is < 1/S of the total individuals of a community or assemblage, where S = species richness (Camargo 1992). However, problems characterize this definition of rarity. First, use of 1/S for a species-poor assemblage, like those of ectoparasites on host individuals, could result in the assignment of relatively abundant species as rare. For example, in an assemblage with S = 5, a species that comprises 19% of the assemblage is rare although it represents a large portion of the assemblage. Second, because all assemblages do not have equal species richness, 1/S defines rareness at different relative abundances for assemblages with different species richness. Third, 1/S requires at least one species be rare in all but the most even of assemblages. Defining rareness using the 5% criterion eliminates these problems.

The definitions of transience and rarity are similar and confused easily, in part because of the operational necessity of a quantitative criterion, such as the 5% rule. Rarity is defined by considerations of incidence: ectoparasite species that occur on < 5% of inspected hosts are rare in that assemblage. In contrast, transience is defined by considerations of relative abundances of ectoparasites: species that comprise < 5% of all individuals in ectoparasite assemblages are transient. Because rareness and transience are defined with respect to different bases, all transient species are not rare and all rare species are not transient. More specifically, the abundance of a particular ectoparasite and the total abundance of all ectoparasites influence its transience, whereas the abundance of a particular ectoparasite and its distribution among host individuals influence its rarity.

Ectoparasite species abundance distributions (SADs) were compiled for each host taxon by pooling all ectoparasite individuals from the same host species into a single sample. Those host taxa whose SAD included $\geq$ 3 primary ectoparasites were analyzed to determine whether a broken stick (BS) or geometric series (GS) model better characterized the empirical SAD. The GS and BS models represent extremes in the context of commonly used models of SADs, including the log series (LS) and log normal

(LN) models (Magurran 1988). It is within this context that the BS and GS models are described and applied to ectoparasite assemblages of bats in Paraguay. The GS model represents the least equitable distribution of individuals among ectoparasite species (i.e., high dominance) and usually is found in species-poor, harsh environments (Magurran 1988). The BS model predicts a more equitable distribution of individuals among ectoparasite species (i.e., high evenness; May 1975, Pielou 1969) and is a "biologically realistic expression of a uniform distribution" (Magurran 1988). Relatively even SADs occur most frequently in communities that are defined from narrow taxonomic, trophic, or geographic perspectives. Ectoparasite assemblages from Paraguayan bats are defined narrowly from all three of these perspectives. The LS and LN models predict intermediate levels of evenness and dominance. Neither of these models was employed for two reasons. First, LS and LN models perform poorly when applied to communities with relatively few species (Pielou 1969), such as those of obligate parasites (e.g., bat ectoparasite assemblages in Paraguay). Second, the application of four (or more) models to 24 empirical SADs (i.e., the number of ectoparasitic assemblages from common and wide-spread bat species) necessitates a large suite of analyses that prove statistically problematic because of inflated error rates. To reduce error rates, I could remove models or SADs from the experimental design. Because I was more interested in examining the SADs of ectoparasites from each of the common bats species, removal of models was preferred to elimination of SADs.

Functions were written in Matlab for the Macintosh V. 4.2c.1 to compare empirical SADs of primary ectoparasites from each of 24 host species to the corresponding BS or GS models. I followed the methodology of Magurran (1988) and used data therein to confirm that the Matlab functions worked properly. A Chi-square goodness-of-fit test compared the empirical distribution to an expected distribution based on the theoretical model in question (i.e., broken stick or geometric series). Because the null hypotheses in these analyses are based on a particular model, and not randomness, significance indicates failure to conform to the theoretical model. For example, significant results (i.e., $p \leq 0.05$) represent empirical distributions that are not

characterized by the underlying distribution. Alternatively, non-significant results (i.e., $p > 0.05$) represent empirical SADs that adequately conform to (i.e., do not significantly differ from) the theoretical model in question.

Results

Ectoparasites were collected from 2,909 of the 4,143 bats captured during the study, representing 44 species and five families of hosts (Table 2.4). Bat assemblages were defined for each of 28 sites, distributed throughout all major biomes of Paraguay (Figure 2.1, Table A.1, Appendix B). Ectoparasites were not collected from dead hosts or specimens that were prepared as entire specimens (wrapped in gauze and injected with formalin). These latter specimens still have their ectoparasite communities preserved with the host specimen for future, more detailed study.

Over 17,500 ectoparasites were collected, representing 104 species and 11 families (Appendix C). In abundance, five of these families (Insecta: Streblidae; Arachnida: Spinturnicidae, Macronyssidae, Chirodiscidae, and Argasidae) accounted for 94.5% of all ectoparasites (Table 2.5, Appendix C). For insects, streblids were found on the majority of noctilionids, phyllostomids, and natalids. However, different insects appeared on vespertilionids (nycteribiids) and molossids (polyctenids), both of which were nearly devoid of streblids. Streblids were highly host-specific. Twenty-two of the 27 streblid species were monoxenous and three were oligoxenous. No streblid occurred on more than two primary host species. Whereas competition may occur within the Arachnida, it has not lead to interspecific exclusion on host species, perhaps because of smaller ectoparasite body sizes. Co-occurrence was common for the arachnids, as nearly all host species were inhabited by macronyssids in addition to at least one other family of arachnid.

In general, the arthropod ectoparasite assemblages of Paraguayan bats are dominated by macronyssid mites, which represented 23 species and 55% of all collected ectoparasites. It is likely that the number of recognized species will increase once these specimens are examined in detail by taxonomic specialists.

Ectoparasite Assemblages on the Noctilionidae

Noctilio possessed an abundance of ectoparasites, averaging > 20 individuals per bat. The primary species composing the ectoparasite assemblage of *N. albiventris* (host N = 68, ectoparasite N = 1460, Table 2.6) were two streblids (*Noctiliostrebla maai* and *Paradyschiria parvula*), a chirodiscid (*Lawrenceocarpus* sp.), and an argasid (*Ornithodoros hasei*). Both streblids were monoxenous. The ectoparasite assemblage of *N. leporinus* (host N = 28, ectoparasite N = 553, Table 2.7) was similar to that of its congener and was dominated by three monoxenous streblids (*Noctiliostrebla aitkeni, N. dubia*, and *Paradyschiria fusca*) and *O. hasei*. In addition, a macronyssid (*Steatonyssus* sp. 1) that appears to be an undescribed species occurred regularly on *N. leporinus*.

Ectoparasite Assemblages on the Phyllostomidae

Only three specimens of *Chrotopterus auritus* (host N = 3, ectoparasite N = 151, Table 2.8) were captured and these individuals were rife with ectoparasites (> 50 per bat). High abundances may account for how a streblid (*Strebla chrotopteri*) and trombiculid (*Trombicula* sp. 1) that infest only this relatively uncommon host species persist through ecological time. Such high infestation rates reduce the chance of local extinction (i.e., all ectoparasites on a host individual dying), which may be an important factor if the only host of an ectoparasite is a rare, long-lived species.

Tonatia possess modest abundances of ectoparasites, with mean numbers between 12 and 14 individuals. *T. bidens* (host N = 3, ectoparasite N = 42, Table 2.9) harbored a monoxenous spinturnicid (*Periglischrus tonatii*) and was home to 70% of all obtained *Parichoronyssus crassipes*, despite the rarity of this host species in Paraguay. Similarly, *T. brasiliense* (host N = 1, ectoparasite N = 12, Table 2.10) was quite rare, but had a monoxenous association with a spinturnicid (*Mastoptera minuta*) and was infested by one of only three *Parichoronyssus sclerus* identified from the bats of Paraguay.

Glossophaga soricina (host N = 54, ectoparasite N = 64, Table 2.11) nearly were devoid of ectoparasites. On average, a host was infested by a single individual.

Nonetheless, three streblids (*Speiseria ambigua*, *Trichobius dugesii*, and *T. uniformis*) and a spinturnicid (*Periglischrus caligus*) had monoxenous associations with *G. soricina*. In addition, 90% of all *Pseudolabidocarpus* were found on *G. soricina*.

Carollia (host N = 75, ectoparasite N = 124, Table 2.12) were infested by slightly higher densities (1.65 individuals/bat) of ectoparasites than were *G. soricina*; however, *C. perspicillata* did not house an assemblage of endemics. *C. perspicillata* were home to 81% and 96% of all *Strebla guajiro* and *Trichobius joblingi*, respectively.

Desmodus rotundus (host N = 51, ectoparasite N = 407, Table 2.13) were infested by an average of eight individuals. This assemblage was dominated by four monoxenous parasites: two streblids (*Strebla weidemanni*, *Trichobius parasiticus*), a spinturnicid (*Periglischrus herrerai*), and a macronyssid (*Radfordiella desmodi*).

Diaemus youngi (host N = 11, ectoparasite N = 114, Table 2.14) were infested by two monoxenous streblids (*Strebla diaemi* and *Trichobius diaemi*) and a monoxenous macronyssid (*Radfordiella oudemansi*). Curiously, *T. diaemi* only occurred on host individuals that also were infested by *S. diaemi*.

Artibeus possessed meager ectoparasite populations, with *A. fimbriatus*, *A. jamaicensis*, and *A. lituratus* averaging 7.1, 7.3, and 3.2 individuals per bat, respectively. *A. lituratus* was by far the most abundant species of *Artibeus* in Paraguay. All ectoparasite species commonly found on the remaining species of *Artibeus* also inhabited *A. lituratus*. Nonetheless, each species of *Artibeus* harbored a distinctive ectoparasite assemblage. A majority of each of three streblid species (*Aspidoptera phyllostomatis*, *Megistopoda aranea*, and *Metelasmus pseudopterus*) inhabited *A. fimbriatus* (host N = 79, ectoparasite N = 561, Table 2.15). In addition, 85% of the remaining *M. aranea* were found on *A. jamaicensis*. Compared to congeners, *A. jamaicensis* (host N = 42, ectoparasite N = 306, Table 2.16) had the highest incidence of chiggers (trombiculids). Six species of streblid were found on *A. lituratus* (host N = 351, ectoparasite N = 1123, Table 2.17), however, only the monoxenous *Paratrichobius longicrus* were common. Although *Periglischrus iheringi*, which probably represents a species complex, occurred

on 12 host species representing three families, 59% of all individuals occurred on *A. lituratus*.

All *Chiroderma doriae* (host N = 3, ectoparasite N = 6, Table 2.18) were infested with *Periglischrus iheringi*. *Platyrrhinus lineatus* (host N = 90, ectoparasite N = 394, Table 2.19) hosted an average of 4.4 individuals, most of which were a spinturnicid (*Periglischrus iheringi*) or a monoxenous macronyssid (*Macronyssoides conciliatus*). In addition, *Platyrrhinus lineatus* were home to a monoxenous streblid (*Trichobius angulatus*). *Pygoderma bilabiatum* (host N = 53, ectoparasite N = 13, Table 2.20) were nearly devoid of ectoparasites, averaging 0.25 individuals per bat and rarely harbored more than one individual on a host. These associations are likely transient.

The greatest ectoparasite richness (23 species) occurred on *Sturnira lilium* (host N = 404, ectoparasite N = 2023, Table 2.21) despite an average of only five individuals per bat. *S. lilium* hosted eight monoxenous ectoparasites including three streblids (*Aspidoptera falcata*, *Megistopoda proxima*, *Metelasmus paucisetus*), one spinturnicid (*Periglischrus ojasti*), one macronyssid (*Parichoronyssus euthysternum*), two trombiculids (*Eutrombicula* sp. and *Perisopalla precaria*), and one myobiid (*Eudusbabekia lepidoseta*).

Ectoparasite Assemblages on the Natalidae

Only one *Natalus stramineus* (host N = 1, ectoparasite N = 7, Table 2.22) was captured during the study. It was infested by two monoxenous ectoparasites; a streblid *(Trichobius galei*) and a spinturnicid (*Periglischrus natali*).

Ectoparasite Assemblages on the Vespertilionidae

The only species of ectoparasite occurring on *Eptesicus* with any frequency was *Steatonyssus joaquimi*, which composed over 85% of all individuals found on this host genus. All ectoparasites on *E. brasiliensis* (host N = 12, ectoparasite N = 78, Table 2.23) and *E. diminutus* (host N = 2, ectoparasite N = 13, Table 2.24) also were on the more common *E. furinalis* (host N = 69, ectoparasite N = 790, Table 2.25). *E. furinalis* were

infested by four monoxenous species including a nycteribiid (*Basilia* sp. 4), two spinturnicids (*Spinturnix orri* and *S. surinamensis*), and a macronyssid (*Parichoronyssus cyrtosternum*).

Histiotus macrotus (host N = 6, ectoparasite N = 120, Table 2.26) were infested heavily, averaging 20 individuals per host. Eighty percent of these individuals were *Steatonyssus joaquimi*, which is common on other vespertilionid genera. Also, *H. macrotus* harbored appreciable numbers of *Chiroptonyssus haematophagus*, which were common on the molossids that dominate bat assemblages in the Chaco where these *H. macrotus* were captured.

Over 95% of all ectoparasites collected from *Lasiurus* were the oligoxenous *Steatonyssus furmani*. Nearly half of all *L. blossevillii* (host N = 11, ectoparasite N = 20, Table 2.27) were not parasitized; those bats that had parasites hosted only one species per individual. *Macronyssus meridionalis* occurred on one of two *L. cinereus* (host N = 2, ectoparasite N = 1, Table 2.28) captured during the study. *L. ega* (host N = 72, ectoparasite N = 411, Table 2.29) was host to 95% of all *S. furmani*.

All species of *Myotis* had similar ectoparasite assemblages. Ectoparasite assemblages of both common species of *Myotis* (*M. albescens* and *M. nigricans*) were dominated by a diversity of nycteribiids, a spinturnicid (*Spinturnix americanus*) and two macronyssids (*Macronyssus crosbyi* and *Steatonyssus joaquimi*). However, *M. albescens* (host N = 87, ectoparasite N = 1550, Table 2.30) had ectoparasite populations over four times as prevalent as those of *M. nigricans* (host N = 128, ectoparasite N = 557, Table 2.31). In addition, *M. albescens* were host to two monoxenous species, *Spinturnix banksi* and a flea, *Myodopsylla wolffsohni*. The rarer species of *Myotis* in Paraguay, *M. riparius* (host N = 11, ectoparasite N = 52, Table 2.32) and *M. simus* (host N = 1, ectoparasite N = 18, Table 2.33), harbored a subset of parasites found on more common congeners.

Ectoparasite Assemblages on the Molossidae

In general, bats of the genus *Eumops* (Tables 2.34 – 2.38) had ectoparasite assemblages dominated by macronyssids, in particular those of the genus *Chiroptonyssus*.

Eumops auripendulus (host N = 2) were host to no ectoparasites (Appendix B). *E. bonariensis* (host N = 5, ectoparasite N = 8, Table 2.34) possessed few ectoparasites, but one individual harbored nearly half of all *Labidocarpus* sp. collected during the study. The two largest species of *Eumops*, *E. dabbenei* (host N = 4, ectoparasite N = 48, Table 2.35) and *E. perotis* (host N = 3, ectoparasite N = 35, Table 2.38), harbored much greater ectoparasite numbers per bat (i.e., prevalence), 12.8 and 11.7, respectively, than did the smaller *E. bonariensis* (1.60) or *E. patagonicus* (3.22), with the medium sized *E. glaucinus* (5.96) having intermediate numbers. *E. glaucinus* (host N = 56, ectoparasite N = 334, Table 2.36) were the primary host of an undescribed polyctenid, *Hesperoctenes* n. sp. 1 (Table 2.36). The ectoparasite assemblage of *E. patagonicus* (host N = 526, ectoparasite N = 1693, Table 2.37) was dominated by *C. haematophagus*, which accounted for 82% of parasites collected from this host, and a monoxenous polyctenid, *H. longiceps*.

Bats of the genus *Molossops* had low levels of parasite infestation. Nonetheless, each species of *Molossops* had an associated monoxenous polyctenid bat fly: *Hesperoctenes cartus* on *M. abrasus* (host N = 14, ectoparasite N = 55, Table 2.39), *H. minor* on *M. planirostris* (host N = 12, ectoparasite N = 20, Table 2.40), and *H. parvulus* on *M. temminckii* (host N = 160, ectoparasite N = 541, Table 2.41). Aside from the polyctenids, macronyssids (*Chiroptonyssus haematophagus* and *C. venezolanus*) and argasids (*Ornithodoros hasei*) were common in ectoparasite assemblages on *Molossops*.

Molossus are the primary host to the only streblid (*Trichobius jubatus*) found on molossids in Paraguay. The ectoparasite assemblage of *M. ater* (host N = 100, ectoparasite N = 911, Table 2.42) was dominated by the monoxenous *C. robustipes* (Table 2.42), whereas those of *M. currentium* (host N = 27, ectoparasite N = 64, Table 2.43) and *M. molossus* (host N = 228, ectoparasite N = 2426, Table 2.44) were dominated by *C. haematophagus*. All three species of *Molossus* commonly hosted the oligoxenous *Hesperoctenes fumarius*.

Nyctinomops laticaudatus (host N = 42, ectoparasite N = 182, Table 2.45) were host to four monoxenous ectoparasites, a polyctenid (*Hesperoctenes setosus*), a myobiid

(*Ewingana* sp. 2), and two ischnopsyllids (*Hormopsylla fosteri* and *Rothschildopsylla noctilionis*). However, *Chiroptonyssus venezolanus* were the most abundant ectoparasite on *Nyctinomops*.

Promops centralis (host N = 4, ectoparasite N = 14, Table 2.46) were host to the monoxenous polyctenid, *Hesperoctenes angustatus*. All *P. nasutus* (host N = 8, ectoparasite N = 227, Table 2.47) were infested with *C. haematophagus*; most individuals were infested heavily, carrying 19 or more parasites.

Host Specificity

Patterns of host specificity were similar regardless of inclusion or omission of ectoparasites that represent contamination and transient taxa; however, inclusion of contamination and transient associations (Table 2.48) may obscure more ecologically important relationships. Consequently, I only will discuss associations under the stricter definition of primary host-ectoparasite relationships (Table 2.49).

Twenty-two of 27 streblids were monoxenous. Of those occurring on more than one host species, two (*Aspidoptera phyllostomatis* and *Megistopoda aranea*) were oligoxenous on *Artibeus* and another (*Trichobius jubatus*) was oligoxenous on *Molossus*. Two streblid species were polyxenous.

Seven of the ten species of polyctenids were monoxenous. The remaining three species were oligoxenous, with two species parasitizing *Molossus* and one species parasitizing *Eumops*.

Nycteribiids were less host-specific than were other families of ectoparasitic insects. Half of the six species were monoxenous. Two species were oligoxenous on *Myotis*. One species was pleioxenous. All ischnopsyllids were monoxenous.

Eight of the ten identified species of spinturnicids were monoxenous. *Spinturnix americanus* were oligoxenous on *Myotis*. *Periglischrus iheringi* were pleioxenous on stenodermatine bats.

Of the 22 species of macronyssids identified from bats of Paraguay, only nine were monoxenous. Three species were oligoxenous, four were pleioxenous, and six were

polyxenous. Among those arthropods specializing as ectoparasites of bats, macronyssids are among the least host specific.

All argasid ticks and chirodiscids mites were polyxenous. Half of the eight trombiculid species were monoxenous on phyllostomids, whereas the other four species were polyxenous, occupying both phyllostomids and molossids. Although myobiids are small (< 450 microns), rarely collected, and probably under represented in these collections, four of the five species were monoxenous and the other was oligoxenous.

Ectoparasite Species Abundance Distributions

Species abundance distributions were compiled for all host species on which ≥ 3 ectoparasite species occurred (Table 2.50, Figs. D.1—D.39). Of the 24 host species whose ectoparasite SAD was compared to the BS and GS models, ten fit neither model, four fit both models, nine fit the BS only, and one fit the GS only (Table 2.51). Of the four that fit both models, three fit the GS better than the BS. Within a bat family, host species were heterogeneous with respect to SADs of their ectoparasite assemblages. Of the three ectoparasite assemblages from species of vespertilionids, one fit the BS and two fit neither model. Of the 11 ectoparasite assemblages from species of phyllostomids, five fit the BS, one fit the GS, two fit both models, and three fit neither model. Of the eight ectoparasite assemblages from species of molossids, two fit the BS, two fit both models, and 4 fit neither model.

Discussion

Host – Parasite Associations and Infestation Levels

The literature is teeming with isolated reports of host-parasite associations. In general, the primary host-parasite relationships between bats and arthropod ectoparasites documented in Paraguay (Tables 2.6 – 2.47) reiterate associations reported numerous times elsewhere (Brennan and Goff 1977, Brennan and Reed 1974, 1975, Brennan and Yunker 1966, de la Cruz 1969, Dusbábek 1969*b*, 1969*c*, Dusbábek and de la Cruz 1966, Fain 1978, Fairchild et al. 1966, Ferris and Usinger 1939, 1945, Guerrero 1993, 1994*a*,

1994*b*, 1995*a*, 1995*b*, 1996, 1997, Guimarães 1966, 1972, Herrin and Tipton 1975, Jones et al. 1972, McDaniel 1970, 1973, Machado-Allison 1965, Pinichpongse 1963a, 1963b, 1963c, 1963d, Radovsky 1967, Reed and Brennan 1975, Ronderos 1959, 1962, Rudnick 1960, Saunders 1975, Ueshima 1972, Wenzel 1976, Wenzel et al. 1966). However, few of these references included material from Paraguay, and none of them were restricted to it.

The streblids are the best known group of mammalian ectoparasites (Guerrero 1993, 1994*a*, 1994*b*, 1995*a*, 1995*b*, 1996, 1997). The culmination of Guerrero's work was a list of host-parasite associations that also contained a list of streblid species recorded from each country or island in the New World. Ten host-parasite associations were documented in Paraguay beyond those reported by Guerrero (1997); however, only two of those represent more than a single infestation. *Metelasmus paucisetus* occurred on *Sturnira lilium* (Table 2.21) and *Strebla weidemanni* occurred frequently on *Desmodus rotundus* (Table 2.13). Twenty-seven species of streblid occurred in Paraguay, seven of these were reported previously (Guerrero 1997).

Despite the substantial literature dedicated to the natural history of bat ectoparasites, reports of ectoparasite infestation levels are limited in depth and breadth, impairing any ability to make comparisons among taxa (either host or ectoparasite) or regions. Most research reports infestation levels of a single ectoparasite species on a single host species. Some report densities or prevalences of a single parasite for many host species or of many parasite species on a single host species. The most comprehensive reports to date are those of Herrin and Tipton (1975), who reported the density, prevalence, and incidence of all spinturnicids occurring on every species of bat collected during a study in Venezuela and Gannon and Willig (1995), who reported the same information for streblids and spinturnicids occurring on bats of Puerto Rico.

Cimicids infesting bats reportedly feed an average of 22 times per day (Overal and Wingate 1976). Although no cimicids were recorded during this study, they are primarily roost dwellers and rarely are found on their host (Marshall 1982*a*), which makes cimicid collection from hosts captured by mist nets improbable. Nonetheless,

cimicids feed on emballonurids, noctilionids, and molossids (Marshall 1982*a*), all of which occur in Paraguay. Failure to detect such roost dwelling ectoparasites would underestimate ectoparasite loads for bats. However, this sampling error is consistent and does not bias ectoparasite assemblage comparisons among Paraguayan bats that are infested by cimicids (i.e., noctilionids and molossids). However, in analyses involving all hosts, the ectoparasite assemblage diversity may be underestimated for these two host families.

Little is known about the ecology of polyctenids. In the only published record, Marshal (1982*b*) documented a density of 13.7 individuals per host for the megadermatid bat, *Megaderma spasma*, in Malaysia. Although molossids and megadermatids share similar autecologies (i.e., both are insectivores and roost in caves or tree cavities), the infestation rate of polyctenids on Paraguayan molossids is quite low, ranging from 0.25 to 3.0 individuals per bat. The difference in infestation rates between megadermatid and molossid bats may be related to the differences in size between host species. More specifically, *M. spasma* weigh about 25 g whereas the more common molossids in Paraguay weigh between 5 g and 13 g. Ecological densities (number of parasites per unit area or biomass) are much more similar than suggested by comparisons of individuals per host.

Many studies have reported prevalences and densities of nycteribiids in South America (see Marshall 1982*a* and sources therein). In general, most hosts are uninfested and prevalences are less than one fly per host individual. Large-bodied genera, such as *Basilia*, have especially low prevalences. Staying on a flying host may be especially difficult for larger bat flies; therefore, *Basilia* may remain in the roost more frequently than do smaller nycteribiids. Infestation rates of nycteribiids in Paraguay are consistent with prior observations: incidence rarely exceeded 10% and prevalence < 1 fly per host.

In general, streblids have higher densities and prevalences than do nycteribiids. *Trichobius corynorhini* had a prevalence of 2.6 flies per bat on *Corynorhinus townsendii* (Kunz 1976), and prevalences of 0.8 (Overal 1980) and 0.55 (Gannon and Willig 1995) flies per bat were reported for *Megistopoda aranea* on *Artibeus jamaicensis* from Panama

and Puerto Rico, respectively. In addition, 0.37 *Aspidoptera phyllostomatis* per bat parasitized the same Puerto Rican *A. jamaicensis* (Gannon and Willig 1995) resulting in nearly one streblid per *A. jamaicensis*. In Paraguay, *M. aranea* and *A. phyllostomatis* commonly occurred on two host species, *A. fimbriatus* and *A. jamaicensis*, and were present at similar densities and prevalences to those reported previously (Tables 2.15 and 2.16). Prevalence for *Trichobius intermedius* on *Monophyllus redmani* are reported for Puerto Rico (Gannon and Willig 1995). Although *Monophyllus* does not occur in Paraguay, a member (*Glossophaga soricina*) of the same subfamily (Glossophaginae) is common there and is host to a species of *Trichobius*. Reported infestation rates (< 1 fly per bat) of *Trichobius* on glossophagine bats are consistent with observations for Paraguay. In this study, streblid prevalences ranged from 0.1 to 4 flies per bat for phyllostomids. However, infestation rates on noctilionids were much higher, with *Noctilio albiventris* hosting > 9 flies per bat and *N. leporinus* > 11 flies per bat (Tables 2.6 and 2.7).

Periglischrus iheringi are pleioxenous spinturnicid mites found on stenodermatine bats, but also have frequent, transient associations with vespertilionids and molossids. *P. iheringi* were reported from two stenodermatine bats and one glossophagine bat in Puerto Rico (Gannon and Willig 1995). In Paraguay, a monoxenous congener, *P. caligus*, infested glossophagines (i.e., *Glossophaga soricina*). In contrast, *P. iheringi* occurred on all stenodermatine bats of Paraguay, with between 1.88 and 2.39 mites per bat on each primary host species (Tables 2.15 – 2.19). These infestation levels occur between those reported for *Stenoderma rufum* (1.48 mites per bat) and *A. jamaicensis* (4.96 mites per bat) of Puerto Rico (Gannon and Willig 1995).

Incidence rates were reported for a collection of *Periglischrus* collected from bats near Brasília, Brazil (Gettinger and Gribel 1989). Four species (*P. caligus*, *P. herrerai*, *P. iheringi*, and *P. ojasti*) infested the same host species as in Paraguay, but each occurred at higher rates of incidence in Brazil (0.83, 0.50, 0.71, 0.57) than in Paraguay (0.11, 0.05, 0.56, 0.48).

Incidence and prevalence values were reported for spinturnicids from phyllostomid bats of Michoacán, Mexico (Sheeler-Gordon and Owen 1999). Four species (*Periglischrus caligus*, *P. herrerai*, *P. iheringi*, and *P. ojasti*) occurred on the same host species as in Paraguay. *P. herrerai*, *P. iheringi*, and *P. ojasti* occurred at similar rates of incidence and prevalence in Paraguay and Mexico (Table 2.52); however, *P. caligus* was more common on *Glossophaga* in Mexico than in Paraguay.

Infestation rates of spinturnicid mites on chiropteran hosts are known from Venezuela (Herrin and Tipton 1975). Noteworthy differences exist between Venezuela and Paraguay (Table 2.52). First, the number of associations that would be considered transient or the result of contamination was more than three times greater in Venezuela than in Paraguay. Host samples in the Venezuelan project were larger than in that for Paraguay, affording more opportunities for detection of transient associations. However, levels of incidence in Venezuela were lower than in Paraguay, which resulted in a higher rate of contamination or transient observation. Although the Venezuelan mammal project had collection of ectoparasites as one of its primary goals, their collection methodology appears to have been less efficient in controlling contamination than was that employed in the Paraguay project. Detailed ectoparasite collection methodology was not published, therefore comparison of specific differences in collection techniques used in Venezuela and Paraguay is not possible. The methodology employed in Paraguay followed that of Sheeler-Gordon and Owen (1999), who reported only one transient association for *Periglischrus* (*P. iheringi* on two *Desmodus rotundus*) from a collection of 305 ectoparasites from 274 hosts representing 18 species.

Rates of infestation for primary associations between collections in Venezuela and Paraguay were not consistent. Incidences and prevalences were higher for species of *Periglischrus* in Paraguay than in Venezuela. In contrast, both metrics were lower for species of *Spinturnix* in Paraguay than in Venezuela.

In a study of ectoparasites that infest mammals of Paraguay, including six bat species, host associations were reported along with data to calculate prevalence and incidence of macronyssids (Whitaker and Abrell 1987). Incidence and prevalence values

were similar to those reported here with three exceptions. First, much greater infestation rates for chiggers were reported (0.64 chiggers per bat) in Whitaker and Abrell 1987 than in this study (0.069 chiggers per bat). Second, in a transient association, *Chiroptonyssus haematophagus* had a higher rate of incidence on *Artibeus lituratus* than did the primary macronyssid (*Macronyssus kochi*) associated with that host. Third, *P. iheringi* infested 67% of *Sturnira lilium*, whereas the primary macronyssid ectoparasite of *Sturnira*, *P. ojasti*, was not observed. *P. ojasti* is the most common and abundant spinturnicid reported from *S. lilium* and is almost exclusively reported from species of *Sturnira* (Herrin and Tipton 1975, Machado-Allison 1965). Moreover, when reported from species of *Sturnira*, *P. iheringi* does not reach incidence or prevalence levels reported by Whitaker and Abrell, (1987) but is observed as a rare transient. Indeed, all reported infestation rates of spinturnicids from *Sturnira* that are similar to those of Whitaker and Abrell are *P. ojasti* (Furman 1966, Gettinger and Gribel 1989, Herrin and Tipton 1975, Machado-Allison 1964, 1965). Most likely, the *P. iheringi* reported by Whitaker and Abrell (1987) were misidentified *P. ojasti*; however, specimens from those collections have not been reviewed and this assertion cannot be verified. These species of *Periglischrus* are very similar and easily misidentified; the relative size and spacing of the first three podosomal setae are the primary distinctive characteristics (Herrin and Tipton 1975).

Ticks found on mammals of Venezuela, documented host associations, and frequency of occurrences on each host species were reported by Jones et al. (1972). However, it is unclear if the authors included all host individuals that were inspected for ticks or only those individuals on which ticks occurred in their calculations of ectoparasite density. Assuming the authors included only hosts from which ticks were found, I compare ectoparasite densities in Paraguay to those reported from Venezuela. *Ornithodoros hasei* occurred in greatest density (10 – 25 individuals per host individual) on *Noctilio albiventris* and *N. leporinus* in Venezuela and Paraguay. All other host species have average densities of 1 - 5 individuals per bat, with a modal value of one tick per bat in each country. Similar to the data from Paraguay, most Venezuelan records of

Amblyomma, *Ixodes*, and *Rhipicephalus* from bats were of single ticks infesting one host individual per host species (Jones et al. 1972). All of these associations are transient.

Trombiculid infestation levels reported in bats appear lower than those in other mammals (Brennan and Reed 1974, 1975, Brennan and Yunker 1966, and Brennan and Goff 1977, Reed and Brennan 1975). Wrenn and Loomis (1984) presented the incidence of chiggers on reptilian, avian, and mammalian hosts for ten regions throughout the New World. Bats were among the least infested in all regions (incidence = 0.4 to 2.8%), whereas mammals as a group were infested between 6.8 and 97.3% of the time. In Paraguay, chiggers were found on 1% of all bats; incidence of chiggers from Paraguayan rodents or marsupials from the project has not been studied. The immature parasitic stage in chiggers crawls on the soil in search of hosts, which may predispose terrestrial vertebrates to higher infestation rates compared to bats.

In Paraguay myobiids occurred on only 12 of 2909 inspected hosts (Appendix C). Myobiids are common and abundant residents of bats (Dusbábek 1969*b*, 1973, Uchikawa 1987, 1988, Uchikawa and Harada 1981); however there are no reports of prevalence or incidence values for these associations. Ninety-seven individuals and 242 eggs were collected from a small lesion on a single *Artibeus phaeotis* (Lukoschus et al. 1981). Six new species of *Eudusbabekia*, each collected from different bat species, were described by Dusbábek and Lukoschus (1974). Each type series ranged from 7 to 33 individuals ($\overline{X}$ = 16.17). Unfortunately, only individuals for the type host were listed. No mention of incidence or density for hosts in general is available.

Myobiid mites remain embedded in mammal skins long after the deaths of host and mite (Fain 1978, Uchikawa and Baker 1993). Mites were collected from already prepared museum specimens that were collected 0 to 79 years before inspection, and generally numbered 1 to 8 ectoparasites per infested bat. However, these numbers represent only specimens still attached to host skins after handling, specimen preparation, and years of storage. It is likely that many myobiids are lost from prepared specimens; therefore, these collections probably represent only a fraction of the myobiids present at the time of host collection. The number of hosts inspected was not listed in either study,

host individuals were only noted if they harbored a new species of myobiid. As a result, it is impossible to estimate incidence, prevalence, or density in these studies. Despite the small numbers of myobiids found in this study, obviously they can reach high densities on hosts. Myobiids are small (0.2 – 0.4 mm), even for ectoparasites. The lack of myobiid documentation in Paraguay likely reflects methodological efficacy and is not an accurate indication of infestation levels.

Host Specificity

Parasitism is an extreme mode of specialization. For every adaptation for parasitism there is a corresponding loss of versatility and increasing dependence on the host; ultimately leading to strict host specificity (i.e., monoxenous parasites). Except for ticks and chiggers, ectoparasites of bats are highly host specific (i.e., monoxenous or pleioxenous). Although some authors (e.g., Wenzel 1976) identify host-parasite associations, and differentiate between primary associations and transient observations or contamination, few assign levels of host specificity to ectoparasites. As such, comparison of host specificity between studies is difficult. Indeed, if transient associations or probable contamination are not removed from consideration, care taken during collection becomes all-important in comparative studies. Moreover, host sample size affects the likelihood of discovering non-primary associations.

Herrin and Tipton (1975), Machado-Allison (1965), and Sheeler-Gordon and Owen (1999) reported host specificity for the genus *Periglischrus* in Venezuela, Venezuela, and Mexico, respectively. All reported similar levels of host specificity to that found in Paraguay (Table 2.53). However, some species (e.g., *P. herrerai*) are reported by Herrin and Tipton (1975) as polyxenous as a result of the inclusion of non-primary associations with *Anoura* spp., *Sturnira lilium*, and *S. ludovici*. *P. herrerai* would have been classified polyxenous in Paraguay if all documented association were considered (Table 2.48). However, this ectoparasite has only one primary association (*Desmodus rotundus* as host) and is functionally monoxenous throughout its distribution. Another complexity arises when comparing host assemblages from different regions.

Differences in the structure of host communities (e.g., number of species in a genus or genera in a subfamily) can affect designations of specificity. For example, *P. tonatii* and *P. caligus* are pleioxenous in Venezuela (Herrin and Tipton 1975). Each infests a single genus represented by multiple species in Venezuela (i.e., *P. tonatii* on *Tonatia* and *P. caligus* on *Glossophaga*). However, only one species of *Glossophaga* occurs in Paraguay. In addition, whereas three species of *Tonatia* occur in Paraguay, each is rare, affording few chances for detecting *P. tonatii*. As a consequence, the designation of these ectoparasites as monoxenous in Paraguay may represent sampling biases or the biogeographic distribution of potential host species.

Tick assemblages on Paraguayan bats were species poor. Over 99.5% of ticks collected from Paraguayan bats were *Ornithodoros hasei* (Appendix C). Single individuals of other species of ticks were rare, occurred on five different bat genera, and represent transient associations. *O. hasei* are specific to bats and occurred on 19 bat species in Paraguay. Ten of those associations are primary, and include four host families (Noctilionidae, Phyllostomidae, Vespertilionidae, Molossidae). In Paraguay, ticks exhibit no host specificity on bats. Indeed, it would have been surprising to find high levels of host specificity given that consecutive feedings of individual argasids often are on different host species (Hoogstrall and Aeschlimann 1982, Oliver 1989). Jones et al. (1972) reported *O. hasei* from numerous bat species that included representatives of each of the four host families from which it was recorded in Paraguay.

Although half of the trombiculid species collected from bats in Paraguay were found from a single host species, it more probable that these ectoparasites are polyxenous than monoxenous. Most likely, chiggers were under sampled because of their small size. Studies focused on chiggers (e.g., Brennan and Reed 1974, 1975) document most trombiculid species from two or more vertebrate orders (e.g., Aves, Reptilia, Amphibia). Therefore, the likelihood that chiggers on bats are more specific than polyxenous is low despite documented occurrences here.

Chirodiscids rarely exhibit host specificity (McDaniel 1973). Although restricted to bats, the common taxa (e.g., *Beamerella* sp., *Trombicula* sp.) usually occur on hosts from > 1 family, as was true in Paraguay (Appendix C).

Myobiids are extremely host specific (Dusbábek 1969*b*, 1973, Uchikawa 1987, 1988, Uchikawa and Baker 1993). Most often, each mite genus is restricted to a single host family and each mite species is restricted to a single host genus. At the ectoparasite taxonomic levels of genus and species, primary host associations were consistent with previous records (Dusbábek 1969*b*, 1973, Uchikawa 1987, 1988, Uchikawa and Baker 1993) for both myobiid genera occurring in Paraguay; *Eudusbabekia* and *Ewingana* were restricted to phyllostomid and molossid bats, respectively. Moreover, each species of myobiid occurred on a different host genus.

Ectoparasites and Safe Spaces

Streblids and nycteribiids have well-developed, flexible legs that allow them to walk rapidly forward, backward, and sideways while clinging to the host, even to flying hosts (Marshall 1982*a*). Nycteribiids and many streblids are wingless; however, modified hind wings used for balance are present in both families. Streblids may be found anywhere on a host, whereas nycteribiids are found only on pelage; both families feed on naked areas (e.g., patagia, ears, lips). Bats are capable of grooming all body parts, and hosts do capture, kill, and consume bat flies (Fritz 1983). Observed flies rarely moved during grooming, even when grooming activity was close to the fly's location. Most fly movements involved intraspecific interactions and were not a response to host initiated stimuli. On roosting hosts, nycteribiids congregate in difficult to groom areas (e.g., between scapulae, under the chin, in the axilla). In contrast, while the host is in flight, nycteribiids move to the dorsal side of the tail (Marshall 1982*a*). Streblids differ in site preference depending on species, season, and roosting habits of the host; some species prefer pelage and other patagia (Kunz 1976, Marshall 1982*a*, Wenzel et al. 1966). Given the complexity of bat fly movements on hosts in response to host behavior or the

environment, multiple safe spaces may be required for each species of bat fly, which may reduce potential bat fly richness.

There are three distinct niches for bat flies based on microhabitat distribution on hosts (i.e, in the fur, on the fur, or on the patagia). In Paraguay, streblids occupy each of these niches, whereas nycteribiids and polyctenids are restricted to niches on the fur and in the fur, respectively. Regardless of ectoparasite taxon, if safe spaces are limiting, no more than three species of bat fly (i.e., one for each distinct niche) should occur on a host species at equilibrium.

Species that occupy any one of these three niches have distinctive adaptations to facilitate movement and attachment to the host. Fur swimmers move within the host pelage and are dorso-ventrally (e.g., *Metelasmus*, *Strebla*) or laterally (e.g., *Nycterophilia*) flattened to facilitate movement. Fur runners move across the surface of host pelage and have greatly elongated hind legs that maintain the abdomen above host fur during rapid movements. Wing crawlers prefer patagia and have a generalized fly morphology (i.e., legs of modest and equal length). Although some genera of streblids have greatly reduced wings, wing development does not affect habitat preference on the host; species from each ecomorphological group may have fully developed or greatly reduced wings. Nycteribiids belong to two ecomorphological groups: fur swimmers and fur runners (Marshall 1982*a*). Smaller species are fur swimmers and larger species are fur runners. All nycteribiids in Paraguay are fur running, large flies of the genus *Basilia*. Competition for safe spaces should limit bat fly species richness on hosts. Polyctenids have modified forelegs with weak claws that part the host's hair to aid in locomotion and two pairs of backward pointing legs. These insects move through the fur with a swimming motion (Marshall 1982*a*). Polyctenids are restricted to pelage and wander widely over the host body. Areas with longer hair that are difficult to groom (e.g., between the scapulae) are preferred (Marshall 1982*b*, Schuh and Slater 1995).

Spinturnicids have two sets of adaptations that facilitate adherence to and movement on bat patagia: 1) strong, thick legs with heavy claws and immovable coxae and 2) dorso-ventrally flattened and slightly concave bodies (Rudnick 1960).

Spinturnicids never leave the host and are incapable of locomotion when not on patagia. Nonetheless, all parts of patagia are not inhabited equally. Spinturnicids occurred most often on the ventral side of the wings, in particular from the angles created by the forearm, metacarpals, and phalanges that appear to be preferred safe spaces.

Macronyssids possess many traits (e.g., flattened bodies, unidirectionally pointing setae, caudally directed spines, coxal spurs, large tarsal claws) that aid in movement through pelage and adhering to the host (Saunders 1975). Host body locations are species-specific for macronyssids. Moreover, one macronyssid species may inhabit distinct host body locations at different developmental stages. For example, larval *Chiroptonyssus robustipes* generally feed on the dorsal surface of the wing, facing anteriorly, whereas adults occur in the pelage (Radovsky 1967). In contrast, all stages of *Steatonyssus antrozoi* remained in the pelage with the preferred location on the lower back of the host (Radovsky 1967).

Predation of ectoparasites by the host limits habitable spaces. Indeed, places on the host where ectoparasites can avoid host grooming (i.e., safe spaces) likely are the limiting resource for which ectoparasites compete. In addition, because of the high degree of specialization required to exploit safe spaces, once a safe space is occupied it is likely that incumbent ectoparasite species prevent successful infestation of additional ectoparasite species via interference competition. Moreover, adaptations that are advantageous for one safe space are unfavorable for other safe spaces, preventing a single ectoparasite species for exploiting all available safe spaces. All of these factors (i.e., host predation, competition, specialization, and limited safe spaces) conspire to constrain both abundance and richness of ectoparasite assemblages on bats. If these mechanisms operate as described, one would expect to observe species poor communities with relatively even SADs. Ectoparasite assemblages from bats of Paraguay conform to these expectations. Assemblages of ectoparasites were species-poor, with individual bats harboring an average of 1.28 primary species of ectoparasite. In addition, the majority of ectoparasite assemblage SADs conformed to the BS model (Table 2.50), which represents a relatively equitable distribution of individuals among ectoparasite species

(i.e., high evenness) and is most commonly found in situations where one resource is being shared fairly evenly in the community.

Streblids and Safe Spaces on *Noctilio*. *Noctilio* have short, sparse fur that lies flat and does not provide habitat for fur swimmers. In addition, the major adaptation (i.e., greatly elongated hind legs) for fur runners is not required for effective movement over *Noctilio* pelage. As a result, *Noctilio* only harbor streblids with the general bat fly ecomorphology typical of wing crawlers. However, each species of *Noctilio* harbors three streblid species (Tables 2.6 and 2.7) that all have wing crawler morphology and prefer patagia to pelage (Carl Dick pers. comm.). *Noctilio* are among the largest Paraguayan bats and may provide sufficient patagial space to reduce competition between wing crawling streblids or provide distinct patagial safe spaces.

The most common and abundant fly on *Noctilio albiventris* is *Paradyschiria parvula*, which occurred on 89% of *Noctilio albiventris* in Paraguay (Table 2.6). *Noctiliostrebla maai* occurred on only 66% of *Noctilio albiventris*, but *P. parvula* occurred on all 45 of the *Noctilio albiventris* that had *Noctiliostrebla maai*. *Paradyschiria* and *Noctiliostrebla* are morphologically similar and should be competitors; however these fly species do not exhibit competitive exclusion and appear to prosper when sharing a host. *Noctilio albiventris* are also host to a tick (*Ornithodoros hasei*), with a mean prevalence of 11.4 ticks per bat (Table 2.6). Interestingly, *Noctilio albiventris* with < 4 *Noctiliostrebla maai* had significantly more *O. hasei* ($F = 4.41$, $p = 0.039$, $df = 1,65$) than did *Noctilio albiventris* with ≥ 4 *Noctiliostrebla maai*. No *Noctilio albiventris* with > 5 *Noctiliostrebla maai* (n = 15) had > 2 ticks, whereas 38% (n = 42) of *Noctilio albiventris* with < 4 *Noctiliostrebla maai* harbored > 10, and as many as 94 ticks. Moreover, there is a significant, negative relationship between the number of *Noctiliostrebla maai* and *O. hasei* on *Noctilio albiventris* ($p = 0.027$, $r^2 = 0.07$). Similarly, *O. hasei* were less abundant on *Noctilio leporinus* in the presence of *Noctiliostrebla* than on hosts without *Noctiliostrebla*; however the differences were not significant, perhaps because of small sample sizes (n = 23). *Noctiliostrebla* and *O. hasei* may compete on *Noctilio*, with *Noctiliostrebla* being competitively dominant.

Noctilio leporinus had similar patterns of streblid co-occurrence among its three streblid species (*Noctiliostrebla* a*itkeni*, *Noctiliostrebla dubia*, and *Paradyschiria fusca*). With the exception of one *Noctiliostrebla dubia*, the streblid assemblages on *Noctilio leporinus* were perfectly nested. If a *Noctilio leporinus* harbored only one species of streblid, it always was *P. fusca*. *Noctiliostrebla aitkeni* did not occur without *P. fusca*; 62% percent of all *Noctilio leporinus* with *P. fusca* also harbored *Noctiliostrebla* a*itkeni*. Moreover, 46% of *Noctilio leporinus* with *P. fusca* and *Noctiliostrebla* a*itkeni* also harbored *Noctiliostrebla dubia*. Instead of illustrating competitive exclusion these flies co-exist frequently and occur in greater abundances when sympatric. For example, *P. fusca* had a prevalence of 3.3 flies per bat on hosts without *Noctiliostrebla*, whereas *P. fusca* had a prevalence of 14.6 flies per bat on hosts with *Noctiliostrebla*. The two most likely explanations for these patterns of co-existence and ectoparasite density are: 1) that the presence of *Paradyschiria* facilitates infestation by *Noctiliostrebla* which facilitates increases in *Paradyschiria* densities, creating a positive feedback loop leading to greater fly densities, or 2) some characteristic of host individuals affects susceptibility to streblid infestation. Although all streblid species on *Noctilio* have wing crawler ecomorphology, short host pelage may allow species of wing crawler ecomorphology to use furred parts of the host effectively. Nonetheless, personal observations (Carl Dick, pers. comm.) of the streblids on *Noctilio* collected from Paraguay, Peru, Honduras, and Venezuela indicate that all of these species usually are found on patagia and not the trunk. The biology of streblids is too poorly studied to explain how one fly species could facilitate the infestation of another. Preliminary analyses of likely host factors (e.g., host sex, host size, host age, collection location) that may affect host susceptibility to streblids were non-significant for assemblages on both species of *Noctilio*. Host health, size of roosting group, and roost type are factors that could affect *Noctilio* vulnerability to streblid infestations that were not measured and are difficult to measure. This ectoparasite assemblage and the interactions among *Noctiliostrebla*, *Paradyschiria*, and *Ornithodoros* warrant further study.

Resource Partitioning on Molossids

In general, weak interspecific competitive interactions characterize ectoparasite assemblages of bats (Marshall 1982*a* and citations therein); however, indirect evidence suggests that families of bat flies exclude one another from particular host species or individuals (Wenzel and Tipton 1966*b*, Marshall 1982*a*). A distinct pattern characterizes bat fly associations on New World bats. Host species with polyctenids harbor neither nycteribiids nor streblids. Similarly, although nycteribiids and streblids may occur on the same host species, both do not occur on the same host individual. These patterns exist for bat ectoparasites in Paraguay with one notable exception. The primary hosts for streblids in Paraguay were generally phyllostomids, however, *Trichobius jubatus*, a wing crawler, occurred only on molossids, and often coexisted on the same host individuals with polyctenids, which are dorso-ventrally flattened fur swimmers. *Hesperoctenes longiceps* occurred with *T. jubatus* on *Eumops patagonicus*, and *H. fumarius* occurred with *T. jubatus* on *Molossus ater* and *M. molossus*. *T. jubatus* occurred on 59 host individuals and co-occurred with a polyctenid on 17 of those hosts. *Trichobius* prefer naked membranes over haired parts of the body (Kunz 1976, Ross 1961). By using a safe space on molossids (i.e., patagia) that is not used by polyctenids, co-existence is facilitated.

Implications to Host Phylogeny Based on Ectoparasites

Specializations resulting from close associations with particular host species make ectoparasites obligate parasites of those hosts. Most often, this reliance increases levels of host specificity. Over evolutionary time, close associations between hosts and ectoparasites make ectoparasites useful tools for understanding host phylogenies. The Spinturnicidae, Macronyssidae, and Myobiidae are ectoparasite families most often used to elucidate host phylogenies at specific to ordinal levels (Dusbábek 1969*a*). Uchikawa and Harada (1981) found myobiids to be more divergent than their hosts (karyotypes), suggesting that these ectoparasites are at least as efficient indicators of bat taxonomy and phylogeny as are karyotypes. Analyses based on myobiid mites produced a phylogeny of

bat hosts comparable to that based on karyologic studies. Moreover, closely related species of myobiids infest closely related species of hosts (Uchikawa and Baker 1993).

Ectoparasite studies have led to the discovery of new host taxa that were cryptic based on considerations of morphology. Eurasian *Miniopterus* were reexamined and seven new species described (Maeda 1982) because of work associated with ectoparasites (Uchikawa 1984)). Similarly, work on the ectoparasites of *Noctilio* indicates that more than two species may exist in the genus (Wenzel 1976, Wenzel et al. 1966, Carl Dick unpub. data).

A study of the myobiids suggested two changes to pteropodid phylogeny (Uchikawa 1986). One suggestion, reassigning *Megaglossus* from the Macroglossinae to the Pteropodinae, was supported by a recent study of bat phylogeny (Jones et al. 2002), whereas the other, reassigning *Eonycteris* from the Macroglossinae to the Pteropodinae, was not. Studies (Uchikawa 1987, Machado-Allison 1967) on two ectoparasite families (i.e., Myobiidae and Spinturnicidae) suggested that the Desmodidae should be relegated to a subfamily within the Phyllostomidae. This arrangement was adopted subsequently and generally is accepted by mammal taxonomists (Jones et al. 2002, Koopman 1993).

Subfamilial Status of *Sturnira*. *Artibeus fimbriatus*, *A. jamaicensis* and *Sturnira lilium* in Paraguay (Tables 2.15, 2.16, and 2.21, Appendices B and C) have primary associations with a streblid from each ecomorphological group; a fur swimmer (*Metelasmus* spp.), fur runner (*Megistopoda* spp.), and wing crawler (*Aspidoptera* spp.). By using different safe spaces, three species from the same ectoparasite family avoid competition and co-exist on the same host. Two species of *Artibeus* (*A. fimbriatus* and *A. jamaicensis*) and *S. lilium* have primary associations with the same three genera of streblids. Interestingly, *A. lituratus* have a primary association with none of these streblid genera, but do have a primary association with *Paratrichobius longicrus*, a fur runner (Table 2.17, Appendices B and C). Moreover, all three species of *Artibeus* have primary associations with the same macronyssid (*Macronyssoides kochi*) and spinturnicid (*Periglischrus iheringi*), whereas *Sturnira* have a primary association with a different macronyssid and spinturnicid, *Parichoronyssus euthysternum* and *Periglischrus ojasti*,

respectively. No explanation for the divergence between streblids on *Artibeus lituratus* and those on other species of *Artibeus* is forthcoming. All three species of *Artibeus* are ecologically similar. In addition, *A. lituratus* and *A. jamaicensis* have nearly identical geographic distributions, whereas the distribution of *A. fimbriatus* is restricted to southern Brazil and Paraguay (Eisenberg 1989, Koopman 1982, Redford and Eisenberg 1992, Reid 1997). The subfamilial status of *Sturnira* is uncertain. Some authors (e.g., Redford and Eisenberg 1992) place *Sturnira* in a separate subfamily, Sturnirinae, however, more recent works (e.g., Jones et al. 2002, Baker et al. 2003) include *Sturnira* in the same subfamily as *Artibeus*, Stenodermatinae. That ectoparasite assemblages of *Artibeus* are more similar to those from *Sturnira* than to those of other stenodermatine bats is evidence that *Sturnira* belongs in the Stenodermatinae.

Relationships among the Vampires, *Glossophaga* and *Carollia*. In Paraguay, *Carollia perspicillata*, *Glossophaga soricina*, and the vampires, *Desmodus rotundus* and *Diaemus youngi*, each harbor fur swimmers of the genus *Strebla* and wing crawlers of the genus *Trichobius* (Tables 2.11-2.14). Desmodontinae is a sister taxon to all other phyllostomid subfamilies as a group (Baker et al. 2003, Jones et al. 2002). Although the streblids of *Carollia* and *Glossophaga* are more similar to those of vampires than their respective sister groups, it is more likely that *Trichobius* and *Strebla* are primitive genera that infested phyllostomid ancestors before speciation than it is that carolline and glossophagine bats are more closely related to desmodontine bats than to stenodermatine and lonchophylline bats, respectively (Jones et al. 2002).

Species Abundance Distributions and Resource Partitioning

In its most basic sense, biodiversity means “life on earth” (Huston 1994). However, the concept of biodiversity is not simple to measure, includes variation at all taxonomic levels, and has genetic, phenotypic, functional, and ecological attributes (Stevens and Willig 2000, Willig 2002*a*, Zak et al. 1994). Measurement of biodiversity began as a simple idea; the number of species in an area. Despite apparent simplicity, even this basic measure presented problems (e.g., taxonomic difficulties, effect of sample

size or area). Measures of biodiversity were expanded to include estimates of relative abundance (e.g., Shannon and Simpson diversity indices – Magurran 1988). Nonetheless, attempts to estimate biodiversity in a single metric (e.g. species richness, Simpson's diversity Index) are criticized because much information is lost (Willig 2002*b*). As data sets containing species richness and relative abundances were accumulated, patterns of species abundance distributions (SADs) were recognized (Magurran 1988). Species abundances are not distributed evenly, rather few species are common, few occur at intermediate abundances, and most are rare. Species abundance models (e.g., broken stick, geometric series) were developed and advocated as the best basis for examination of taxonomic components of biodiversity because SADs use all of the information gathered about a community or assemblage (May 1975, Southwood 1978). SADs usually are compared to four models (i.e., geometric series (GS), logseries, lognormal, and broken stick (BS)), which represent a continuum from less even (GS) to the more even (BS) distributions.

The lognormal distribution is the most common model used to describe SADs (May 1975). However, "the lognormal distribution reflects the statistical Central Limit Theorem; conversely, in those special circumstances where broken-stick, geometric series, or logseries distributions are observed, they reflect features of the community biology." (May 1975). This interpretation of the lognormal may be somewhat misleading, as the lognormal may suggest that many independent and additive factors contribute to observed abundance distributions within a group of species. Nonetheless these factors are difficult to distinguish in the present study. By fitting an empirical SAD of the ectoparasite assemblage of each of the 24 common host species to the GS and BS models, I can evaluate whether: (1) hosts are harsh environments that promote species-poor assemblages with high levels of dominance (i.e., consistent with the GS model), or (2) a single limiting resource is shared relatively evenly by ectoparasite species (i.e., consistent with the BS model). Ectoparasite assemblage richness is usually low (i.e., fewer than six species); therefore analyses of these assemblages lack power. Generally,

SADs that fit both models are examples of situations for which analyses were not powerful enough to distinguish between competing models.

Visual inspection of the SADs of ectoparasites from common bat hosts of Paraguay (Figs. D1 – D39) evince two noteworthy patterns. First, SADs that fit a BS model had one or more of the following traits: A) co-dominant species (i.e., species with high and similar abundances), B) co-subdominant species (i.e., multiple species with similar and intermediate abundances), and C) several rare species (i.e., species composing < 5% of the total number of individuals). Second, SADs that fit the GS model had one dominant species, one subdominant species, and few rare species.

If empirical SADs fit the BS model, the interpretation often is that species are sharing a single limiting resource in a relatively even manner compared to SADs that fit the other three common theoretical models (i.e., LS, LN, and GS). The resource for which bat ectoparasites compete likely is space on the host, in particular locations where mortality from grooming is unlikely (i.e., safe space). The "sharing" of a resource implies that participating species are not engaged in intense competition or that competition has led to niche partitioning in the past. A generally accepted view of parasite coexistence considers most parasite communities to be unsaturated; interspecific competition does not play a major structuring role as seen in demographics (Mouillot et al. 2003). In Paraguay, 13 of the 24 SADs for bat ectoparasites fit the BS model. There are three probable explanations: 1) these assemblages are not structured by competitive interactions, 2) competitors already have been excluded from the assemblage, or 3) competitors have diverged to take advantage of distinct safe spaces.

Only one assemblage fit the GS model but not the BS model. The k-value (% of remaining niche space pre-empted by each species) for the five SADs that fit the GS model ranged from 0.45 – 0.73 ($\bar{k}$ = 0.59). In general, assemblages with higher k-values have fewer species because higher rates of niche space pre-emption leave less niche space for subsequent species (Magurran 1988). The assemblage of primary ectoparasites for those SADs that fit the GS averaged 4.4 species per assemblage. In contrast, a relatively simple marine fish assemblage had 70 species and a k of 0.14 (Fujita et al.

1993), whereas an assemblage of epiphytic chironomids had nine species and a k of 0.507 (Tokeshi 1986, 1990). Ectoparasite species partition safe spaces relatively evenly, as described by the BS, and not by dominant species pre-empting a constant proportion of the available safe space, as in the GS. Because each type of safe space requires distinctive specialization, all available safe space cannot be used by a single ectoparasite species as modeled by the GS. For example, bat flies, spinturnicids (wing mites), and macronyssids each have unique safe spaces to which they are adapted (i.e., a safe space for a spinturnicid is not safe for a streblid or macronyssid), which in turn leads to a relatively even SAD. Trade-offs exist. Because each safe space requires a particular suite of adaptations, each parasite species may only effectively avail itself of one safe space, leaving other niches open for other specialists. In addition, priority rules (e.g., Paine 1977) likely are in effect (i.e., the first ectoparasite species to use a particular safe space has a distinct advantage over new colonizers) in ecological and evolutionary contexts. Evolutionarily, once safe spaces on host species are occupied, it likely is difficult for alternative ectoparasite species to evict well-adapted species or evade a hosts' grooming activity, effectively leading to competitive exclusion. Ecologically, immigration rates are sufficiently low so that early colonists can reproduce and saturate a safe space prior to the arrival of potential competitors.

Of Birds and Bats

Few investigations (e.g., Gannon and Willig 1995) have attempted to determine the effect of host ecology or morphology on bat ectoparasite assemblages; however, many studies of the effect of bird biology on avian parasite assemblages have been published. Ecologically, birds and bats are similar and present ectoparasites with comparable host opportunities. Many birds and bats roost in trees, many species are colonial for at least part of the year, some species of each migrate, and both are volant homeotherms. Therefore, bat ectoparasite assemblages may be more comparable to those of birds than to other mammalian taxa.

Although bird ectoparasite assemblages have been more thoroughly studied than those of bats, basic information (e.g., incidence, prevalence, density) is published rarely. The effect of ectoparasite infestations on avian hosts include investigations of breeding success (e.g. Allander 1998, Darlová et al. 1997, Santos Alves 1997), long-term survival (Brown et al. 1995), nest-site choice (e.g., Loye and Carrol 1991, Mappes et al. 1994), mate choice (e.g., Spurrier et al. 1991), mating behavior (e.g., Møller 1991*a*, 1991*b*), and the cost of colonial living (e.g., Brown and Brown 1986, Poulin 1991). Despite the tremendous quantity of data concerning avian hosts, few studies focus on ectoparasites or their assemblage structure. Even less is available concerning comparative ecology of ectoparasite assemblages on different bird species. This is unfortunate, considering that birds harbor the most studied ectoparasite communities on wild animals.

Pruett-Jones and Pruett-Jones (1991) analyzed tick burdens of 115 bird species from New Guinea and concluded little other than adult ticks do not parasitize birds, with > 95% of individuals harboring $\leq$ 1 tick, and only one tick species was present on the entire host assemblage. Similar to the situation characterizing ectoparasite assemblages of bats, ticks are not key components of avian ectoparasite assemblages, are not host specific or abundant, and lack taxonomic richness (Pruett-Jones and Pruett-Jones 1991).

The most noteworthy difference between ectoparasite assemblages on bats and birds is that the latter may host orders of magnitude more individuals that do the former. Indeed, infestations of over 30,000 mites per nest have been documented to have no effect on fledgling mortality in passerines (Burtt et al. 1991). Most studies find only minor differences in fledgling survivorship and weight as a function of parasite load (Loye and Zuk 1991 and sources therein).

There are many reasons birds harbor more species rich and dense ectoparasite assemblages than do bats. Feathers provide a more complex habitat than does hair. This allows for more specialization in bird ectoparasites than in bat ectoparasites (Crompton 1991). The complex anatomical structure of feathers allows parasites to live on, among, and inside feathers. Indeed, many feather types have shafts large enough to house

ectoparasites (Proctophyllodids) that spend nearly their entire lives inside a feather, only exiting during molting phases.

In terms of ambient temperature, birds provide a more stable habitat than do bats. Bats are capable of heterothermy; most bat species are torpid (Altringham 1996, Crichton and Krutzsch 2000, Findley 1993, Fleming 1988, Hill and Smith 1984, Humphrey and Cope 1976) and many bat species hibernate (Altringham 1996, Findley 1993, Hill and Smith 1984, Humphrey and Cope 1976) for extended periods of time (Fleming and Eby 2003). Compared to bird ectoparasites, bat ectoparasites must deal with greater temperature fluctuations for longer periods.

Most birds build nests with complex structure providing "off-host" refuges for ectoparasites. Moreover, nests are integral to birds for protection and rearing young. Birds use the same nest throughout egg incubation and rearing of the young (Gill 1990), which lasts several months and is longer than the life cycle of most ectoparasites. In addition, many bird species use the same nest for consecutive years. All of these factors (e.g., complex structure, reliable return, extended use) make birds more reliable hosts than bats for ectoparasites that spend time off-host. In contrast, foliage roosting bats use multiple (usually 3-7) locations for roosting during short time intervals and frequently switch roosts (i.e., use different day-roosts on consecutive days), which results in roosts being unoccupied for several days at a time (Kunz 1982, Kunz and Lumsden 2003). Indeed, most bats that roost in foliage, tree cavities, or beneath exfoliated bark switch roosts daily, often never returning to a roost (Kunz and Lumsden 2003). Because most bat ectoparasites survive < 2 days without a meal, roost switching habits enhance risk for nest-parasites of bats. Nest-parasites are an appreciable component of bird ectoparasite assemblages (Allander 1998, Brown and Brown 1986, Darlová et al. 1997, Loye and Carrol 1991, Mappes et al. 1994, Møller 1991*a*, 1991*b*, Poulin 1991, Santos Alves 1997); however, bats (even relatively roost-faithful cave-dwelling bats) have few ectoparasites (e.g., trombiculids and some bat flies) that do not spend nearly all of their time on the host. Because space on the host is a limiting resource for bat ectoparasites, the lack of a

nest or reliable roost location further reduces the number of ectoparasite species and individuals in bat ectoparasite assemblages.

Conclusions

The ectoparasite collection methodology employed during this study resulted in less cross-host contamination (< 1/3 the contamination rate) than in previous studies (Herrin and Tipton 1975). Nonetheless, families of smaller ectoparasites (e.g., Myobiidae, Chirodiscidae) are under-represented here because their collection requires more time-consuming, careful inspection than the method employed in Paraguay. In general, host-parasite associations in Paraguay corroborate previously reported associations. Analysis of the SADs of ectoparasite assemblages (restricted to primary associations) revealed that the limiting resource for ectoparasites (i.e., space on the host) is relatively evenly divided among component taxa, within the context of commonly used models of SADs such as the broken stick, geometric series, log normal, and log series models. Ectoparasite SADs are not consistent with models (i.e., geometric series) based on niche preemption hypotheses. Observations of insects ectoparasitic on bats demonstrate that competition is reduced by specializations for locomotion on particular parts of the host (i.e., microhabitats). Three suites of ecomorphological specializations (e.g., fur swimmers, fur runners, wing crawlers) characterize streblids. Co-existence of multiple fly species on individual hosts often is attained by microhabitat specialization in this taxon. Host grooming activity is a major cause of bat fly mortality. Nonetheless, observations of bat flies on live hosts indicate that most ectoparasite movements result from inter- and intra-specific interactions among ectoparasites, and are not responses to host grooming. Therefore, competition may play a major role in limiting ectoparasite diversity on bat hosts. Indeed, there is evidence that some bat flies protect their host from infestation by other ectoparasite species. Ecological understanding of microhabitat use by arachnid ectoparasites of bats is minimal. Therefore, it is difficult to hypothesize ecological mechanisms that limit ectoparasitic arachnid richness or abundance.

No previous studies have considered the entire ectoparasite assemble of an entire host assemblage. Therefore, comparisons with ectoparasite assemblages from other host species or geographic regions are difficult. Bats are more similar to birds than to other mammals, and bird ectoparasites are better known than are those of other mammals. However, many differences in behavior and anatomy reduce parasite richness and abundance on bats in comparison to birds. Bats do not build nests and frequently change roosts, which essentially eliminates nest-type parasites from bat ectoparasite assemblages. In addition, bat pelage is not as complex as bird plumage, providing fewer safe spaces for ectoparasites.

Ectoparasite assemblages provide many opportunities for the study of mechanisms that structure communities. Continued, conscientious collection and analysis of complete ectoparasite assemblages from diverse collections of hosts from many geographic regions will broaden scientific understanding of community assembly rules, co-speciation, and co-evolution, as well as host and ectoparasite phylogenies.

Literature Cited

Allander, K. 1998. The effects of an ectoparasite on reproductive success in the great tit: a 3-year experimental study. Canadian Journal of Zoology 76:19-25.

Altringham, J. D. 1996. Bats: biology and behaviour. Oxford University Press, New York, New York.

Anderson, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History 231:1-652.

Baker, E. W., T. M. Evans, D. J. Gould, W. B. Hull, and H. L. Keegan. 1956. A manual of parasitic mites of medical or economic importance. National Pest Control Association, Inc., Washington D. C.

Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche. 2003. Diversification among New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:1-32.

Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham. 1988. Genetic studies of Lasiurus (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University 117:1-15.

Barquez, R. M., M. A. Mares, and J. K. Braun. 1999. The bats of Argentina. Special Publications, The Museum, Texas Tech University 42:1-275.

Bertoni, G. T., and J. R. Gorham. 1973. The geography of Paraguay. Pp. 9-31 in Paraguay: ecological essays (J. R. Gorham, ed.), Academy of Arts and Sciences of the Americas, Miami, Florida.

Brennan, J. M. 1958. *Beamerella* and *Kaaia*, two new genera of chiggers from South America (Acarina, Trombiculidae). Journal of Kansas Entomological Society 31:71-75

Brennan, J. M. 1970. Chiggers from the Bolivian-Brazilian border (Acarina: Trombiculidae). The Journal of Parasitology 56:807-812.

Brennan, J. M., and M. L. Goff. 1977. Keys to the genera of chiggers of the Western Hemisphere (Acarina: Trombiculidae). The Journal of the Parasitology 63:554-566.

Brennan, J. M., and J. T. Reed. 1974. The genus Eutrombicula in Venezuela (Acarina: Trombiculidae). The Journal of Parasitology 60:699-711.

Brennan, J. M., and J. T. Reed. 1975. A list of Venezuela chiggers, particularly of small mammalian hosts (Acarina: Trombiculidae). Brigham Young University Science Bulletin, Biological Series 20(1):45-75.

Brennan, J. M., and C. E. Yunker. 1966. The chiggers of Panama (Acarina: Trombiculidae). Pp. 221-266 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Brown, C. R., and M. B. Brown. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). Ecology 67:1206-1218.

Brown, C. R., M. B. Brown, and B. Rannala. 1995. Ectoparasites reduce long-term survival of their avian host. Proceedings of the Royal Society of London, Series B 262:313-319.

Burtt, E. H., Jr., W. Chow, and G. A. Babbitt. 1991. Occurrence and demography of mites of tree swallow, house wren, and eastern bluebird nests. Pp. 104-122 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M Zuk, eds.). Oxford University Press, Oxford, Great Britain.

Camargo, J. A. 1992. Can dominance influence stability in competitive interactions? Oikos 64:605-609.

Chalcraft, D. R., J. W. Williams, M. D. Smith, and M. R. Willig. 2004. Scale dependence in the relationship between species richness and productivity: the role of spatial and temporal turnover. Ecology (In Press).

Crampton, A., I. McKay, and S. C. Barker. 1996. Phylogeny of ticks (Ixodida) inferred from nuclear ribosomal DNA. International Journal of Parasitology 26:511-517.

Crichton, E. G., and P. H. Krutsch. 2000. Reproductive biology of bats. Academic Press, Cambridge, Great Britain.

Crompton, D. W. T. 1991. Birds as habitat for parasites. Pp. 253-270 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M Zuk, eds.). Oxford University Press, Oxford, Great Britain.

Darlová, A., H. Hoi, and B. Schleicher. 1997. The effect of ectoparasite nest load on the breeding biology of the Punduline tit *Remiz pendulinus*. Ibis 139:115-120.

de la Cruz, J. 1969. Nueva especie de acaro (Acarina: Listrophoridae) parásito de murciélagos cubanos. Poeyana, Seria A 62:1-8.

Dusbábek, F. 1969*a*. To the phylogeny and zoogeography of bats (Chiroptera) based on the study of their parasitic mites (Acarina). Proceedings of the First International Bat Conference 19-24.

Dusbábek, F. 1969*b*. To the phylogeny of genera of the family Myobiidae. Acarologia 11:537-574.

Dusbábek, F. 1969*c*. Generic revision of the myobiid mites (Acarina: Myobiidae) parasitic on bats. Folia Parasitologica 16:1-17.

Dusbábek, F. 1973. A sytematic review of the genus *Pteracarus* (Acariformes: Myobiidae). Acarologia 15:240-288.

Dusbábek, F., and J. de la Cruz. 1966. Nuevos géneros y espécies de acaros (Acarina: Listrophoridae) parásitos de murciélagos cubanos. Poeyana, Seria A 31:1-20.

Dusbábek, F., and F. S. Lukoschus. 1974. Parasitic mites of Surinam XXVI. Mites of the genus *Eudusbabekia* (Myobiidae: Trombidiformes) of the leaf-nosed bat subfamily Phyllostominae. Acarologia 16:476-499.

Eisenberg, J. F. 1989. Mammals of the neotropics: the northern neotropics. Volume 1, Panamá, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, Illinois.

Fain, A. 1978. Mites of the family Myobiidae (Acarina: Prostigmata) from mammals in the collection of the British Museum (Natural History). Bulletin of the British Museum of Natural History, Zoological Series 33:193-229.

Fain, A. 1982*a*. The labidocarpine mites (Acari, Chirodiscidae) from oriental bats. III. Genera *Paralabidocarpus* Pinichpongse, 1963, *Labidocarpoides* Fain, 1970, *Labidocarpus* Troussart, 1895, and *Alabidocarpus* Ewing, 1929. Systematic Parasitology 4:303-336.

Fain, A. 1982*b*. The labidocarpine mites (Acari, Chirodiscidae) from oriental bats. IV. Genera *Olabidocarpus* Lawrence, 1948, *Dentocarpus* Dusbábek & Cruz, 1966, *Labidocarpellus* Fain, 1976, and *Pteropiella* Fain, 1970, with a key to the genera of Chirodiscidae. Systematic Parasitology 4:337-360.

Fairchild, G. B., G. M. Kohls, and V. J. Tipton. 1966. The ticks of Panama (Acarina: Ixodoidea). Pp. 167-220 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Fariña Sanchez, T. 1973. The climate of Paraguay. Pp. 33-38 in Paraguay: ecological essays (J. R. Gorham, ed.), Academy of Arts and Sciences of the Americas, Miami, Florida.

Ferris, G. F., and R. L. Usinger. 1939. The family Polyctenidae (Hemiptera: Heteroptera). Microentomology 4:1-50.

Ferris, G. F., and R. L. Usinger. 1945. Notes and descriptions of American Polyctenidae (Hemiptera). Pan Pacific Entomologist 21:121-124.

Findley, J. S. 1993. Bats: a community perspective. Cambridge University Press, Cambridge, Great Britain.

Fleming, T. H. 1988. The short-tailed fruit bat: a study in plant-animal interactions. The University of Chicago Press, Chicago, Illinois.

Fleming, T. H., and P. Eby. 2003. Ecology of bat migration. Pp. 156-208 in Bat ecology (T. H. Kunz and M. B. Fenton, eds). University of Chicago Press, Chicago, Illinois.

Freeland, W. J. 1983. Parasites and the coexistence of animal host species. The American Naturalist 121:223-236.

Fritz, G. N. 1983. Biology and ecology of bat flies (Diptera: Streblidae) on bats in the genus *Carollia*. Journal of Medial Entomology 20:1-10.

Fujita, T., T. Inada, and Y. Ishito. 1993. Density, biomass, and community structure of demersal fishes off the Pacific coast of northeastern Japan. Journal of Oceanography 49:211-229.

Furman, D. P. 1966. The spinturnicid mites of Panama (Acarina: Spinturnicidae). Pp. 125-166 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Gannon, M. R., and M. R. Willig. 1995. Ecology of ectoparasites from tropical bats. Environmental Entomology 25:1495-1503.

Gannon, M.R., and M.R. Willig. 1997. The effect of lunar illumination on movement and activity of the red fig-eating bat (*Stenoderma rufum*). Biotropica 29:525-529.

Gaston, K. 1996. Species-range-size distributions: patterns, mechanisms and implications. Trends in Ecology and Evolution 11:197-200.

Gettinger, D., and K. A. Ernest. 1995. Small-mammal community structure and the specificity of ectoparasite associations in central Brazil. Revista Brasiliera de Biologia 55:331-341.

Gettinger, D., and R. Gribel. 1989. Spinturnicid mites (Gamasida: Spinturnicidae) associated with bats in central Brasil. Journal of Medical Entomology 26:491-493.

Gill, Frank B. 1990. Ornithology. W. H. Freeman and Company, New York, New York.

Gorham, J. R. 1973. The Paraguayan Chaco and its rainfall. Pp. 39-60 in Paraguay: ecological essays (J. R. Gorham, ed.), Academy of Arts and Sciences of the Americas, Miami, Florida.

Gorresen, P. M., and M. R. Willig. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. Journal of Mammalogy 85:688-697.

Graciolli, G., and C. W. Dick. 2004. A new species of *Metelasmus* (Diptera: Streblidae: Streblinae) from southern South America. Zootaxa 509:1-8.

Guerrero, R. 1993. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. I. Clave para los géneros y Nycterophiliinae. Acta Biológica Venezuelica 14 (4):61-75.

Guerrero, R. 1994*a*. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. II. Los grupos: *pallidus*, *caecus*, *major*, *uniformis* y *longipes* del género *Trichobius* Gervais, 1844. Acta Biológica Venezuelica 15 (1):1-18.

Guerrero, R. 1994*b*. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. IV. Trichobiinae con alas desarrolladas. Boletín de Entomología Venezolana 9 (2):161-192.

Guerrero, R. 1995*a*. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. III. Los grupos: *dugesii*, *dunni*, y *phyllostomae* del género *Trichobius* Gervais, 1844. Acta Biológica Venezuelica 15 (3/4):1-27.

Guerrero, R. 1995*b*. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. V. Trichobiinae con alas reducidas o ausentes y miscelaneos. Boletín de Entomología Venezolana 10 (2):135-160.

Guerrero, R. 1996. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. VI. Streblinae. Acta Biológica Venezuelica 16 (2):1-26.

Guerrero, R. 1997. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. VII. Lista de espécies, hospedadores y paises. Acta Biológica Venezuelica 17 (1):9-24.

Guimarães, L. R. 1966. Nycteribiid bat flies from Panama (Diptera: Nycteribiidae). Pp. 393-404 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Guimarães, L. R. 1972. Venezuelan nycteribiid batflies (Diptera: Nycteribiidae). Brigham Young University Science Bulletin, Biological Series 17 (1):1-11.

Hagan, H. R. 1951. Embryology of the viviparous insects. Ronald Press, New York, New York.

Handley, C. O., Jr. 1987. New species of mammals from northern South America: fruit-eating bats, genus *Artibeus* Leach. Pp. 163-172 in Studies in neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana, Zoology (New Series) 39:1-506.

Hayes, F. E. 1995. Status, distribution and biogeography of the birds of Paraguay. Monographs in Field Ornithology No. 1, 1-230.

Herrin, C. S., and V. J. Tipton. 1975. Spinturnicid mites of Venezuela. Brigham Young University Science Bulletin, Biological Series 20 (2):1-72.

Hill, J. E., and J. D. Smith. 1984. Bats: a natural history. Heffers Printers Ltd., Cambridge, Great Britain.

Hoogstraal, H. 1985. Argasid and nuttalliellid ticks as parasites and vectors. Advances in Parasitology 24:135-238.

Hoogstraal, H., and A. Aeschlimann. 1982. Tick-host specificity. Bulletin de la Société Entomologique Suisse 55:5-32.

Hoskins, J. D. 1991. Ixodid and argasid ticks: keys to their identification. Veterinary Clinics of North America: Small Animal Practice 21:185-196.

Hueck, K. 1972. As florestas da América do Sul: ecologia, composição e importância econômica. Editôra da Universidade de Brasília, Editôra Polígono S. A., São Paulo, Brazil.

Humphrey, S. R., and J. B. Cope. 1976. Population ecology of the little brown bat, Myotis lucifugus, in Indiana and North-central Kentucky. The American Society of Mammalogists, Special Publications 4:1-81.

Huston, Michael, A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, New York.

Jones, E. K, C. M. Clifford, J. E. Keirans, and G. M. Kohls. 1972. Ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of *Amblyomma* in the Western Hemisphere. Brigham Young University Science Bulletin, Biological Series 17(4):1-40.

Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biological Review 77:223-259.

Kim, K. C. 1985. Evolutionary relationships of parasitic arthropods and mammals. Pp. 3-82 in Coevolution of parasitic arthropods and mammals (K. C. Kim, ed.). John Wiley & Sons, New York, New York.

Koopman, K. F. 1982. Biogeography of the bats of South America. Pp. 273-302 in Mammalian Biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications of Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh 6:1-539.

Koopman, K. F. 1993. Order Chiroptera. Pp. 137-241 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D. C.

Krantz, G. W. 1970. A manual of acarology, First edition. Oklahoma State University. Book Stores, Inc., Corvalis, Oregon.

Kunz, T. H. 1976. Observations on the winter ecology of the bat fly *Trichobius corynorhini* Chockerell (Diptera: Streblidae). Journal of Medical Entomology 12:631-636

Kunz, T. H. 1982. Roosting ecology. Pp. 1-56 in Ecology of bats. (T. H. Kunz, ed.). Plenum Press, New York, New York.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3-89 in Bat ecology (T. H. Kunz and M. B. Fenton, eds). University of Chicago Press, Chicago, Illinois.

Loomis, R. B., and W. J. Wrenn. 1984. Systematics of the pest chigger genus *Eutrombicula* (Acari: Trombiculidae). Pp. 152-165 in Acarology VI (D. A. Griffiths and C. E. Bowman, eds.). Chichester: E. Horwood, Halsted Press, New York, New York.

López-González, C. 1998. Systematics and Zoogeography of the Bats of Paraguay. Ph.D. dissertation, Texas Tech University, Lubbock, Texas.

López-González, C. 2005. Los murciélagos de Paraguay. Publicaciones Comité Español MAB y Red Ibero MAB (in press).

Loye, J. E., and S. P. Carrol. 1991. Nest ectoparasite abundance and cliff swallow colony site selection, nestling development, and departure time. Pp. 222-241 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M Zuk, eds.). Oxford University Press, Oxford, Great Britain.

Loye, J. E., and M. Zuk. 1991. Bird-parasite interactions: ecology, evolution, and behaviour. Oxford University Press, Oxford, Great Britain.

Lukoschus, F. S., G. Scheperboer, E. Méndez, and A. Fain. 1981. *Eudusbabekia* (*Synoecomyobia*) *artibei*, new subgenus, new species (Acarina: Prostigmata: Myobiidae), infesting the phyllostomids bat *Artibeus phaeotis* in Panama. Pacific Insects 23:478-486.

McDaniel, B. 1970. The labidocarpid batmites of Nicaragua (Listrophoroidea : Labidocarpidae). Acarologia 12:803-823.

McDaniel, B. 1973. Labidocarpid bat-mites of Venezuela (Listophoroidea: Labidocarpidae). Brigham Young University Science Bulletin, Biological Series 17(2):15-32.

Machado-Allison, C. E. 1964. Notas sobre Mesostigmata Neotropicales. II. Cuatro nuevas especies de *Periglischrus* Kolenati, 1857. (Acarina, Spinturnicidae). Revista de la Sociedad Mexicana de Historia Natural 25:193-207.

Machado-Allison, C. E. 1965. Las espécies Venezolanas del género *Periglischrus* Kolenati 1857. Acta Biología Venezuelica 4:259-348.

Machado-Allison, C. E. 1967. The systematic position of the bats *Desmodus* and *Chilonycteris*, based on host-parasite relationships (Mammalia; Chiroptera). Proceedings of the Biological Society of Washington 80:223-226.

Maeda, K. 1982. Studies on the classification of *Miniopterus* in Eurasia, Australia and Melanesia. Mammalian Science Supplement 1: 1-176.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

Mappes, T., J. Mappes, and J. Kotiaho. 1994. Ectoparasites, nest site choice and breeding success in the pied flycatcher. Oecologia 98:147-149.

Margolis, L., R. Anderson, and J. Holmes. 1982. The use of ecological terms in parasitology. (Report of an ad-hoc committee of the American Society of Parasitologists). Journal of Parasitology 68:131-133.

Marshall, A. G. 1970. The life cycle of *Basilia hispida* Theodor 1967 (Diptera: Nycteribiidae) in Malaysia. Parasitology 61:1-18.

Marshall, A. G. 1971. The ecology of *Basilia hispida* (Diptera: Nycteribiidae) in Malaysia. Journal of Animal Ecology 40:141-154.

Marshall, A. G. 1976. Host-specificity amongst arthropods ectoparasitic upon mammals and birds in the New Hebrides. Ecological Entomology 1:189-199.

Marshall, A. G. 1982*a*. Ecology of insects ectoparasitic on bats. Pp. 369-401 in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, New York.

Marshall, A. G. 1982*b*. The ecology of *Eoctenes spasmae* (Hemiptera: Polyctenidae) in Malaysia. Biotropica 14:50-55.

Matheson, R. 1935. Three new species of ticks, *Ornithodorus* (Acarina: Ixodoidea). The Journal of Parasitology 21:347-353.

Matheson, R. 1941. A new species of tick, *Ornithodoros anduzei* (Ixodoidea, Argasidae) from bat caves in Venezuela. Boletín de Entomología Venezolana 1:3-5.

May, R. M. 1975. Patterns of species abundance and diversity. Pp. 81-120 in Ecolgy and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap Press of Harvard University, Cambridge, Massachusetts.

Møller, A. P. 1991*a*. Parasites, sexual ornaments, and mate choice in the barn swallow. Pp. 328-343 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M Zuk, eds.). Oxford University Press, Oxford, Great Britain.

Møller, A. P. 1991*b*. Parasite load reduces song output in a passerine bird. Animal Behaviour 41:723-730.

Mouillet, D., M. George-Nascimento, and R. Poulin. 2003. How parasites divide resources: a test of the niche apportionment hypothesis. Journal of Animal Ecology 72:757-764.

Myers, P. 1982. Origins and affinities of the mammal fauna of Paraguay. Pp. 85-93 in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications, Pymatuning Laboratory of Ecology 6:1-539.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 10:99-109.

Oliver, J. H. Jr. 1989. Biology and systematics of ticks (Acari: Ixodida). Annual Review of Ecology and Systematics 20:397-430.

Overal, W. L. 1980. Host-relations of the batfly *Megistopoda aranea* (Diptera: Streblidae) in Panama. University of Kansas Science Bulletin 51:1-20.

Overal, W. L., and L. R. Wingate. 1976. The biology of the batbug *Stricticimex antennatus* (Hemiptera: Cimicidae) in South Africa. Annals of the National Museum 22:821-828.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Special Publications of the Academy of Natural Sciences, Philadelphia 12:245-270.

Pianka, E. R. 1970. On r- and k-selection. The American Naturalist 104:592-597.

Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley & Sons, New York, New York.

Pielou, E. C. 1975. Ecological Diversity. John Wiley & Sons, New York, New York.

Pik, A. J., I. Oliver, and A. J. Beattie. 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Australian Journal of Ecology 24:555-562.

Pinichpongse, S. 1963*a*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (1st series). Acarologia 5:81-91.

Pinichpongse, S. 1963*b*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part Two). Acarologia 5:266-278.

Pinichpongse, S. 1963*c*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part three). Acarologia 5:397-404.

Pinichpongse, S. 1963*d*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part four). Acarologia 5:620-627.

Poulin, R. 1991. Group-living and infestation by ectoparasites in passerines. The Condor 93:418-423.

Pruett-Jones, M., and S. Pruett-Jones. 1991. Analysis and ecological correlates of tick burdens in a New Guinea avifauna. Pp. 154-176 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M. Zuk, eds.). Oxford University Press, Oxford, Great Britain.

Radovsky, F. J. 1966. Revision of the macronyssid and laelapid mites of bats: outline of classification with descriptions of new genera and new type species. Journal of Medical Entomology 3:93-99.

Radovsky, F. J. 1967. The Macronyssidae and Laelapidae (Acarina: Mesostigmata) parasitic on bats. University of California Publications in Entomology 46:1-288.

Redford, K. H., and J. F. Eisenberg. 1992. Mammals of the Neotropics: the southern cone. Volume 2, Chile, Argentina, Uruguay, Paraguay. The University of Chicago Press, Chicago, Illinois.

Reed, J. T., and J. M. Brennan. 1975. The subfamily Leeuwenhoekinae in the Neotropics (Acarina: Trombiculidae). Brigham Young University Science Bulletin, Biological Series 20(1):1-42.

Reid, F. A. 1997. A field guide to the mammals of Central America and southeast Mexico. Oxford University Press, New York, New York.

Ronderos, R. A. 1959. Polycténidae americanos. I. (Hemiptera). Actas y Trabajos del Primer Congreso Sudamericano de Zoologia 3:173-180.

Ronderos, R. A. 1962. Polycténidae americanos. II. (Hemiptera). Acta Zoologica Lilloana 18:259-262.

Ross, A. 1961. Biological studies on bat ectoparasites of the genus *Trichobius* (Diptera: Streblidae) in North America, North of Mexico. The Wasmann Journal of Biology 19:229-246.

Rudnick, A. 1960. A revision of the mites of the family Spinturnicidae (Acarina). University of California Publications in Entomology 17: 157-283.

Santos Alves, M. A. 1997. Effects of ectoparasites on the sand martin *Riparia riparia* nestlings. Ibis 139:494-496.

Saunders, R. C. 1975. Venezuelan Macronyssidae (Acarina: Mesostigmata). Brigham Young University Science Bulletin, Biological Series 20 (2):75-90.

Schuh, R. T., and J. A. Slater. 1995. True bugs of the world (Hemiptera: Heteroptera): Classification and Natural History. Cornell University Press, Ithaca, New York.

Sheeler-Gordon, L. L., and R. D. Owen. 1999. Host tracking or resource tracking? The case of *Periglischrus* wing mites (Acarina: Spinturnicidae) of leaf-nosed bats (Chiroptera: Phyllostomidae) from Michoacan, Mexico. Acta Zoológica Mexicana (nueva serie) 76:85-102.

Simmons, N. B., and R. S. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 1. Bats. Bulletin of the American Museum of Natural History 237:1-219.

Southwood, T. R. E. 1978. Ecological Methods. Chapman and Hall, London, Great Britain.

Spurrier, M. F., M. S. Boyce, and B. F. J. Manly. 1991. Effects of parasites on mate choice by captive sage grouse. Pp. 389-399 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M Zuk, eds.). Oxford University Press, Oxford, Great Britain.

Stevens, R. D., and M. R. Willig. 2000. Community structure, abundance, and morphology. Oikos 88:48-56.

Tokeshi, M. 1986. Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. Journal of Animal Ecology 55:491-506.

Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. Journal of Animal Ecology 59:1129-1146.

Uchikawa, K. 1984. Revision of the genus *Calcarmyobia* Radford (Trombidiformes: Myobiidae) and application of the mites to the systematics of their hosts (Chiroptera). Pp. 196-201 in Acarology VI (D. A. Griffiths and C. E. Bowman, eds.). Chichester: E. Horwood, Halsted Press, New York, New York.

Uchikawa, K. 1986. Myobiid mites of the genus *Pteropimyobia* Fain (Trombidiformes, Myobiidae) and information on host taxonomy deduced from them. Journal of Parasitology 72:249-256.

Uchikawa, K. 1987. Myobiid mites (Trombidiformes: Myobiidae) associated with vampire bats (Chiroptera: Phyllostomatidae) and information on host taxonomy deduced from them. Journal of Parasitology 73:640-645.

Uchikawa, K. 1988. Myobiidae (Acarina, Trombidiformes) associated with minor families of Chiroptera (Mammalia) and a discussion of phylogeny of chiropteran myobiid genera. Journal of Parasitology 74:159-176.

Uchikawa, K. and A. Baker. 1993. A new classification for the subgenera of the genus *Acanthophthirius* Perkins, with descriptions of twelve new taxa (Acarina, Trombidiformes, Myobiidae). Systematic Parasitology 25:81-108.

Uchikawa, K., and M. Harada. 1981. Evaluation of bat-infesting Myobiidae (Acarina, Trombidiformes) as indicators in taxonomy and phylogeny of host bats (Chiroptera). Zoological Magazine 90:351-361.

Ueshima N. 1972. New World Polyctenidae (Hemiptera), with special reference to Venezuelan species. Brigham Young University Science Bulletin, Biological Series 17 (1):13-21.

Universidad Nacional de Asuncion. 1994. Uso de la tierra y deforestación en la region oriental del Paraguay periodo 1984-1991. Vol. 1. Facultad de Ingenieria Agronómica, Carrera de Ingenieria Forestal, San Lorenzo, Paraguay.

Unruh, R. G. 1973. Colonization and agriculture in the Paraguayan Chaco. Pp. 105-108 in Paraguay: ecological essays (J. R. Gorham, ed.). Academy of Arts and Sciences of the Americas, Miami, Florida.

Webb, J. P., and R. B. Loomis. 1977. Ectoparasites. Pp. 57-119 in Biology of bats of the New World family Phyllostomatidae. Part II (R. J. Baker, J. K. Jones, Jr., D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University 13:1-364.

Wenzel, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin, Biological Series 20 (4):1-177.

Wenzel, R. L., and V. J. Tipton, editors. 1966*a*. Ectoparasites of Panama. Field Museum of Natural History, Chicago, Illinois.

Wenzel, R. L., and V. J. Tipton. 1966*b*. Some relationships between mammal hosts and their ectoparasites. Pp. 677-723 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Wenzel, R. L., V. J. Tipton, and A. Kiewlicz. 1966. The streblid batflies of Panama (Diptera: Streblidae). Pp. 405-675 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Whitaker, J. O., Jr, and D. B. Abrell. 1987. Notes on some ectoparasites from mammals of Paraguay. Entomological News 98:198-204.

Willig, M.R. 2002*a*. Exploring biodiversity in time and space: profitable directions for mammalogy in the 21st century. Mastozoologia Neotropical 8:107-109.

Willig, M.R. 2002*b*. Challenges to understanding dynamics of biodiversity in time and space. Paleobiology 29:30-33.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution and Systematics 34: 273-309.

Willig, M. R., S. J. Presley, R. D. Owen, and C. López-González. 2000. Composition and structure of bat assemblages in Paraguay: a subtropical – temperate interface. Journal of Mammalogy 81:386-401.

Wrenn, W. J., and R. B. Loomis. 1984. Host selectivity in the Genus *Eutromicula* (Acari: Trombicula). Pp. 160-165 in Acarology VI: volume 1 (D. A. Griffiths and C. E. Bowman, eds.). Halsted Press, New York, New York.

Zak, J.C., M.R. Willig, D.L. Moorhead, and H.G. Wildman. 1994. Functional diversity of microbial communities: a quantitative approach. Soil Biology and Biochemistry 26:1101-1108.

Table 2.1. Ecological characteristics of the seven biomes (Figure 2.1) that occur in Paraguay (Hayes 1995); east and west designate locations of biomes with respect to the Río Paraguay.

	Biome	Topography	Vegetation	Precipitation	Inundation	Humidity
West						
	Matogrosense (MG)	Flat	Forest	Medium	Seasonal	Sub-humid
	Alto Chaco (AC)	Flat	Forest	Low	None	Semi-arid
	Bajo Chaco (BC)	Flat	Palm	Medium	Seasonal	Semi-humid
East						
	Campos Cerrados (CC)	Hills	Forest	High	None	Semi-humid
	Central Paraguay (CP)	Hills	Forest	High	None	Humid
	Alto Paraná (AP)	Hills	Forest	Very high	None	Humid
	Ñeembucú (NE)	Hills	Grassland	High	Seasonal	Semi-humid

Table 2.2. Bat species known from Paraguay (López-González 1998, Willig et al. 2000) and their primary feeding preferences (Eisenberg 1989, Redford and Eisenberg 1992, Anderson 1997).

Taxon	Feeding preference
Family Emballonuridae	
Pteropteryx macrotis	Insectivore
Family Noctilionidae	
Noctilio albiventris	Insectivore
Noctilio leporinus	Piscivore
Family Phyllostomidae	
Anoura caudifer	Nectarivore
Artibeus fimbriatus	Frugivore
Artibeus jamaicensis	Frugivore
Artibeus lituratus	Frugivore
Carollia perspicillata	Frugivore
Chiroderma doriae	Frugivore
Chrotopterus auritus	Carnivore
Desmodus rotundus	Sanguinivore
Diaemus youngi	Sanguinivore
Glossophaga soricina	Nectarivore
Macrophyllum macrophullum	Insectivore
Phyllostomus discolor	Insectivore
Phyllostomus hastatus	Insectivore
Platyrrhinus lineatus	Frugivore
Pygoderma bilabiatum	Frugivore
Sturnira lilium	Frugivore
Tonatia bidens	Insectivore
Tonatia brasiliense	Insectivore
Tonatia sylvicola	Insectivore
Vampyressa pusilla	Frugivore
Family Natalidae	
Natalus stramineus	Insectivore

Table 2.2. Continued

Taxon	Feeding preference
Family Vespertilionidae	
Eptesicus brasiliensis	Insectivore
Eptesicus diminutus	Insectivore
Eptesicus furinalis	Insectivore
Histiotus macrotus	Insectivore
Histiotus velatus	Insectivore
Lasiurus blossevillii	Insectivore
Lasiurus cinereus	Insectivore
Lasiurus ega	Insectivore
Myotis albescens	Insectivore
Myotis nigricans	Insectivore
Myotis riparius	Insectivore
Myotis ruber	Insectivore
Myotis simus	Insectivore
Family Molossidae	
Eumops auripendulus	Insectivore
Eumops bonariensis	Insectivore
Eumops dabbenei	Insectivore
Eumops glaucinus	Insectivore
Eumops patagonicus	Insectivore
Eumops perotis	Insectivore
Molossops abrasus	Insectivore
Molossops planirostris	Insectivore
Molossops temminckii	Insectivore
Molossus ater	Insectivore
Molossus currentium	Insectivore
Molossus molossus	Insectivore
Nyctinomops laticaudatus	Insectivore
Nyctinomops macrotis	Insectivore
Promops centralis	Insectivore
Promops nasutus	Insectivore
Tadarida brasiliensis	Insectivore

Table 2.3. The geographical distribution and host families of insects ectoparasitic on bats (Marshall, 1982*a*). Asterisks indicate New World Associations.

Insect family	Geographic distribution	Host family
Arixeniidae	Oriental	Molossidae
Cimicidae	Cosmopolitan	Emballonuridae*
		Molossidae*
		Noctilionidae*
		Pteropodidae
		Rhinolophidae
		Vespertilionidae*
Polyctenidae	Cosmopolitan	Emballonuridae*
		Megadermatidae
		Molossidae*
		Nycteridae*
		Rhinolophidae
Nycteribiidae	Cosmopolitan	Emballonuridae*
		Phyllostomidae*
		Pteropodidae
		Rhinolophidae
		Thyropteridae
		Vespertilionidae*
Streblidae	Cosmopolitan	Emballonuridae*
		Fruipteridae*
		Megadermatidae
		Molossidae*
		Mormoopidae*
		Natalidae*
		Noctilionidae*
		Nycteridae*
		Phyllostomidae*

Table 2.3. Continued

Insect family	Geographic distribution	Host family
Ischnopsyllidae	Cosmopolitan	Emballonuridae*
		Megadermatidae
		Molossidae*
		Noctilionidae*
		Pteropodidae
		Rhinolophidae
		Rhinopomatidae
		Vespertilionidae*

Table 2.4. Species composition of bat assemblages in the seven biomes of Paraguay (Willig et al. 2000). Proportional abundances (as percentages) of each species within each biome are provided based on the total number of captured specimens; nomenclature generally follows Koopman (1993; for exceptions, see text).

Taxon	Biomes						
	West			East			
	Mato-grosense	Alto Chaco	Bajo Chaco	Campos Cerrados	Central Paraguay	Alto Paraná	Ñeembucú
Family Noctilionidae							
Noctilio albiventris	30.37		9.21	0.34			11.44
Noctilio leporinus		1.40	0.84	0.85			
Family Phyllostomidae							
Artibeus fimbriatus				0.85	2.61	10.22	3.39
Artibeus jamaicensis				6.47	1.05	0.34	
Artibeus lituratus				13.29	35.54	34.17	5.08
Carollia perspicillata				2.56	3.48	9.05	
Chiroderma doriae					0.52		
Chrotopterus auritus					0.52		
Desmodus rotundus	4.44	0.73		1.02	4.88		1.27
Diaemus youngi	0.37		4.18				
Glossophaga soricina				11.93	4.88		2.54
Platyrrhinus lineatus			0.84	14.48	2.96	0.17	1.69
Pygoderma bilabiatum				1.36	6.79	2.01	0.42
Sturnira lilium		0.06		21.47	29.62	36.18	18.22
Tonatia bidens		0.18					
Tonatia brasiliense			0.42				

Table 2.4. Continued

Taxon	Biomes						
	West			East			
	Mato-grosense	Alto Chaco	Bajo Chaco	Campos Cerrados	Central Paraguay	Alto Paraná	Ñeembucú
Family Natalidae							
Natalus stramineus				0.17			
Family Vespertilionidae							
Eptesicus brasiliensis		0.37		1.02			
Eptesicus diminutus		0.12					
Eptesicus furinalis		1.16	4.60	3.92	1.05	0.17	5.08
Histiotus macrotus		0.37					
Lasiurus blossevillii		0.12	0.84	0.51	0.52	0.17	0.42
Lasiurus cinereus						0.34	0.42
Lasiurus ega	1.48	2.01	12.55	0.34			2.97
Myotis albescens	21.48	1.22	12.97				2.97
Myotis nigricans	7.41	2.20	21.34	1.70	1.05	0.34	5.08
Myotis riparius				0.85	0.70	0.17	0.42
Myotis simus							0.42
Family Molossidae							
Eumops auripendulus		0.06				0.17	
Eumops bonariensis			0.84	0.17		0.34	
Eumops dabbenei		0.18					0.42
Eumops glaucinus		1.83		1.70		2.85	
Eumops patagonicus	9.26	60.12	9.21	3.58	0.35	1.68	15.25
Eumops perotis		0.12					
Molossops abrasus				0.85		0.17	3.39

Table 2.4. Continued

Taxon	Biomes						
	West			East			
	Mato-grosense	Alto Chaco	Bajo Chaco	Campos Cerrados	Central Paraguay	Alto Paraná	Ñeembucú
Molossops planirostris		0.30		0.34			2.12
Molossops temminckii	0.74	7.87	4.18	2.73	1.74	1.17	1.69
Molossus ater	10.74	1.59	7.11	0.17	1.05		14.83
Molossus currentium	13.70						
Molossus molossus		14.57	10.88	7.16	0.52	0.17	
Nyctinomops laticaudatus		2.87					
Promops centralis		0.06		0.17	0.17	0.17	0.42
Promops nasutus		0.49					
Number of individuals	270	1640	239	587	574	597	236

Table 2.5. Summary of ectoparasite assemblage composition for each host family and species.

Taxon	Number of hosts inspected	Ectoparasite richness		Number of species of each of common ectoparasite family				
		Mean	Total	Streblidae	Polyctenidae	Nycteribiidae	Spinturnicidae	Macronyssi
Noctilionidae	96	0.98	44	6				6
Noctilio albiventris	68	2.50	11	3				6
Noctilio leporinus	28	2.36	8	3				2
Phyllostomidae	1220	1.43	59	20			7	15
Phyllostominae								
Chrotopterus auritus	3	1.67	3	1				1
Tonatia bidens	3	2.33	3	1			1	1
Tonatia brasiliense	1	2.00	2	1				1
Glossophaginae								
Glossophaga soricina	54	0.48	10	4			2	2
Carollinae								
Carollia perspicillata	75	0.99	14	3			3	6
Desmodontinae								
Desmodus rotundus	51	1.04	8	2			2	3
Diaemus youngi	11	1.91	5	2				3
Stenodermatinae								
Artibeus fimbriatus	79	2.27	12	6			2	2
Artibeus jamaicensis	42	2.00	12	3			1	2
Artibeus lituratus	351	1.19	17	6			2	5
Chiroderma doriae	3	1.00	1				1	
Platyrrhinus lineatus	90	1.18	14	4			3	7
Pygoderma bilabiatum	53	0.23	7				2	4
Sturnirinae								
Sturnira lilium	404	1.87	23	6			2	6
Natalidae	1	2.00	2	1			1	
Natalus stramineus	1	2.00	2	1			1	

Table 2.5. Continued

Taxon	Number of hosts inspected	Ectoparasite richness		Number of species of each of common ectoparasite family				
		Mean	Total	Streblidae	Polyctenidae	Nycteribiidae	Spinturnicidae	Macronyssi
Family Vespertilionidae	401	1.15	33			7	6	13
Eptesicus brasiliensis	12	1.17	5			2		2
Eptesicus diminutus	2	2.00	3			1		1
Eptesicus furinalis	69	1.33	16			5	3	6
Histiotus macrotus	6	1.00	3			1		2
Lasiurus blossevillii	11	0.55	3					3
Lasiurus cinereus	2	0.50	1					1
Lasiurus ega	72	0.68	5					1
Myotis albescens	87	1.70	15			5	2	5
Myotis nigricans	128	0.99	16			3	2	9
Myotis riparius	11	1.27	6			2	1	3
Myotis simus	1	2.00	2				1	1
Family Molossidae	1192	0.98	44	2	10	1	3	12
Eumops auripendulus	2	0.00						
Eumops bonariensis	5	0.60	3					2
Eumops dabbenei	4	2.00	5		1			2
Eumops glaucinus	56	1.16	8	1	1		1	2
Eumops patagonicus	526	0.81	17	2	1		2	4
Eumops perotis	3	1.00	2		1			1
Molossops abrasus	14	1.14	5		1			3
Molossops planirostris	12	0.67	4		1			2
Molossops temminckii	160	0.88	15	1	1		1	6
Molossus ater	100	1.30	16	1	2		1	5
Molossus currentium	27	1.04	4		1			2
Molossus molossus	228	1.26	15	1	2	1		5
Nyctinomops laticaudatus	42	0.95	9		1			2
Promops centralis	4	0.75	2		1			1
Promops nasutus	8	1.00	1					1

Table 2.6. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Noctilio albiventris* (n = 68). SD = standard deviation.

Ectoparasite Taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Noctiliostrebla maai	66.18	3.13	3.60	4.73	3.47	1.00
Paradyschiria parvula	89.71	6.38	8.07	7.11	8.21	1.00
Xenotrichobius noctilionis	8.82	0.09	0.29	1.00	0.00	1.00
Chiroptonyssus haematophagus	1.47	0.03	0.24	2.00	--	0.00
Chiroptonyssus robustipes	8.82	0.19	0.72	2.17	1.33	0.02
Macronyssus crosbyi	1.47	0.01	0.12	1.00	--	0.00
Steatonyssus sp. 1	1.47	0.01	0.12	1.00	--	0.09
Steatonyssus sp. 2	2.94	0.03	0.17	1.00	0.00	0.08
Unknown macronyssid	1.47	0.01	0.12	1.00	--	0.01
Ornithodoros hasei	61.76	11.35	20.19	18.38	23.11	0.65
Lawrenceocarpus sp.	5.88	0.22	0.91	3.75	0.96	0.79

Table 2.7. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Noctilio leporinus* (n = 28). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Noctiliostrebla aitkeni	46.43	2.82	4.89	6.08	5.69	0.99
Noctiliostrebla dubia	25.00	0.57	1.20	2.29	1.38	1.00
Paradyschiria fusca	75.00	8.11	10.84	10.81	11.31	1.00
Chiroptonyssus haematophagus	10.71	0.57	2.30	5.33	5.77	0.00
Steatonyssus sp. 1	10.71	0.36	1.25	3.33	2.52	0.91
Ornithodoros hasei	57.14	6.14	10.78	10.75	12.51	0.14
Parkosa tadarida	7.14	1.14	4.23	16.00	2.83	0.03
Unknown mites	3.57	0.04	0.19	1.00	--	0.08

Table 2.8. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Chrotopterus auritus* (n = 3). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Strebla chrotopteri	66.67	5.00	7.00	7.50	7.78	1.00
Unknown macronyssid	33.33	22.33	38.68	67.00	--	0.85
Trombicula sp. 1	66.67	23.00	38.12	34.50	45.96	1.00

Table 2.9. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Tonatia bidens* (n = 3). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Trichobius joblingi	66.67	1.00	1.00	1.50	0.71	0.04
Periglischrus tonatii	66.67	2.00	2.00	3.00	1.41	1.00
Parichoronyssus crassipes	100.00	11.00	12.29	11.00	12.29	0.70

Table 2.10. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Tonatia brasiliense* (n = 1). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Mastoptera minuta	100.00	11.00	--	11.00	--	1.00
Parichoronyssus sclerus	100.00	1.00	--	1.00	--	0.33

Table 2.11. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Glossophaga soricina* (n = 54). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Speiseria ambigua	1.85	0.02	0.14	1.00	--	1.00
Strebla guajiro	5.56	0.09	0.45	1.67	1.15	0.16
Trichobius dugesii	9.26	0.15	0.49	1.60	0.55	1.00
Trichobius uniformis	11.11	0.15	0.45	1.33	0.52	1.00
Periglischrus caligus	11.11	0.19	0.65	1.67	1.21	1.00
Periglischrus ojasti	1.85	0.02	0.14	1.00	--	0.00
Chiroptonyssus venezolanus	1.85	0.02	0.14	1.00	--	0.00
Unknown macronyssid	1.85	0.02	0.14	1.00	--	0.01
Pseudolabidocarpus sp.	1.85	0.50	3.67	27.00	--	0.90
Unknown mites	1.85	0.04	0.27	2.00	--	0.15

Table 2.12. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Carollia perspicillata* (n = 75). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Megistopoda proxima	2.67	0.03	0.16	1.00	0.00	0.01
Strebla guajiro	22.67	0.33	0.70	1.47	0.72	0.81
Trichobius joblingi	44.00	0.85	1.30	1.94	1.32	0.96
Periglischrus iheringi	2.67	0.03	0.16	1.00	0.00	0.00
Periglischrus ojasti	1.33	0.01	0.12	1.00	--	0.00
Unknown spinturnicid	1.33	0.01	0.12	1.00	--	0.33
Macronyssoides conciliatus	1.33	0.03	0.23	2.00	--	0.01
Macronyssoides kochi	2.67	0.04	0.26	1.50	0.71	0.00
Macronyssus sp. 3	1.33	0.04	0.35	3.00	--	0.50
Parichoronyssus crassipes	5.33	0.05	0.23	1.00	0.00	0.09
Parichoronyssus euthysternum	8.00	0.15	0.61	1.83	1.33	0.01
Unknown macronyssid	2.67	0.03	0.16	1.00	0.00	0.03
Unknown ixodid	1.33	0.01	0.12	1.00	--	1.00
Pseudolabidocarpus sp.	1.33	0.04	0.35	3.00	--	0.10

Table 2.13. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Desmodus rotundus* (n = 51). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Strebla weidemanni	23.53	1.49	3.91	6.33	5.99	1.00
Trichobius parasiticus	31.37	4.29	9.13	13.69	11.86	1.00
Periglischrus herrerai	5.88	0.06	0.24	1.00	0.00	0.60
Unknown spinturnicid	1.96	0.02	0.14	1.00	--	0.33
Parichoronyssus euthysternum	1.96	0.04	0.28	2.00	--	0.00
Parichoronyssus sclerus	1.96	0.04	0.28	2.00	--	0.67
Radfordiella desmodi	35.29	2.02	4.37	5.72	5.82	0.98
Ornithodoros hasei	1.96	0.02	0.14	1.00	--	0.00

Table 2.14. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Diaemus youngi* (n = 11). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Strebla diaemi	72.73	3.36	3.26	4.63	2.92	0.97
Trichobius diaemi	27.27	0.45	0.82	1.67	0.58	1.00
Macronyssus crosbyi	9.09	0.18	0.60	2.00	--	0.00
Radfordiella desmodi	9.09	0.18	0.60	2.00	--	0.02
Radfordiella oudemansi	72.73	6.18	6.95	8.50	6.82	1.00

Table 2.15. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Artibeus fimbriatus* (n = 79). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Aspidoptera falcata	1.27	0.01	0.11	1.00	--	0.00
Aspidoptera phyllostomatis	18.99	0.24	0.58	1.27	0.70	0.66
Megistopoda aranea	53.16	0.78	0.90	1.48	0.71	0.58
Megistopoda proxima	2.53	0.03	0.16	1.00	0.00	0.01
Metelasmus pseudopterus	18.99	0.22	0.47	1.13	0.35	0.81
Strebla guajiro	1.27	0.01	0.11	1.00	--	0.03
Periglischrus iheringi	69.62	2.39	2.73	3.44	2.67	0.17
Periglischrus ojasti	1.27	0.01	0.11	1.00	--	0.00
Macronyssoides kochi	54.43	3.35	5.56	6.16	6.29	0.37
Parichoronyssus euthysternum	2.53	0.03	0.16	1.00	0.00	0.00
Beamerella acutascuta	1.27	0.01	0.11	1.00	--	0.04
Eudusbabekia viguerasi	1.27	0.01	0.11	1.00	--	0.25

Table 2.16. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Artibeus jamaicensis* (n = 42). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Aspidoptera phyllostomatis	14.29	0.19	0.51	1.33	0.52	0.28
Megistopoda aranea	38.10	0.93	1.70	2.44	2.00	0.36
Metelasmus pseudopterus	4.76	0.07	0.34	1.50	0.71	0.14
Periglischrus iheringi	61.90	2.07	2.59	3.35	2.56	0.08
Chiroptonyssus haematophagus	2.38	0.12	0.77	5.00	--	0.00
Macronyssoides kochi	52.38	2.83	6.21	5.41	7.79	0.17
Ornithodoros hasei	9.52	0.69	2.56	7.25	5.12	0.02
Beamerella acutascuta	7.14	0.19	0.94	2.67	2.89	0.30
Trombicula dicrura	2.38	0.10	0.62	4.00	--	0.06
Trombicula sp.	2.38	0.05	0.31	2.00	--	0.07
Parkosa maxima	2.38	0.02	0.15	1.00	--	0.01
Eudusbabekia viguerasi	2.38	0.02	0.15	1.00	--	0.25

Table 2.17. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Artibeus lituratus* (n = 351). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Aspidoptera falcata	0.28	0.00	0.05	1.00	--	0.00
Aspidoptera phyllostomatis	0.57	0.01	0.08	1.00	0.00	0.07
Megistopoda aranea	0.57	0.01	0.12	1.50	0.71	0.03
Megistopoda proxima	0.57	0.01	0.08	1.00	0.00	0.01
Metelasmus pseudopterus	0.28	0.00	0.05	1.00	--	0.05
Paratrichobius longicrus	23.93	0.44	0.97	1.85	1.17	0.97
Periglischrus iheringi	56.41	1.88	2.74	3.33	2.91	0.59
Periglischrus ojasti	0.28	0.02	0.37	7.00	--	0.01
Chiroptonyssus haematophagus	0.28	0.00	0.05	1.00	--	0.00
Chiroptonyssus venezolanus	0.57	0.01	0.15	2.00	0.00	0.01
Macronyssoides kochi	31.91	0.77	2.12	2.41	3.19	0.38
Parichoronyssus euthysternum	1.14	0.01	0.14	1.25	0.50	0.01
Steatonyssus joaquimi	0.28	0.01	0.21	4.00	--	0.00
Euschoengastia megastyrax	0.28	0.00	0.05	1.00	--	1.00
Parkosa maxima	0.57	0.01	0.19	2.50	0.71	0.03
Eudusbabekia viguerasi	0.57	0.01	0.08	1.00	0.00	0.50
Unknown mites	0.28	0.00	0.05	1.00	--	0.08

Table 2.18. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Chiroderma doriae* (n = 3). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevelance		Density		SI
		Mean	SD	Mean	SD	
Periglischrus iheringi	100.00	2.00	1.00	2.00	1.00	0.01

Table 2.19. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Platyrrhinus lineatus* (n = 90). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Aspidoptera falcata	1.11	0.01	0.11	1.00	--	0.00
Megistopoda proxima	1.11	0.01	0.11	1.00	--	0.00
Paratrichobius longicrus	3.33	0.03	0.18	1.00	0.00	0.02
Trichobius angulatus	6.67	0.11	0.48	1.67	1.03	1.00
Periglischrus iheringi	52.22	1.88	3.31	3.60	3.85	0.15
Periglischrus ojasti	2.22	0.03	0.23	1.50	0.71	0.01
Spinturnix orri	1.11	0.01	0.11	1.00	--	0.07
Chiroptonyssus haematophagus	1.11	0.02	0.21	2.00	--	0.00
Macronyssoides conciliatus	28.89	1.52	4.22	5.27	6.56	0.98
Macronyssoides kochi	13.33	0.54	1.90	4.08	3.68	0.07
Macronyssus crosbyi	1.11	0.02	0.21	2.00	--	0.00
Parichoronyssus crassipes	3.33	0.10	0.67	3.00	2.65	0.19
Steatonyssus furmani	1.11	0.01	0.11	1.00	--	0.00
Steatonyssus joaquimi	1.11	0.07	0.63	6.00	--	0.00

Table 2.20. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Pygoderma bilabiatum* (n = 53). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Periglischrus iheringi	3.77	0.06	0.30	1.50	0.71	0.00
Unknown spinturnicid	1.89	0.02	0.14	1.00	--	0.33
Chiroptonyssus haematophagus	3.77	0.04	0.19	1.00	0.00	0.00
Macronyssoides kochi	3.77	0.04	0.19	1.00	0.00	0.00
Macronyssoides sp. 1	1.89	0.02	0.14	1.00	--	1.00
Parichoronyssus euthysternum	3.77	0.04	0.19	1.00	0.00	0.00
Eudusbabekia sp.	3.77	0.04	0.19	1.00	0.00	1.00

Table 2.21. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Sturnira lilium* (n = 404). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Aspidoptera falcata	29.95	0.57	1.22	1.90	1.56	0.99
Megistopoda aranea	0.25	0.01	0.15	3.00	--	0.03
Megistopoda proxima	48.27	0.88	1.27	1.83	1.27	0.98
Metelasmus paucisetus	0.99	0.01	0.13	1.25	0.50	1.00
Noctiliostrebla aitkeni	0.25	0.00	0.05	1.00	--	0.01
Paratrichobius longicrus	0.25	0.00	0.05	1.00	--	0.01
Periglischrus iheringi	0.25	0.00	0.05	1.00	--	0.00
Periglischrus ojasti	48.27	1.21	1.96	2.51	2.16	0.97
Chiroptonyssus haematophagus	0.50	0.01	0.16	2.00	1.41	0.00
Macronyssoides kochi	0.25	0.01	0.15	3.00	--	0.00
Parichoronyssus crassipes	0.25	0.00	0.05	1.00	--	0.02
Parichoronyssus euthysternum	53.47	2.04	4.52	3.81	5.61	0.95
Steatonyssus joaquimi	0.74	0.03	0.43	4.33	3.06	0.01
Unknown macronyssid	0.25	0.01	0.15	3.00	--	0.04
Ornithodoros hasei	0.25	0.01	0.15	3.00	--	0.00
Rhipicephalus sp.	0.25	0.00	0.05	1.00	--	0.50
Beamerella acutascuta	0.25	0.00	0.05	1.00	--	0.04
Eutrombicula sp.	0.25	0.00	0.05	1.00	--	1.00
Hooperella vesperuginus	0.50	0.00	0.07	1.00	0.00	0.50
Perisopalla precaria	0.25	0.00	0.05	1.00	--	1.00
Trombicula dicrura	0.74	0.15	2.62	20.33	27.65	0.87
Trombicula sp.	0.25	0.04	0.80	16.00	--	0.59
Eudusbabekia lepidoseta	0.74	0.01	0.09	1.00	0.00	1.00

Table 2.22. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Natalus stramineus* (n = 1). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Trichobius galei	100.00	6.00	--	6.00	--	1.00
Periglischrus natali	100.00	1.00	--	1.00	--	1.00

Table 2.23. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eptesicus brasiliensis* (n = 12). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia sp. 5	8.33	0.50	1.73	6.00	--	0.55
Chiroptonyssus venezolanus	8.33	0.08	0.29	1.00	--	0.00
Steatonyssus joaquimi	75.00	5.83	7.13	7.78	7.28	0.04
Ornithodoros hasei	8.33	0.08	0.29	1.00	--	0.00

Table 2.24. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eptesicus diminutus* (n = 2). SD = standard deviation. Male specimens of different species are indistinguishable using phenotypic traits, therefore *Basilia* on hosts with only males were simply identified as *Basilia* spp.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia spp. (males only)	50.00	0.50	0.71	1.00	--	0.02
Steatonyssus joaquimi	100.00	5.50	2.12	5.50	2.12	0.01
Ornithodoros hasei	50.00	0.50	0.71	1.00	--	0.00

Table 2.25. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eptesicus furinalis* (n = 69). SD = standard deviation. Male specimens of different species are indistinguishable using phenotypic traits, therefore *Basilia* on hosts with only males were simply identified as *Basilia* spp.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia sp. 1	1.45	0.03	0.24	2.00	--	0.40
Basilia sp. 3	1.45	0.01	0.12	1.00	--	0.02
Basilia sp. 4	8.70	0.17	0.62	2.00	0.89	1.00
Basilia sp. 5	2.90	0.07	0.43	2.50	0.71	0.45
Basilia spp. (males only)	11.59	0.13	0.38	1.13	0.35	0.21
Periglischrus iheringi	1.45	0.01	0.12	1.00	--	0.00
Spinturnix orri	7.25	0.20	0.80	2.80	1.30	0.93
Spinturnix surinamensis	7.25	0.41	1.78	5.60	4.16	1.00
Chiroptonyssus haematophagus	1.45	0.03	0.24	2.00	--	0.00
Chiroptonyssus venezolanus	1.45	0.12	0.96	8.00	--	0.01
Macronyssus crosbyi	2.90	0.07	0.49	2.50	2.12	0.00
Parichoronyssus cyrtosternum	1.45	0.03	0.24	2.00	--	1.00
Steatonyssus furmani	1.45	0.09	0.72	6.00	--	0.01
Steatonyssus joaquimi	72.46	9.93	15.54	13.98	16.86	0.40
Ornithodoros hasei	8.70	0.12	0.40	1.33	0.52	0.01
Beamerella acutascuta	1.45	0.03	0.24	2.00	--	0.07

Table 2.26. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Histiotus macrotus* (n = 6). SD = standard deviation. Male specimens of different species are indistinguishable using phenotypic traits, therefore *Basilia* on hosts with only males were simply identified as *Basilia* spp.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia spp. (males only)	16.67	0.17	0.41	1.00	--	0.02
Chiroptonyssus haematophagus	33.33	3.83	6.59	11.50	6.36	0.01
Steatonyssus joaquimi	50.00	16.00	33.05	32.00	44.31	0.06

Table 2.27. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Lasiurus blossevillii* (n = 11). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Chiroptonyssus haematophagus	18.18	0.18	0.40	1.00	0.00	0.00
Steatonyssus furmani	27.27	1.09	2.07	4.00	2.00	0.03
Steatonyssus joaquimi	9.09	0.55	1.81	6.00	--	0.00

Table 2.28. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Lasiurus cinereus* (n = 2). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Macronyssus meridionalis	50.00	0.50	0.71	1.00	--	0.02

Table 2.29. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Lasiurus ega* (n = 72). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Steatonyssus furmani	62.50	5.56	8.82	8.89	9.76	0.95
Labidocarpus sp.	1.39	0.10	0.82	7.00	--	0.54
Parkosa tadarida	1.39	0.03	0.24	2.00	--	0.00
Unknown mites	2.78	0.03	0.17	1.00	0.00	0.15

Table 2.30. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Myotis albescens* (n = 87). SD = standard deviation. Male specimens of different species are indistinguishable using phenotypic traits, therefore *Basilia* on hosts with only males were simply identified as *Basilia* spp.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia sp. 1	1.15	0.03	0.32	3.00	--	0.60
Basilia sp. 2	1.15	0.03	0.32	3.00	--	0.14
Basilia sp. 3	13.79	0.29	0.78	2.08	0.79	0.40
Basilia sp. 6	1.15	0.01	0.11	1.00	--	1.00
Basilia spp. (males only)	16.09	0.21	0.53	1.29	0.61	0.43
Spinturnix americanus	18.39	0.28	0.74	1.50	1.10	0.38
Spinturnix banksi	6.90	0.07	0.25	1.00	0.00	1.00
Chiroptonyssus haematophagus	1.15	0.01	0.11	1.00	--	0.00
Macronyssus crosbyi	54.02	9.70	14.13	17.96	14.89	0.77
Parichoronyssus euthysternum	1.15	0.18	1.72	16.00	--	0.02
Steatonyssus joaquimi	33.33	6.53	18.54	19.59	28.12	0.33
Steatonyssus sp. 2	1.15	0.15	1.39	13.00	--	0.50
Ornithodoros hasei	3.45	0.03	0.18	1.00	0.00	0.00
Myodopsylla wolffsohni	16.09	0.28	0.79	1.71	1.20	0.92
Unknown mites	1.15	0.01	0.11	1.00	--	0.08

Table 2.31. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Myotis nigricans* (n = 128). SD = standard deviation. Male specimens of different species are indistinguishable using phenotypic traits, therefore *Basilia* on hosts with only males were simply identified as *Basilia* spp.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia sp. 2	7.03	0.14	0.66	2.00	1.66	0.82
Basilia sp. 3	7.81	0.22	0.88	2.80	1.69	0.45
Basilia spp. (males only)	5.47	0.08	0.37	1.43	0.79	0.24
Periglischrus ojasti	0.78	0.02	0.18	2.00	--	0.00
Spinturnix americanus	11.72	0.21	0.78	1.80	1.57	0.43
Chiroptonyssus haematophagus	2.34	0.04	0.26	1.67	0.58	0.00
Chiroptonyssus robustipes	0.78	0.01	0.09	1.00	--	0.00
Macronyssus crosbyi	25.00	1.52	4.27	6.09	6.78	0.18
Macronyssus meridionalis	3.13	0.14	1.07	4.50	4.73	0.38
Macronyssus sp. 2	0.78	0.02	0.27	3.00	--	1.00
Steatonyssus furmani	0.78	0.02	0.18	2.00	--	0.00
Steatonyssus joaquimi	25.00	1.71	5.29	6.84	8.86	0.13
Steatonyssus sp. 2	1.56	0.09	0.89	5.50	6.36	0.42
Unknown macronyssid	3.13	0.03	0.17	1.00	0.00	0.05
Ornithodoros hasei	2.34	0.09	0.82	4.00	4.36	0.01
Myodopsylla wolffsohni	1.56	0.02	0.12	1.00	0.00	0.08

Table 2.32. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Myotis riparius* (n = 11). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Basilia sp. 2	9.09	0.09	0.30	1.00	--	0.05
Basilia sp. 3	36.36	0.73	1.19	2.00	1.15	0.13
Spinturnix americanus	9.09	0.09	0.30	1.00	--	0.02
Macronyssus crosbyi	9.09	0.82	2.71	9.00	--	0.01
Macronyssus meridionalis	54.55	2.55	3.36	4.67	3.27	0.58
Steatonyssus joaquimi	9.09	0.45	1.51	5.00	--	0.00

Table 2.33. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Myotis simus* (n = 1). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Spinturnix americanus	100.00	10.00	--	10.00	--	0.16
Macronyssus sp. 1	100.00	8.00	--	8.00	--	1.00

Table 2.34. Incidence, prevalance, density, and specificity index (SI) of ectoparasites of *Eumops bonariensis* (n = 5). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Chiroptonyssus haematophagus	20.00	0.20	0.45	1.00	--	0.00
Parichoronyssus euthysternum	20.00	0.20	0.45	1.00	--	0.00
Labidocarpus sp.	20.00	1.20	2.68	6.00	--	0.46

Table 2.35. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eumops dabbenei* (n = 4). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes n. sp. 1	75.00	3.00	2.94	4.00	2.65	0.07
Chiroptonyssus haematophagus	75.00	6.50	9.81	8.67	10.79	0.01
Chiroptonyssus venezolanus	25.00	1.75	3.50	7.00	--	0.01
Ornithodoros hasei	25.00	0.50	1.00	2.00	--	0.00
Parkosa tadarida	25.00	1.00	2.00	4.00	--	0.00

Table 2.36. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eumops glaucinus* (n = 56). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Trichobius jubatus	1.79	0.02	0.13	1.00	--	0.01
Hesperoctenes n. sp. 1	42.86	2.73	11.80	6.65	17.91	0.93
Periglischrus iheringi	3.57	0.04	0.19	1.00	0.00	0.00
Chiroptonyssus haematophagus	55.36	2.20	4.40	3.84	5.27	0.04
Chiroptonyssus robustipes	1.79	0.16	1.20	9.00	--	0.02
Ornithodoros hasei	3.57	0.09	0.44	1.67	1.15	0.00
Beamerella acutascuta	1.79	0.11	0.80	6.00	--	0.22
Parkosa tadarida	5.36	0.63	3.16	11.67	9.02	0.03

Table 2.37. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eumops patagonicus* (n = 526). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Strebla diaemi	0.19	0.00	0.04	1.00	--	0.03
Trichobius jubatus	4.37	0.06	0.29	1.26	0.69	0.36
Hesperoctenes longiceps	16.92	0.28	0.78	1.65	1.15	1.00
Periglischrus herrerai	0.19	0.00	0.09	2.00	--	0.40
Periglischrus iheringi	0.19	0.00	0.04	1.00	--	0.00
Chiroptonyssus haematophagus	49.43	2.64	9.49	5.33	12.96	0.42
Chiroptonyssus venezolanus	0.57	0.01	0.13	1.67	0.58	0.01
Macronyssus crosbyi	0.19	0.01	0.22	5.00	--	0.00
Macronyssus sp. 3	0.19	0.00	0.04	1.00	--	0.17
Ornithodoros hasei	3.80	0.05	0.29	1.35	0.75	0.02
Rhipicephalus sp.	0.19	0.00	0.04	1.00	--	0.50
Beamerella acutascuta	0.19	0.01	0.13	3.00	--	0.11
Trombicula dicrura	0.19	0.01	0.22	5.00	--	0.07
Trombicula sp.	0.76	0.01	0.12	1.25	0.50	0.19
Parkosa maxima	0.57	0.01	0.13	1.67	0.58	0.03
Parkosa tadarida	2.28	0.13	1.23	5.58	6.23	0.06
Ewingana sp. 1	0.38	0.00	0.06	1.00	0.00	1.00

Table 2.38. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Eumops perotis* (n = 3). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes n. sp. 2	33.33	1.67	2.89	5.00	--	1.00
Chiroptonyssus haematophagus	66.67	10.00	8.72	15.00	1.41	0.01

Table 2.39. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Molossops abrasus* (n = 14). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes cartus	35.71	0.50	0.76	1.40	0.55	1.00
Chiroptonyssus robustipes	21.43	0.64	1.65	3.00	2.65	0.02
Chiroptonyssus venezolanus	28.57	1.00	1.84	3.50	1.73	0.02
Steatonyssus joaquimi	7.14	0.21	0.80	3.00	--	0.00
Ornithodoros hasei	21.43	1.57	3.92	7.33	6.03	0.02

Table 2.40. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Molossops planirostris* (n = 12). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes minor	25.00	0.75	1.42	3.00	1.00	1.00
Chiroptonyssus venezolanus	25.00	0.75	1.76	3.00	2.65	0.00
Chiroptonyssus sp. 1	8.33	0.08	0.29	1.00	--	0.50
Ornithodoros hasei	8.33	0.08	0.29	1.00	--	0.00

Table 2.41. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Molossops temminckii* (n = 160). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Trichobius jubatus	0.63	0.01	0.16	2.00	--	0.03
Hesperoctenes parvulus	18.75	0.33	1.11	1.77	2.03	1.00
Spinturnix americanus	0.63	0.01	0.08	1.00	--	0.02
Chiroptonyssus haematophagus	4.38	0.28	2.16	6.29	8.90	0.01
Chiroptonyssus robustipes	0.63	0.01	0.16	2.00	--	0.00
Chiroptonyssus venezolanus	45.63	2.31	4.39	5.05	5.34	0.64
Macronyssus crosbyi	0.63	0.01	0.08	1.00	--	0.00
Macronyssus meridionalis	0.63	0.01	0.08	1.00	--	0.02
Steatonyssus joaquimi	1.88	0.06	0.50	3.00	2.65	0.01
Ornithodoros hasei	10.63	0.34	1.35	3.18	2.90	0.05
Amblyomma sp.	0.63	0.01	0.08	1.00	--	0.33
Trombicula sp.	0.63	0.01	0.08	1.00	--	0.04
Unknown mites	1.88	0.02	0.14	1.00	0.00	0.23

Table 2.42. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Molossus ater* (n = 100). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Trichobius jubatus	17.00	0.27	0.74	1.59	1.06	0.34
Hesperoctenes fumarius	13.00	0.41	1.49	3.15	3.00	0.25
Hesperoctenes n. sp. 3	2.00	0.02	0.14	1.00	0.00	0.67
Periglischrus iheringi	2.00	0.02	0.14	1.00	0.00	0.00
Chiroptonyssus robustipes	67.00	5.26	11.16	7.85	12.89	0.94
Chiroptonyssus venezolanus	1.00	0.07	0.70	7.00	--	0.01
Chiroptonyssus sp. 1	1.00	0.01	0.10	1.00	--	0.50
Macronyssus crosbyi	1.00	0.01	0.10	1.00	--	0.00
Unknown macronyssid	1.00	0.01	0.10	1.00	--	0.01
Ornithodoros hasei	17.00	0.60	2.10	3.53	4.05	0.05
Hooperella vesperuginus	1.00	0.02	0.20	2.00	--	0.50
Trombicula sp.	1.00	0.02	0.20	2.00	--	0.07
Lawrenceocarpus sp.	1.00	0.04	0.40	4.00	--	0.31
Parkosa maxima	1.00	0.01	0.10	1.00	--	0.01
Parkosa tadarida	3.00	2.33	16.29	77.67	66.08	0.21
Unknown mites	1.00	0.01	0.10	1.00	--	0.08

Table 2.43. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Molossus currentium* (n = 27). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes fumarius	7.41	0.07	0.27	1.00	0.00	0.01
Chiroptonyssus haematophagus	81.48	2.00	2.25	2.45	2.26	0.02
Steatonyssus joaquimi	3.70	0.07	0.38	2.00	--	0.00
Ornithodoros hasei	11.11	0.22	0.80	2.00	1.73	0.01

Table 2.44. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Molossus molossus* (n = 228). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Trichobius jubatus	7.46	0.09	0.38	1.24	0.75	0.26
Hesperoctenes fumarius	26.75	0.53	1.14	1.97	1.43	0.74
Hesperoctenes n. sp. 3	0.44	0.00	0.07	1.00	--	0.33
Chiroptonyssus haematophagus	56.58	5.68	11.33	10.03	13.54	0.40
Macronyssoides conciliatus	0.44	0.00	0.07	1.00	--	0.01
Macronyssus crosbyi	2.63	0.11	0.76	4.33	2.07	0.02
Macronyssus sp. 3	0.44	0.01	0.13	2.00	--	0.33
Steatonyssus furmani	0.44	0.00	0.07	1.00	--	0.00
Ornithodoros hasei	3.07	0.05	0.35	1.71	1.11	0.01
Beamerella acutascuta	1.32	0.03	0.28	2.00	1.73	0.22
Parkosa maxima	11.84	0.76	3.11	6.41	6.86	0.94
Parkosa tadarida	13.60	3.36	14.27	24.74	31.52	0.68
Unknown mites	0.88	0.01	0.09	1.00	0.00	0.15

Table 2.45. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Nyctinomops laticaudatus* (n = 42). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevalence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes setosus	9.52	0.10	0.30	1.00	0.00	1.00
Chiroptonyssus haematophagus	7.14	0.26	1.06	3.67	2.08	0.00
Chiroptonyssus venezolanus	54.76	3.69	8.47	6.74	10.59	0.27
Ornithodoros hasei	7.14	0.07	0.26	1.00	0.00	0.00
Amblyomma sp.	2.38	0.02	0.15	1.00	--	0.33
Trombicula sp.	2.38	0.02	0.15	1.00	--	0.04
Ewingana sp. 2	2.38	0.02	0.15	1.00	--	1.00
Hormopsylla fosteri	2.38	0.02	0.15	1.00	--	1.00
Rothschildopsylla noctilionis	7.14	0.12	0.50	1.67	1.15	1.00

Table 2.46. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Promops centralis* (n = 4). SD = standarad deviation.

Ectoparasite taxon	Incidence (%)	Prevelence		Density		SI
		Mean	SD	Mean	SD	
Hesperoctenes angustatus	25.00	0.75	1.50	3.00	--	1.00
Chiroptonyssus haematophagus	50.00	2.75	4.86	5.50	6.36	0.00

Table 2.47. Incidence, prevalence, density, and specificity index (SI) of ectoparasites of *Promops nasutus* (n = 8). SD = standard deviation.

Ectoparasite taxon	Incidence (%)	Prevelence		Density		SI
		Mean	SD	Mean	SD	
Chiroptonyssus haematophagus	100.00	28.38	25.29	28.38	25.29	0.07

Table 2.48. Host specificity of arthropods ectoparasitic on bats of Paraguay using all observed associations from this study

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
Streblidae	*Aspidoptera falcata*	Polyxenous	4	3	1
	Aspidoptera phyllostomatis	Oligoxenous	3	1	1
	Mastoptera minuta	Monoxenous	1	1	1
	Megistopoda aranea	Polyxenous	4	2	1
	Megistopoda proxima	Polyxenous	5	4	1
	Metelasmus pseudopterus	Oligoxenous	3	1	1
	Metelasmus paucisetus	Monoxenous	1	1	1
	Noctiliostrebla aitkeni	Polyxenous	2	2	2
	Noctiliostrebla dubia	Monoxenous	1	1	1
	Noctiliostrebla maai	Monoxenous	1	1	1
	Paradyschiria fusca	Monoxenous	1	1	1
	Paradyschiria parvula	Monoxenous	1	1	1
	Paratrichobius longicrus	Polyxenous	3	3	1
	Speiseria ambigua	Monoxenous	1	1	1
	Strebla chrotopteri	Monoxenous	1	1	1
	Strebla diaemi	Polyxenous	2	2	2
	Strebla guajiro	Polyxenous	3	3	1
	Strebla weidemanni	Monoxenous	1	1	1
	Trichobius angulatus	Monoxenous	1	1	1
	Trichobius diaemi	Monoxenous	1	1	1
	Trichobius dugesii	Monoxenous	1	1	1
	Trichobius galei	Monoxenous	1	1	1
	Trichobius joblingi	Polyxenous	2	2	1
	Trichobius jubatus	Pleioxenous	5	3	1
	Trichobius parasiticus	Monoxenous	1	1	1
	Trichobius uniformis	Monoxenous	1	1	1

Table 2.48. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Xenotrichobius noctilionis	Monoxenous	1	1	1
Polyctenidae	*Hesperoctenes angustatus*	Monoxenous	1	1	1
	Hesperoctenes cartus	Monoxenous	1	1	1
	Hesperoctenes fumarius	Oligoxenous	3	1	1
	Hesperoctenes longiceps	Monoxenous	1	1	1
	Hesperoctenes minor	Monoxenous	1	1	1
	Hesperoctenes parvulus	Monoxenous	1	1	1
	Hesperoctenes setosus	Monoxenous	1	1	1
	Hesperoctenes n. sp. 1	Oligoxenous	2	1	1
	Hesperoctenes n. sp. 2	Monoxenous	1	1	1
	Hesperoctenes n. sp. 3	Oligoxenous	2	1	1
Nycteribiidae	*Basilia* sp. 1	Pleioxenous	2	2	1
	Basilia sp. 2	Oligoxenous	3	1	1
	Basilia sp. 3	Pleioxenous	4	2	1
	Basilia sp. 4	Monoxenous	1	1	1
	Basilia sp. 5	Oligoxenous	2	1	1
	Basilia sp. 6	Monoxenous	1	1	1
Ischnopsyllidae	*Hormopsylla fosteri*	Monoxenous	1	1	1
	Myodopsylla wolffsohni	Oligoxenous	2	1	1
	Rothschildopsylla noctilionis	Monoxenous	1	1	1
Spinturnicidae	*Periglischrus caligus*	Monoxenous	1	1	1
	Periglischrus herrerai	Polyxenous	2	2	2

Table 2.48. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Periglischrus iheringi	Polyxenous	12	9	3
	Periglischrus natali	Monoxenous	1	1	1
	Periglischrus ojasti	Polyxenous	7	6	2
	Periglischrus tonatii	Monoxenous	1	1	1
	Spinturnix americanus	Polyxenous	5	2	2
	Spinturnix banksi	Monoxenous	1	1	1
	Spinturnix orri	Polyxenous	2	2	2
	Spinturnix surinamensis	Monoxenous	1	1	1
Macronyssidae	*Chiroptonyssus haematophagus*	Polyxenous	23	14	4
	Chiroptonyssus robustipes	Polyxenous	6	5	3
	Chiroptonyssus venezolanus	Polyxenous	11	7	3
	Chiroptonyssus sp. 1	Pleioxenous	2	2	1
	Macronyssoides conciliatus	Polyxenous	3	3	2
	Macronyssoides kochi	Polyxenous	7	5	1
	Macronyssoides sp. 1	Monoxenous	1	1	1
	Macronyssus crosbyi	Polyxenous	11	8	4
	Macronyssus meridionalis	Polyxenous	4	3	2
	Macronyssus sp. 1	Monoxenous	1	1	1
	Macronyssus sp. 2	Monoxenous	1	1	1
	Macronyssus sp. 3	Polyxenous	3	3	2
	Parichoronyssus crassipes	Polyxenous	4	4	1
	Parichoronyssus cyrtosternum	Monoxenous	1	1	1
	Parichoronyssus euthysternum	Polyxenous	8	7	3
	Parichoronyssus sclerus	Polyxenous	2	2	1
	Radfordiella desmodi	Pleioxenous	2	2	1

Table 2.48. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Radfordiella oudemansi	Monoxenous	1	1	1
	Steatonyssus furmani	Polyxenous	6	5	3
	Steatonyssus joaquimi	Polyxenous	14	9	3
	Steatonyssus sp. 1	Oligoxenous	2	1	1
	Steatonyssus sp. 2	Polyxenous	3	2	2
Argasidae	*Ornithodoros hasei*	Polyxenous	19	10	4
	Amblyomma sp.	Polyxenous	3	3	2
	Rhipicephalus sp.	Polyxenous	2	2	2
Ixodidae	Unknown ixodid	Monoxenous	1	1	1
Trombiculidae	*Beamerella acutascuta*	Polyxenous	7	5	3
	Euschoengastia megastyrax	Monoxenous	1	1	1
	Eutrombicula sp.	Monoxenous	1	1	1
	Hooperella vesperuginus	Polyxenous	2	2	2
	Trombicula dicrura	Polyxenous	3	3	2
	Trombicula sp. 1	Monoxenous	1	1	1
	Trombicula sp.	Polyxenous	6	6	2
Chirodiscidae	*Labidocarpus* sp.	Polyxenous	2	2	2
	Lawrenceocarpus sp.	Polyxenous	2	2	2
	Perisopalla precaria	Monoxenous	1	1	1
	Parkosa maxima	Polyxenous	5	3	2
	Parkosa tadarida	Polyxenous	7	4	3
	Pseudolabidocarpus sp.	Polyxenous	2	2	1

Table 2.48. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
Myobiidae	*Eudusbabekia lepidoseta*	Monoxenous	1	1	1
	Eudusbabekia viguerasi	Oligoxenous	3	1	1
	Eudusbabekia sp.	Monoxenous	1	1	1
	Ewingana sp. 1	Monoxenous	1	1	1
	Ewingana sp. 2	Monoxenous	1	1	1

Table 2.49. Host specificity of arthropods ectoparasitic on bats of Paraguay using only primary host associations (i.e., ignoring probable transient relationships and contamination).

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
Streblidae	*Aspidoptera falcata*	Monoxenous	1	1	1
	Aspidoptera phyllostomatis	Oligoxenous	2	1	1
	Mastoptera minuta	Monoxenous	1	1	1
	Megastopoda aranea	Oligoxenous	2	1	1
	Megastopoda proxima	Monoxenous	1	1	1
	Metelasmus pseudopterus	Monoxenous	1	1	1
	Metelasmus paucisetus	Monoxenous	1	1	1
	Noctiliostrebla aitkeni	Monoxenous	1	1	1
	Noctiliostrebla dubia	Monoxenous	1	1	1
	Noctiliostrebla maai	Monoxenous	1	1	1
	Paradyschiria fusca	Monoxenous	1	1	1
	Paradyschiria parvula	Monoxenous	1	1	1
	Paratrichobius longicrus	Monoxenous	1	1	1
	Speiseria ambigua	Monoxenous	1	1	1
	Strebla chrotopteri	Monoxenous	1	1	1
	Strebla diaemi	Monoxenous	1	1	1
	Strebla guajiro	Polyxenous	2	2	1
	Strebla weidemanni	Monoxenous	1	1	1
	Trichobius angulatus	Monoxenous	1	1	1
	Trichobius diaemi	Monoxenous	1	1	1
	Trichobius dugesii	Monoxenous	1	1	1
	Trichobius galei	Monoxenous	1	1	1
	Trichobius joblingi	Polyxenous	2	2	1
	Trichobius jubatus	Oligoxenous	2	1	1
	Trichobius parasiticus	Monoxenous	1	1	1

Table 2.49. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Trichobius uniformis	Monoxenous	1	1	1
	Xenotrichobius noctilionis	Monoxenous	1	1	1
Polyctenidae	*Hesperoctenes angustatus*	Monoxenous	1	1	1
	Hesperoctenes cartus	Monoxenous	1	1	1
	Hesperoctenes fumarius	Oligoxenous	3	1	1
	Hesperoctenes longiceps	Monoxenous	1	1	1
	Hesperoctenes minor	Monoxenous	1	1	1
	Hesperoctenes parvulus	Monoxenous	1	1	1
	Hesperoctenes setosus	Monoxenous	1	1	1
	Hesperoctenes n. sp. 1	Oligoxenous	2	1	1
	Hesperoctenes n. sp. 2	Monoxenous	1	1	1
	Hesperoctenes n. sp. 3	Oligoxenous	2	1	1
Nycteribiidae	*Basilia* sp. 1	Pleioxenous	2	2	1
	Basilia sp. 2	Oligoxenous	2	1	1
	Basilia sp. 3	Oligoxenous	3	1	1
	Basilia sp. 4	Monoxenous	1	1	1
	Basilia sp. 5	Monoxenous	1	1	1
	Basilia sp. 6	Monoxenous	1	1	1
Ischnopsyllidae	*Hormopsylla fosteri*	Monoxenous	1	1	1
	Myodopsylla wolffsohni	Monoxenous	1	1	1
	Rothschildopsylla noctilionis	Monoxenous	1	1	1
Spinturnicidae	*Periglischrus caligus*	Monoxenous	1	1	1

Table 2.49. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Periglischrus herrerai	Monoxenous	1	1	1
	Periglischrus iheringi	Pleioxenous	5	3	1
	Periglischrus natali	Monoxenous	1	1	1
	Periglischrus ojasti	Monoxenous	1	1	1
	Periglischrus tonatii	Monoxenous	1	1	1
	Spinturnix americanus	Oligoxenous	4	1	1
	Spinturnix banksi	Monoxenous	1	1	1
	Spinturnix orri	Monoxenous	1	1	1
	Spinturnix surinamensis	Monoxenous	1	1	1
Macronyssidae	*Chiroptonyssus haematophagus*	Polyxenous	13	7	3
	Chiroptonyssus robustipes	Polyxenous	3	3	2
	Chiroptonyssus venezolanus	Polyxenous	6	4	2
	Chiroptonyssus sp. 1	Pleioxenous	2	2	1
	Macronyssoides conciliatus	Monoxenous	1	1	1
	Macronyssoides kochi	Pleioxenous	4	2	1
	Macronyssoides sp. 1	Monoxenous	1	1	1
	Macronyssus crosbyi	Oligoxenous	3	1	1
	Macronyssus meridionalis	Pleioxenous	2	2	1
	Macronyssus sp. 1	Monoxenous	1	1	1
	Macronyssus sp. 2	Monoxenous	1	1	1
	Macronyssus sp. 3	Polyxenous	3	3	2
	Parichoronyssus crassipes	Polyxenous	2	2	1
	Parichoronyssus cyrtosternum	Monoxenous	1	1	1
	Parichoronyssus euthysternum	Monoxenous	1	1	1
	Parichoronyssus sclerus	Monoxenous	1	1	1

Table 2.49. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Radfordiella desmodi	Monoxenous	1	1	1
	Radfordiella oudemansi	Monoxenous	1	1	1
	Steatonyssus furmani	Oligoxenous	2	1	1
	Steatonyssus joaquimi	Pleioxenous	8	4	1
	Steatonyssus sp. 1	Oligoxenous	2	1	1
	Steatonyssus sp. 2	Polyxenous	3	2	2
Argasidae	*Ornithodoros hasei*	Polyxenous	11	7	4
	Amblyomma sp.	Polyxenous	3	3	2
	Rhipicephalus sp.	Polyxenous	2	2	2
Ixodidae	Unknown ixodid	Monoxenous	1	1	1
Trobiculidae	*Beamerella acutascuta*	Polyxenous	7	5	3
	Euschoengastia megastyrax	Monoxenous	1	1	1
	Eutrombicula sp.	Monoxenous	1	1	1
	Hooperella vesperuginus	Polyxenous	2	2	2
	Trombicula dicrura	Polyxenous	3	3	2
	Trombicula sp. 1	Monoxenous	1	1	1
	Trombicula sp.	Polyxenous	6	6	2
Chirodiscidae	*Labidocarpus* sp.	Polyxenous	2	2	2
	Lawrenceocarpus sp.	Polyxenous	2	2	2
	Perisopalla precaria	Monoxenous	1	1	1
	Parkosa maxima	Polyxenous	5	3	2
	Parkosa tadarida	Polyxenous	7	4	3

Table 2.49. Continued

Ectoparasite family	Ectoparasite species	Host specificity	Number of hosts		
			Species	Genera	Families
	Pseudolabidocarpus sp.	Polyxenous	2	2	1
Myobiidae	*Eudusbabekia lepidoseta*	Monoxenous	1	1	1
	Eudusbabekia viguerasi	Oligoxenous	3	1	1
	Eudusbabekia sp.	Monoxenous	1	1	1
	Ewingana sp. 1	Monoxenous	1	1	1
	Ewingana sp. 2	Monoxenous	1	1	1

Table 2.50. Empirical species abundance distributions of the ectoparasite communities on each of 39 host species. Numbers are absolute abundances and arranged from most to least abundant within each host species such that S1 is the most abundant ectoparasite species from a given host and S23 the least abundant. S1 need not represent the same ectoparasite species for different host species. Ectoparasite N = total number of ectoparasites collected from all individual of a host species. Asterisks indicate non-primary associations.

Host family	Ectoparasite species												
Host species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
Noctilionidae													
Noctilio albiventris	772	434	213	15	13	6	2*	2*	1*	1*	1*		
Noctilio leporinus	227	172	79	32	16	16	10	1*					
Phyllostomidae													
Chrotopterus auritus	69	67	15										
Tonatia bidens	33	6	3										
Tonatia brasiliense	11	1											
Glossophaga soricina	27	10	8	8	5	2*	1	1*	1*	1*			
Carollia perspicillata	64	25	11*	4	3	3*	3*	2*	2*	2*	2*	1*	1*
Desmodus rotundus	219	103	76	3	2*	2*	1*	1*					
Diaemus youngi	68	37	5	2*	2*								
Artibeus fimbriatus	265	189	62	19	17	2*	2*	1	1*	1*	1*	1*	
Artibeus jamaicensis	119	87	39	29	8	8	5*	4*	3*	2*	1	1*	
Artibeus lituratus	659	270	155	7*	5*	5*	4*	4*	3*	2	2*	2*	1
Platyrrhinus lineatus	169	137	49	10	9*	6*	3*	3*	2*	2*	1*	1*	1*
Pygoderma bilabiatum	3*	2*	2*	2*	2*	1*	1*						
Sturnira lilium	823	489	357	230	61	16	13*	5	4*	3	3*	3*	3*
Natalidae													
Natalus stramineus	6	1											

Table 2.50. Continued

Host family	Ectoparasite species										Total
Host species	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	ectoparasite N
Noctilionidae											
Noctilio albiventris											1460
Noctilio leporinus											553
Phyllostomidae											
Chrotopterus auritus											151
Tonatia bidens											42
Tonatia brasiliense											12
Glossophaga soricina											64
Carollia perspicillata	1*										124
Desmodus rotundus											407
Diaemus youngi											114
Artibeus fimbriatus											561
Artibeus jamaicensis											306
Artibeus lituratus	1*	1*	1*	1*							1123
Platyrrhinus lineatus	1*										394
Pygoderma bilabiatum											13
Sturnira lilium	3*	2	1	1	1	1*	1*	1*	1*	1*	2023
Natalidae											
Natalus stramineus											7

Table 2.50. Continued

Host family	Ectoparasite species												
Host species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
Vespertilionidae													
Eptesicus brasiliensis	70	6	2*	1*	1*								
Eptesicus diminutus	11	1*	1*										
Eptesicus furinalis	685	28	14	12	9*	8*	8	6*	5	5*	2	2	2*
Histiotus macrotus	96	23	1*										
Lasiurus blossevillii	12	6	2										
Lasiurus ega	400	7	2*	2*									
Myotis albescens	844	568	25	24	24	18*	16*	13*	6	3	3*	3*	1
Myotis nigricans	219	195	28	27	18	18	12*	11	10*	5*	4*	3*	2*
Myotis riparius	28	9*	8	5*	1*	1*							
Myotis simus	10	8											
Molossidae													
Eumops bonariensis	6*	1*	1*										
Eumops dabbenei	26	12	7	4	2								
Eumops glaucinus	156	122	35	9*	6*	4*	2*	1*					
Eumops patagonicus	1387	147	67	29	27*	5*	5*	5*	5*	5*	3*	2	2*
Eumops perotis	30	5											
Molossops abrasus	22	14	9	7	3								
Molossops planirostris	9*	9*	1*	1*									
Molossops temminckii	369	54	53	44*	9*	3*	2*	2*	1*	1*	1*	1*	1*
Molossus ater	526	233	60	41	27	7*	4	2	2	2*	2*	1*	1*
Molossus currentium	54	6	2*	2*									
Molossus molossus	1294	767	173	120	26*	21	12*	6	2*	2*	1*	1*	1*
Nyctinomops laticaudatus	155	11	5	4	3	1*	1*	1*	1*				
Promops centralis	11	3											

Table 2.50. Continued

Host family	Ectoparasite species										Total
Host species	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	ectoparasite N
Vespertilionidae											
Eptesicus brasiliensis											80
Eptesicus diminutus											13
Eptesicus furinalis	2*	1*	1*								790
Histiotus macrotus											120
Lasiurus blossevillii											20
Lasiurus ega											411
Myotis albescens	1*	1*									1550
Myotis nigricans	2*	2*	1*								557
Myotis riparius											52
Myotis simus											18
Molossidae											
Eumops bonariensis											8
Eumops dabbenei											51
Eumops glaucinus											335
Eumops patagonicus	1	1*	1*	1*							1693
Eumops perotis											35
Molossops abrasus											55
Molossops planirostris											20
Molossops temminckii											541
Molossus ater	1*	1*	1*								911
Molossus currentium											64
Molossus molossus	1*										2427
Nyctinomops laticaudatus											182
Promops centralis											14

Table 2.51. Comparisons of the primary ectoparasite species abundance distributions (SADs) of 24 each of host species with the predictions of the geometric series and broken broken stick models showing the Chi-square statistic (X^2), degrees of freedom (df) and significance (p-value). If SADs conformed to a particular model, the values are in bold. One asterisk indicates host species whose ectoparasite SAD conformed to neither model; two asterisks indicate those that conformed to both.

Host species	Geometric series			Broken stick		
	X^2	df	p-value	X^2	df	p-value
*Noctilio albiventris**	138.8	5	0.0000	34.13	9	0.0001
Noctilio leporinus	20	6	0.0028	**13.8**	**7**	**0.0549**
Chrotopterus auritus	29.9	2	0.0000	**4.4**	**6**	**0.6227**
*Tonatia bidens***	**1.64**	**2**	**0.4404**	**7.3**	**5**	**0.1993**
*Glossophaga soricina***	**10.98**	**5**	**0.0518**	**3.46**	**4**	**0.4840**
Carollia perspicillata	**2.48**	**3**	**0.4789**	14.95	5	0.0106
*Desmodus rotundus**	319.3	3	0.0000	17.4	7	0.0150
Diaemus youngi	16.4	2	0.0003	**4.75**	**6**	**0.5763**
Artibeus fimbriatus	164.8	5	0.0000	**13.8**	**8**	**0.0871**
Artibeus jamaicensis	54.6	6	0.0000	**7.97**	**6**	**0.2403**
*Artibeus lituratus**	658	4	0.0000	108	9	0.0000
Platyrrhinus lineatus	70	3	0.0000	**4.96**	**7**	**0.6648**
*Sturnira lilium**	138.4	11	0.0000	127.8	9	0.0000
*Eptesicus furinalis**	428	7	0.0000	67.1	9	0.0000
*Myotis albescens**	244	7	0.0000	51.4	9	0.0000
Myotis nigricans	82.8	6	0.0000	**13.48**	**7**	**0.0612**
*Eumops dabbenei***	**0.18**	**4**	**0.9962**	**0.47**	**4**	**0.9764**
Eumops glaucinus	26.6	2	0.0000	**1.05**	**7**	**0.9940**
*Eumops patagonicus**	103.5	5	0.0000	127.8	10	0.0000
*Molossops abrasus***	**0.97**	**4**	**0.9143**	**1.35**	**4**	**0.8528**
Molossops temminckii	57.98	2	0.0000	**9.59**	**8**	**0.2950**
*Molossus ater**	27.2	7	0.0003	56.1	9	0.0000
*Molossus molossus**	245.2	5	0.0000	24.99	10	0.0054
*Nyctinomops laticaudatus**	57.4	4	0.0000	29.4	7	0.0001

Table 2.52. Comparison of spinturnicid infestation rates (incidence and prevalence) on chiropteran hosts from Venezuela (Herrin and Tipton 1975), Mexico (Sheeler-Gordon and Owen 1999), and Paraguay. Host N = number of host individuals inspected for ectoparasites. Inc (%) = ectoparasite incidence. Prev = ectoparasite prevalence. See text for definitions.

Host taxon	Venezuela			Paraguay			Mexico		
Ectoparasite taxon	Host N	Inc (%)	Prev	Host N	Inc (%)	Prev	Host N	Inc (%)	Pre
Noctilio albiventris	535			68					
Periglischrus iheringi		0.37	0.01		--	--			
Noctilio leporinus	87			28					
Periglischrus ojastii		1.15	0.02		--	--			
Tonatia bidens	19			3					
Periglischrus paratorrealbai		5.26	0.32		--	--			
Periglischrus tonatii		5.26	0.05		66.67	11.00			
Glossophaga soricina	866			54			18		
Periglischrus caligus		10.62	0.29		11.11	0.19		27.78	0.8
Periglischrus iheringi		0.23	0.00		1.85	0.02		--	--
Periglischrus ojastii		0.23	0.00		--	--		--	--
Carollia perspicillata	4305			75					
Cameronieta elongatus		0.02	0.00		--	--			
Periglischrus sp.		0.02	0.00		1.33	0.01			
Periglischrus acutisternus		0.02	0.00		--	--			
Periglischrus iherringi		0.14	0.00		2.67	0.04			
Periglischrus ojastii		0.07	0.00		1.33	0.04			
Periglischrus torrealbai		0.09	0.00		--	--			
Desmodus rotundus	964			51			15		
Periglischrus sp.		--	--		1.96	0.02		--	--
Periglischrus acutisternus		0.52	0.01		--	--		--	--
Periglischrus caligus		0.21	0.00		--	--		--	--
Periglischrus gameroi		0.10	0.00		--	--		--	--
Periglischrus herrerai		6.33	0.12		5.88	0.06		6.67	0.0

Table 2.52. Continued

Host taxon	Venezuela			Paraguay			Mexico		
Ectoparasite taxon	Host N	Inc (%)	Prev	Host N	Inc (%)	Prev	Host N	Inc (%)	Pre
Periglischrus iherringi		0.31	0.01		--	--		13.33	0.5
Periglischrus ojastii		0.41	0.01		--	--		--	--
Periglischrus tonatii		0.10	0.00		--	--		--	--
Periglischrus torrealbai		0.31	0.01		--	--		--	--
Artibeus jamaicensis	2302			42			20		
Periglischrus acutisternus		0.22	0.00		--	--		--	--
Periglischrus caligus		0.09	0.00		--	--		--	--
Periglischrus gameroi		0.04	0.00		--	--		--	--
Periglischrus iherringi		15.20	0.49		61.90	2.07		40.00	0.9
Periglischrus ojastii		0.26	0.00		--	--		--	--
Periglischrus torrealbai		0.09	0.00		--	--		--	--
Artibeus lituratus	1620			351					
Periglischrus iherringi		25.19	0.67		56.41	1.88			
Periglischrus ojastii		0.12	0.00		0.28	0.02			
Sturnira lilium	363			404			39		
Cameronieta elongatus		0.13	0.00		--	--		--	--
Periglischrus sp.		0.17	0.00		--	--		--	--
Periglischrus acutisternus		0.04	0.00		--	--		--	--
Periglischrus caligus		0.04	0.00		--	--		--	--
Periglischrus herrerai		0.04	0.00		--	--		--	--
Periglischrus iherringi		0.44	0.01		0.25	0.00		--	--
Periglischrus ojastii		21.87	0.62		48.27	1.21		33.33	0.5
Eptesicus brasiliensis	64			12					
Spinturnix surinamensis		10.94	0.20		--	--			

Table 2.52. Continued

Host taxon	Venezuela			Paraguay			Mexico		
Ectoparasite taxon	Host N	Inc (%)	Prev	Host N	Inc (%)	Prev	Host N	Inc (%)	Prev
Eptesicus furinalis	16			69					
Periglischrus gameroi		6.25	0.06		--	--			
Periglischrus iherringi		--	--		1.45	0.01			
Spinturnix orri		--	--		7.25	0.20			
Spinturnix surinamensis		--	--		7.25	0.41			
Myotis albescens	86			87					
Periglischrus iherringi		1.16	0.01		--	--			
Spinturnix americanus		39.53	0.72		18.39	0.28			
Spinturnix banksi		--	--		6.90	0.07			
Myotis nigricans	153			128					
Periglischrus iherringi		0.65	0.01		--	--			
Periglischrus ojastii		--	--		0.78	0.01			
Spinturnix americanus		50.98	1.64		11.72	0.21			
Eumops glaucinus	81			56					
Periglischrus iherringi		1.23	0.01		3.57	0.04			
Spinturnix americanus		1.23	0.01		--	--			
Molossops planirostris	241			12					
Periglischrus acutisternus		0.41	0.00		--	--			
Periglischrus torrealbai		0.41	0.00		--	--			
Molossus ater	410			100					
Periglischrus iherringi		0.24	0.00		2.00	0.02			
Periglischrus sp.		0.24	0.00		--	--			

Table 2.53. Comparison of *Periglischrus* host specificity on chiropteran hosts from Venezuela (Herrin and Tipton 1975, Machado-Allison 1965), Mexico (Sheeler-Gordon and Owen 1999), and Paraguay using only primary associations. HT = Herrin and Tipton, MA = Machado-Allsion.

	Host specificity			
	Venezuela		Paraguay	Mexico
Ectoparasite taxon	HT	MA		
P . caligus	Oligoxenous		Monoxenous	Oligoxenous
P . herrerai	Monoxenous	Monoxenous	Monoxenous	Monoxenous
P . iheringi	Pleioxenous	Pleioxenous	Pleioxenous	Pleioxenous
P . natali	Monoxenous		Monoxenous	
P . ojastii	Oligoxenous	Oligoxenous	Monoxenous	Oligoxenous
P . tonatii	Oligoxenous		Monoxenous	

CHAPTER III
FLYING ISLANDS I: THE EFFECT OF HOST BODY SIZE ON ECTOPARASITE ASSEMBLAGE BIODIVERSITY

Introduction

Biogeography is an integrated discipline that requires understanding of ecological and evolutionary elements to define patterns and identify causal mechanisms at regional, continental, and global scales. Biogeographic processes *per se* may not exist; rather, large-scale geoclimatic (e.g., tectonic plate movements, changes in sea level, climate, and oceanic circulation), evolutionary (e.g., adaptation, speciation, extinction), and ecological (e.g., predation, competition) processes operate in concert to produce biogeographic patterns. These processes do not operate in isolation. For example, as geoclimatic characteristics change overtime, species must adapt (i.e., evolve) to remain competitive or avoid predation. These interactions may result in extinction or speciation. Consequently, the dynamic nature of interactions at large scales of space and time make it difficult to determine which mechanisms are dominant driving forces in structuring communities.

Islands possess many tractable qualities that make them attractive foci for biogeographic study (Shoener 1988). An island is a more feasible study unit than is a continent or ocean, and is visibly discreet so that resident populations may be distinguished more easily along natural boundaries. In addition, islands are abundant and differ in shape, size, degree of isolation, history, and ecology; consequently they provide the replication necessary to conduct non-manipulative experiments. Low primary diversity on islands (i.e., species richness due to immigration) promotes *in situ* diversification, with the most isolated islands evincing the largest adaptive radiations (Paulay, 1994). Whether intra-island or inter-island speciation is more important depends on the dispersal ability of the taxon and opportunities for isolation from parent populations (Paulay, 1994). The small size and isolation of islands results in relatively small populations, which makes island species especially vulnerable to local extinction.

Therefore, islands provide biotas with opportunities for larger radiations and more frequent *in situ* diversification than occur on mainlands, while simultaneously subjecting them to higher extinction rates. Because of these phenomena, islands provide insight into assemblage rules.

In the 1960s, MacArthur and Wilson (1963, 1967) proposed the equilibrium theory of island biogeography (ETIB) in an attempt to explain patterns of species richness on islands. The primary predictions of ETIB are two fold: 1) larger islands maintain greater species richness than do smaller islands, and 2) islands more distant from a source of colonization support fewer species than do closer islands. Distance from a source population primarily affects richness by molding immigration rates, whereas island size primarily affects richness by molding extinction rates.

The ETIB has been much debated (for review see Whitaker 1998). Despite executing one of the more successful tests of ETIB (Simberloff and Wilson 1970), Simberloff (1976) was foremost among the critics claiming that ETIB gained paradigm status despite numerous studies that failed to conform to its predictions. These failures often are explained by faulting deductive logic or by "willful suspension of belief in the experimental result" (Simberloff 1976). Early work (Simberloff 1983) with development and application of null models attempted to discount the dynamic equilibrium facet of ETIB (i.e., that extinction and immigration rates converge to form a stable equilibrium). Unfortunately, the design of Simberloff's model predisposes a finding of randomness and is not an unbiased test of dynamic equilibria (Colwell and Winkler 1984). Many (Gilbert 1980, Schrader-Frechette and McCoy 1993, Simberloff 1976) remain frustrated by the continued application of ETIB to various types of islands (e.g., habitat patches, lakes, parasite hosts) in diverse theoretical and applied situations. Nonetheless, prominent biologists have endorsed it as being useful and insightful despite simplifying assumptions (Brown 1971, Rosenzweig 1995). Contention has lasted for decades because of the different ways that researchers employ ETIB. Detractors often test predictions of ETIB based on natural history data (e.g., Gilbert 1980, Johnson and Simberloff 1974, Bush and Whittaker 1991) and discredit the theory because data fail to conform to predictions.

However, the failure of these tests should not be surprising given the simplicity of the theory and the complexity of natural systems (Sismondo 2000). A different perspective (Haila and Järvinen 1982) views ETIB as a heuristic model that provides opportunities to explore patterns rather than as a suite of hypotheses to falsify.

Although the ETIB has been applied to a multitude of taxa, few investigations have focused on ectoparasite assemblages. In evolutionary studies, the focus often is on a single ectoparasite species and its co-evolutionary relationship with a host and not the community or assemblage. I use ETIB as a model for understanding host characteristics that determine community structure of arthropod ectoparasite assemblages on chiropteran hosts.

Bats and Their Ectoparasites as Model Systems

Generally, bats come in contact with few non-bats, thereby isolating bat ectoparasites from potential non-bat hosts. In addition, bat species rarely come into contact with each other, except in multispecific colonies, which usually contain species from the same family (Kunz 1982), restricting potential inter-specific host transfer of ectoparasites to members of the same host family. Finally, with the exception of colonial species, individual bats may be in contact with conspecifics only during periods of mating and rearing, reducing opportunities for ectoparasite transfer among individuals. Prolonged periods of host isolation in solitary bat species may increase the likelihood of local extinction of ectoparasites on the host.

Four host characteristics affect parasite species richness within the context of ETIB (Kuris et al. 1980): 1) host size, 2) host age, 3) habitat complexity (often correlated with host age or size), and 4) distance to potential sources of infestation. Host size, and its relationship to habitat complexity, is evaluated in this chapter, whereas host population density is considered in chapter IV. Because bats essentially reach adult size in a few (4 – 7) months (Barclay and Harder 2003), which is only a small fraction of average life expectancy of bats (11 – 15 years), the effect of size and age can be de-coupled. This is not possible in work on ectoparasites of fishes (Kennedy 1978*a*, 1978*b*,

Newbound and Knott 1999), because these hosts exhibit indeterminate growth. Moreover, bats have long life expectancies compared to animals of similar size (Barclay and Harder 2003). Such long life may provide ectoparasite assemblages on individual hosts with opportunities to experience processes similar to those on habitat or oceanic islands (e.g., local extinction, colonization, rescue effect).

When considering individuals as islands, five aspects of host biology must be addressed to accommodate traditional interpretations of ETIB (Kuris et al. 1980). First, inter-island distances fluctuate over time. These fluctuations may occur over short time frames for vagile hosts such as bats and may create only sporadic opportunities for infestation. Although host individuals and species are like islands in being discrete and easily identifiable units, they are not like islands in that the level of isolation is dynamic. Indeed, considering hosts as islands is complicated because the distances among islands are changing continually and some islands even make temporary physical contact. Moreover, physical contact differs in frequency, regularity, and duration depending on season, as well as host species identity, age, sex, and mating and social systems.

Second, seasonal changes in behavior or physiology may affect the presence of parasites. Host behavior could have a significant effect on distance to source populations for bat species that form maternity colonies as well as for those that hibernate individually or in colonies. Conversely, physiological peculiarities of bats may expose ectoparasites to phenomena similar to those experienced by inhabitants of temperate islands. For example, daily changes in bat body temperature (from torpor to activity) are analogous to daily fluctuations in ambient temperature. Similarly, seasonal changes in bat body temperature related to hibernation in temperate species or to extended periods of torpor in sub-tropical or tropical species are analogous to seasonal changes in climate that are characteristic of temperate islands. Seasonal or daily changes in bat behavior do not require modification of theory applied to oceanic islands.

Third, quality of the host island changes over ecological time as a result of growth and aging. Host islands may change over much shorter time frames than do those that characterize true islands; however, the effects of these changes with respect to invading

species are similar. Indeed, fewer complications arise due to age of hosts than due to successional changes related to the age of islands On true islands, early colonizers may facilitate invasion by other species, leading to a more predictable order of invasion and community structure than may occur on host islands. Because all hosts, from birth to death, are inhabitable islands for potential parasites, evaluations of ETIB for host-parasite systems are not complicated by host (i.e., island) age.

Fourth, presence of certain parasites may affect characteristics of host islands, including survival. Characteristics of true islands change with the presence of every species, either enhancing or diminishing the chance of other species establishing populations on the island. Still, it is difficult to imagine a scenario where an invading species would cause the "death" of an island. Furthermore, it is unlikely that the presence of ectoparasite species commonly facilitates the infestation of others. Fortunately, little evidence suggests that species ectoparasitic on bats have deleterious effects on their hosts as to commonly cause death of an otherwise healthy individual. Indeed, bat host survival is affected marginally by ectoparasite load, although energy demands may be significantly increased by heavy ectoparasite loads (Marshall 1982). Nonetheless, all hosts die. How death of an island affects evaluations of ETIB in host-parasite systems is unclear.

Finally, Kuris et al. (1980) consider hosts to be sufficiently ephemeral to prevent parasite assemblages from reaching equilibrium. Nonetheless, bats have remarkably long life spans, with species documented to live 20 years or longer (Barclay and Harder 2003). Because the life-span of most ectoparasite species is only a few months, bat hosts may be sufficiently long-lived as to support equilibrial assemblages.

In summary, the only characteristic of bats that may require significant modification of ETIB for application to ectoparasite assemblages is the potential for distance from sources to fluctuate quickly and with varying frequency and regularity. Whereas ectoparasite residency was considered the host individual from which it was collected, it is possible that individuals residing on one host communicate with other hosts via direct invasion or the dispersal of offspring, especially species that are vagile

and regularly leave the host (e.g., streblids). As such, extinction (i.e., no ectoparasites on a host individual) and extinction rates, which are fundamental to the equilibrium theory of island biogeography, may be difficult to define. This is also true of highly interactive islands (Coleman et al. 1982), such as archipelagos in which mobile members of biotas move among islands on a daily or monthly basis.

A Host Is an Island, Entire of Itself

Islands have large adaptive radiations of species and high levels of *in situ* diversification compared to mainland communities (Paulay 1994). Bat ectoparasite assemblages exhibit both of these island characteristics, implying that they may have evolved as isolated evolutionary units. Ectoparasite faunas of mammalian hosts contain relatively few species, many of which are monoxenous (i.e., occur on only one host species), indicating evolution of ectoparasite species on the host island (i.e., *in situ* diversification). In addition, many ectoparasite families contain hundreds of species, but all are restricted to a single family of host, indicating relatively recent and large adaptive radiations. Together, these observations are evidence, albeit circumstantial, that ectoparasite faunas on bat hosts experience similar ecological and evolutionary mechanisms to those of biotas on true islands.

Limiting Factors

The most important factor inhibiting ectoparasites from interspecific host transfer is physical isolation (Kuris et al. 1980, Marshall 1971, 1982, Wenzel and Tipton 1966). Indeed, many ectoparasite species have virtually no chance to move to another host species because direct body contact likely is rare between host species. Moreover, survival away from the host is brief (< 1 day for most bat ectoparasites). Hence, even ectoparasites that do not require direct body contact of hosts for transfer would have only brief windows of opportunity to infest alternative host species. When opportunities for infestation do exist, many factors inhibit successful infestation (i.e., survival and reproduction) of new host species. In experimental transfers of ectoparasitic insects to

non-primary bat host species, nycteribiids starved and bat flies fell victim to predation by hosts (Marshall 1971, 1982). Often, ectoparasites even find potential host species that are closely related to their typical host to be unsuitable. Two sets of ideas account for these observations. First, ectoparasites have specialized adaptations for life on their host and these may be unsuitable on other host species. More specifically, claws may be unsuitable for attachment, or body form, setae, and combs may be inappropriate for movement through hair. Failure to match proper morphological adaptations to the microhabitat will enhance exposure to predation. Second, parasites may starve because their mouthparts are unsuitable for feeding or the host's blood may be inadequate nutritionally (Marshall 1982).

I used host (i.e., bat) morphology and ecology to explore questions about biodiversity of ectoparasite assemblages within the framework of the ETIB. A suite of analyses was designed to determine: 1) the number of ectoparasites that inhabit a host individual of a particular size and 2) the diversity (e.g., measures of richness, evenness, dominance) of the ectoparasite assemblage that inhabits a host individual of particular size.

Materials and Methods

Field Methods

Mammals and their associated ectoparasites were collected from July 1995 to June 1997, and again from July to August in 1998, as part of a scientific expedition entitled "Paraguayan Mammals and Their Ectoparasites: an Intensive Survey in a Temperate-Subtropical Interface" (Willig et al. 2000). Bats were surveyed at 28 sites (Table A.1), representing all major biomes, including many protected areas, and spanning gradients of moisture and temperature in Paraguay (Figure 2.1). Because of the potential importance of the Río Paraguay as a biogeographic barrier (Myers 1982), approximately one-half of the sites were on each side (east or west) of the river. In general, mist nets were erected in all habitats at a site and were monitored from dusk until 0100 h. Much of the time, nets were monitored until dawn. Rates of capture for bats in the field depend on

a variety of factors including net characteristics (e.g., mesh size, length, condition, placement, configuration), temporal factors (e.g., length of time, particular hours of the night, period in the lunar cycle; Gannon and Willig 1997), local weather conditions (especially with respect to temperature and precipitation), and history (i.e., number of consecutive nights at a site; Simmons and Voss 1998). Captured bats were sacrificed and prepared as standard museum specimens. Specific bat identification was initiated in the field but verified after comparison with systematic reference materials by C. López-González (López-González 1998, 2005).

Host and Parasite Systematics

The systematic recommendations of López-González (1998, 2005) were followed for bat taxa in Paraguay. Ectoparasites were identified using the most recent, comprehensive information about South American representatives for each family including Wenzel (1976) and Wenzel et al. (1966) for the Streblidae; Guimarães (1966, 1972) for the Nycteribiidae; Ueshima (1972), Ferris and Usinger (1939, 1945), and Ronderos (1959, 1962) for the Polyctenidae; Rudnick (1960), Machado-Allison (1965), and Herrin and Tipton (1975) for the Spinturnicidae; Radovsky (1967) and Saunders (1975) for the Macronyssidae; Dusbábek (1969*a*, 1969*b*) and Fain (1978) for the Myobiidae; Jones et al. (1972) and Fairchild et al. (1966) for the Ixodidae and Argasidae; Reed and Brennan (1975), Brennan and Reed (1974, 1975), Brennan and Yunker (1966), and Brennan and Goff (1977) for the Trombiculidae; McDaniel (1970, 1973), Pinichpongse (1963a, 1963b, 1963c, 1963d), de la Cruz (1969) and Dusbábek and de la Cruz (1966) for the Chirodiscidae. Details about field and laboratory methods appear in chapter II.

At the individual level, I used host body size as a surrogate for island area. Because of the exploratory nature of these analyses and differences in body and wing shapes among host species, especially those in different families, host mass (MA) and forearm length (FA) were used to estimate host body size. All analyses in this chapter consider host individuals to be “islands.”

Host-parasite associations with an incidence $\geq$ 0.05 were considered primary, with hosts and parasites of these associations referred to as primary hosts and primary ectoparasites, respectively. An exception to this rule was made for small mite taxa (e.g., Myobiidae, Chirodiscidae, Trombiculidae) that were rare on all host species. The host on which these parasites most often were found was considered to be the primary association.

Statistical Methods

Analysis of Ectoparasite Abundance. To evaluate the effect of host body size on ectoparasite abundance, analyses were performed at multiple taxonomic levels within the context of ectoparasites and of hosts. For each host individual, three levels of ectoparasite abundance were calculated: 1) total number of ectoparasites, 2) number of ectoparasites for each ectoparasite family, and 3) number of ectoparasites for each ectoparasite species. These three levels of ectoparasite abundance were evaluated with respect to each of three distinct host pools: 1) all host individuals, 2) host individuals for a particular family, and 3) host individuals for each of the 22 host species that had $\geq$ 25 individuals inspected for ectoparasites. *Desmodus rotundus*, *Glossophaga soricina*, and *Pygoderma bilabiatum* were not analyzed beyond the level of total ectoparasite abundance, despite more than 50 captures each, because each taxon had low ectoparasite abundances per host individual. Within host families or species, analyses were performed only for those ectoparasite families or species that have primary relationships with the particular host group. For example, streblid abundance was analyzed for the Noctilionidae and both species of *Noctilio*, but not for any vespertilionids because in Paraguay, vespertilionids are not primary hosts for streblids. In cases where host size significantly affected ectoparasite abundance among individuals within a host species, the observed relationship could have resulted from a variety of host-related factors including, but not limited to, sexual dimorphism, age, or body size. In addition to size measures, data on the sex of each host individual were available, whereas host age was unknown. To better determine host characteristics that lead to differences in ectoparasite load, I

employed a multivariate analysis of variance (MANOVA) to determine if sexual size dimorphism (using MA and FA) existed for a particular host species and an analysis of covariance (ANCOVA) to evaluate the effect of sex on ectoparasite abundance, while accounting for sex-related differences in size. In the ANCOVAs, ectoparasite abundance was the dependent variable, sex the treatment factor, and FA and MA the covariates.

Bat ectoparasites have relatively strict host associations at multiple taxonomic levels. Therefore, multiple levels of analysis, from the perspective of both the host and ectoparasite, were necessary to provide a comprehensive assessment of the role of host size on the structure of ectoparasite communities. Although such detailed analyses may seem redundant, they elucidate ecological and evolutionary factors that may go unnoticed with more simple analytical designs.

Analysis of Ectoparasite Biodiversity. A suite of analyses evaluated the effect of host body size on biodiversity of ectoparasites. Biodiversity comprises a variety of attributes (Brower et al. 1990, Peet 1974): diversity, richness, evenness, dominance, and rarity (Table 3.1). These evince various degrees of correlation and are each estimated by a number of metrics (Camargo 1993, 1995, Magurran 1988, May 1975, Southwood 1978).

Four indices estimated richness. MeanS was defined as the average ectoparasite richness on host individuals of a particular host species. Accumulative S (AccumS) was defined as the total number of ectoparasite species found on all individuals of a particular host species. Chao1 is an abundance-based estimate of cumulative species richness (Chao 1984) calculated using EstimateS (Colwell 2001). LogS was calculated using Matlab ver. 4.2c.1 for the Macintosh (The Math Works, Inc. 1994; script files available from the author, Appendix E) as an alternative abundance-based cumulative estimate of richness. This function used a jackknife sampling regime to produce a mean species-accumulation curve from 1000 random permutations of individuals based on the ectoparasite species-abundance distribution (SAD) from a particular host species. In each iteration, individuals were ordered randomly and sampled without replacement. An iterative process was used to determine the best-fit logistic curve to the mean species-

accumulation curve. The asymptote of that curve is the number of species predicted to occur in an assemblage after infinite sampling (= LogS). Preliminary investigations of this metric revealed that it was overly sensitive to rare species, especially those that occur only once (i.e., singletons), likely leading to overestimates of richness. To diminish the effect of singletons, one individual was added to each species in the SAD at the beginning of the simulation. This modification better predicted richness for known universes (Presley, unpublished data) than did the original incarnation.

Five additional indices (Table 3.1) measured other aspects of ectoparasite SADs. Shannon Diversity (Shannon), Shannon Evenness (Even), and Berger-Parker Dominance (Dom) were calculated using Matlab. Following Whitaker (1960), beta diversity (Betadiv) was calculated as the difference between gamma diversity, as estimated by LogS (i.e., LogS is the cumulative species richness estimate previously discussed, not Log[S]), and alpha diversity as estimated by MeanS. Rare ectoparasite species were defined separately for each ectoparasite taxon (i.e., species, family, or class). Rare species richness (Rare) was equal to the number of ectoparasite species whose separate proportional abundances < 0.05. A common definition of rarity (e.g. Chalcraft et al. 2004, Stevens and Willig 2000, Willig et al. 2003) considers a species to be rare if its abundance is < 1/S of the total individuals of a community or assemblage, where S = species richness (Camargo 1992). However, problems characterize this definition of rarity. First, use of 1/S for a species-poor assemblage, like those of ectoparasites on host individuals, could result in the assignment of relatively abundant species as rare. For example, in an assemblage with S = 5, a species that comprises 19% of the assemblage is rare although it represents a large portion of the assemblage. Second, because all assemblages do not have equal species richness, 1/S defines rareness at different relative abundances for assemblages with different species richness. Third, 1/S requires at least one species be rare in all but the most even of assemblages. Defining rareness using the 5% criterion eliminates these problems. Regardless of the employed definition of rare, species of ectoparasites defined as rare may represent transients or contamination in addition to identifying species of ectoparasite that are naturally rare on their primary host.

Simple linear regressions quantified the effect of host body size on each of these nine indices of biodiversity. Analyses were performed for all bats, as well as for molossids, phyllostomids, and vespertilionids, separately. Unless otherwise stated, regression analyses, MANOVAs, and ANCOVAs for all experiments were conducted using SPSS 4.0 for the Macintosh (SPSS, Inc. 1990).

An ongoing debate characterizes the ecological literature on the use of methods to maintain type I error rate at a reasonable level for suites of analyses (Hurlbert 2003, Moran 2003). Chief among the misconceptions that lead to the idea of a need to account for multiple tests is the view that every test increases overall likelihood of a Type I error. In actuality, the likelihood of such an error only increases in instances for which the null hypothesis is rejected (Hurlbert 2003). The Bonferroni sequential adjustment (BSA) is a common method used to maintain experiment-wise error rate (EWER) at a predetermined, albeit arbitrary, rate (i.e., alpha). However, this method is conservative and leads to elevated type II error rates (i.e., failure to reject a null hypothesis that is false). An alternate approach to the use of BSA is to present exact p-values and make "reasonable" interpretations of results based on experimental design, differences in treatment responses, and logic based on experience and scientific understanding (Moran 2003). Hurlbert (2003) stated, "Without knowing how many, if any, of the null hypotheses being tested are true, it is not possible to calculate the probability of making one or more Type I errors. For most investigations that probability is likely to be zero." Nonetheless, most statisticians and ecologists prefer to maintain EWER at a predetermined level (i.e., alpha). Therefore, I applied BSA separately to each independent variable (e.g., host forearm length and mass) in each suite of analyses (i.e., table of analyses) and included those results in each table. I was more concerned about the consequences of ignoring results that could have biological implications than about the potential for type I errors. Because of the exploratory nature of analyses, I interpreted results before application of the BSA, with the understanding that a few significant results contributing to the overall pattern in each discussion may represent type I errors.

In most cases, general patterns are the same, just not as strong, when EWER is maintained at alpha (i.e., 0.05).

Results

Total Ectoparasite Abundance. In the analysis for all bat species as a group, total ectoparasite abundance (TEA) did not respond significantly to body size (Table 3.2). However, analyses restricted to phyllostomids and to molossids, the two most abundant and species-rich families of Paraguayan bats, larger species of bat did harbor more ectoparasites than did smaller species of bat. There was no effect of size at the familial level for noctilionids or vespertilionids. At the level of host species, host size did not affect TEA for 17 species. On two host species, *Sturnira lilium* and *Molossus ater*, smaller bats had greater TEA, whereas on three host species, *Artibeus fimbriatus*, *Myotis albescens* and *Molossops temminckii*, larger bats had greater TEA. Three of the host species (*S. lilium*, *M. albescens*, and *M. ater*) for which body size affected TEA were dimorphic (Table 3.3). When the effect of size was removed via ANCOVA, only *S. lilium* had a significant relationship between sex and ectoparasite infestation, with males harboring significantly fewer ectoparasites than did females ($p = 0.008$). That neither *M. albescens* nor *M. ater* had significant effects of sex in ANCOVAs, and that *A. fimbriatus* and *M. temminckii* were not sexually dimorphic, implies that the difference in ectoparasite load between smaller and larger individuals of those species is size- and not sex-related.

Familial Ectoparasite Abundance. For all bats as a group, the effect of host body size on familial ectoparasite abundance (FEA) was significant in 17 of 24 analyses (Table 3.4). Significance reflected the body size of the primary host species of each ectoparasite family, and not an effect of host size, *per se*. For example, the Streblidae occur mostly on phyllostomids and noctilionids, which include most of the larger bat species in Paraguay. Therefore, host size had a significant positive effect on streblid FEA. Alternatively, nycteribiids occur on vespertilionids, and thus had a significant negative response to host body size. Of the eight common ectoparasite families, only the

Polyctenidae did not have a significant response to host size. Nonetheless, large species of *Eumops* (e.g., *E. dabbenei*, Table 2.35, and *E. glaucinus*, Table 2.36) had polyctenid prevalences > 2.0, whereas other molossids had prevalences < 1.0 (Tables 2.39 – 2.47). Spinturnicids occur mostly on phyllostomids and had a positive response to host body size. Macronyssids inhabit small molossids and vespertilionids and had a negative response to host body size. Argasids dwell mostly on noctilionids and had a positive response to host body size.

For each host family, the effect of host body size on FEA was significant in 16 of 42 analyses (Table 3.4). Significance reflected the body size of the primary host species of each ectoparasite family, and was not an effect of host size, *per se*. For example, among phyllostomids, streblids were most abundant on *Sturnira lilium*, which is a relatively small phyllostomid. Therefore, FEA evinced a significant negative response to host size. Alternatively, for phyllostomids, spinturnicids occurred mostly on species of *Artibeus*, which are among the largest and most common phyllostomids in Paraguay. As a result, there was a significant positive response of spinturnicid FEA to phyllostomid body size. FEA was not significant if ectoparasites occurred on all members of a host family regardless of body size (e.g., macronyssids on molossids).

Body size affected FEA in eight host species (*Noctilio albiventris*, *Artibeus lituratus*, *Sturnira lilium*, *Myotis albescens*, *Myotis nigricans*, *Eumops patagonicus Molossops temminckii*, and *Molossus molossus*; Table 3.4). Three families of ectoparasite on *Sturnira lilium* had significant responses to host body size, and two families of ectoparasite on *Myotis albescens* had significant responses to host body size (Table 3.4). Of those host species with at least one significant response of FEA to body size, males were larger than females in *Noctilio albiventris*, *Sturnira lilium*, and *Molossus molossus*, whereas females were larger than males in *Artibeus lituratus*, *Myotis albescens*, and *Myotis nigricans*. *Eumops patagonicus* and *Molossops temminckii* were not dimorphic (Table 3.3). Quite unexpectedly, in six of 11 cases, smaller bats had significantly greater ectoparasite abundances than did larger bats. In instances where more ectoparasites were found on larger bats, sex was not significant (i.e., larger bats,

regardless of sex, possessed higher ectoparasite abundances). Where smaller bats had greater ectoparasite loads, female hosts generally were significantly smaller than males. On *Noctilio albiventris*, ecological interactions between two ectoparasite families appear to have resulted in one family occurring in greater abundance on females and the other on males (see chapter II).

ANCOVA Results for FEA. Four host species evinced significant effects of host sex on FEA while accounting for host size (Table 3.5). Streblids occurred on female *Noctilio albiventris* at densities twice that found on males, whereas ticks occurred on males at densities three times that on females. Macronyssids and spinturnicids were more abundant on female *Artibeus fimbriatus* and female *A. lituratus*, respectively, than on males of corresponding species. Similarly, female *Lasiurus ega* harbored more macronyssids than did males.

Specific Ectoparasite Abundance. For all bats as a group, the effect of host body size on specific ectoparasite abundance (SEA) was significant in 68 of 84 analyses (Table 3.6). If the primary host species of an ectoparasite species was smaller than 30 g, host body size had a significant negative effect on SEA. Alternatively, if the primary host species was larger than 30 g, host body size had a significant positive effect. However, significance in these analyses reflected the body size of the primary host species of each ectoparasite species and was not a response of ectoparasite abundance to host body size, *per se*.

Analyses of the effects of host body size on SEA that included all host species within particular host families were nearly all significant, with the direction (negative or positive) of the response indicating the body size of the primary host species of each ectoparasite species (i.e., negative responses indicate smaller hosts and positive responses indicate larger hosts). Results for SEA at the specific host level mirrored those of FEA, and identified the particular ectoparasite species that was responsible for relationships at the level of FEA. For example, FEA of streblids on *Artibeus lituratus* had a significant positive response. *Paratrichobius longicrus*, which had a significant positive response to

host body size at the SEA level, likely is the principle species responsible for the differences in streblid abundances on *A. lituratus*.

ANCOVA Results for SEA. Host sex affected SEA of 13 ectoparasite species on nine host species while accounting for host size (Table 3.7). In 11 of 13 cases, females harbored significantly more ectoparasites than did males. Two cases represent possible resource partitioning of hosts by ectoparasite species or competitive exclusion. Tick (*Ornithodoros hasei*) abundances on male *Noctilio albiventris* averaged more than three times that of females. In contrast, abundance of *Paradyschiria parvula* on female *N. albiventris* was more than twice that of males. *Myotis nigricans* is primary host to two species of macronyssid, *Macronyssus crosbyi* and *Steatonyssus joaquimi*. However, *M. crosbyi* occurred almost exclusively on female *M. nigricans*, whereas *S. joaquimi* occurred almost exclusively on males.

Ectoparasite Biodiversity. For simple regression analyses of all bat species as a group, average richness (MeanS) was the only metric of ectoparasite biodiversity that had a significant response: larger bats exhibited higher MeanS than did smaller bats (Table 3.8). Within the Phyllostomidae, host size did not affect ectoparasite biodiversity (Table 3.8). Indeed, no analysis even approached significance. In analyses restricted to vespertilionids, smaller bats had higher Shannon diversity than did larger bats. Alternatively, larger vespertilionids had higher Berger-Parker dominance than did smaller vespertilionids. These results reflect the greater biodiversity of ectoparasite assemblages on *Myotis* than on either *Lasiurus* or *Eptesicus*. For molossids, host size significantly affected MeanS, with larger bats having greater MeanS than did smaller bats (Table 3.8).

Multi-level analyses in this chapter introduce two forms of bias that require consideration. Some analyses (i.e., those for all host species as a group) necessarily have larger sample sizes than others (i.e., those that are taxonomically restricted to a particular host family or species). Because statistical power is greater for analyses with larger sample sizes, increases in sample size predispose analyses to be statistically significant. For example, in analyses of the effect of host body size on FEA (Table 3.4), most analyses for all bats as well as common families and species were significant, whereas

analyses of less abundant host species (i.e., those with smaller sample sizes were mostly non-significant). Similarly, analyses of all host species as a group span a greater range of host body sizes than does any taxonomically restricted analysis. Reduced variation in the independent variable (i.e., body size) predisposes analyses to non-significance (e.g., analyses restricted to individual host species).

Discussion

Methodological Considerations

Mass (MA) and forearm length (FA) were chosen to estimate the effects of host body size on ectoparasite abundance and diversity. Host body size reflects habitat area available to ectoparasites. However, these measures (i.e., MA or FA) are not two dimensional and do not have a linear relationship with area. In general, body surface area should scale as $MA^{2/3}$, and wing surface area as FA^2; such transformations should induce linear relationships between body and wing area and MA or FA, respectively (Emerson et al. 1994). Nonetheless, such transformations may not improve (i.e., linearize) the relationships between estimates of body size and ectoparasite abundance or biodiversity. Bat body and wing shapes are complex and differ among species so that any general transformation may not improve the ability of MA or FA to estimate body or wing surface area. Moreover, that the relationships between length, area, and mass are positive and monotonic may be sufficient to justify not transforming MA and FA into two dimensional equivalents. Indeed, species-area curves have many forms including the exponential, power, and logistic curves (Scheiner 2003). In general, species-area curves are positive and monotonic, but non-linear (Scheiner 2003, Scheiner et al. 2000). However, many species-area curves are linear in log-log space (Rosenzweig 1995). Finally, visual inspection of the data revealed that diversity-body size plots were linear and flat, or linear with a positive or negative slope. No plots suggested that a linear model was inappropriate. Consequently, data were not transformed prior to analyses.

With no evidence of a more complex relationship between ectoparasite diversity and host body size, I chose to use a linear model for its simplicity and ease of interpretation.

Effects of Host Size on Ectoparasite Biodiversity

Although analyses for all ectoparasite species regardless of host species showed that larger bats harbor more ectoparasite individuals and species than do smaller bats, these effects were weak (Tables 3.2 and 3.8). In fact, larger hosts within bat species did not harbor more ectoparasite individuals or species than did smaller hosts. Significance arose because larger host species harbored more ectoparasite individuals and species (Tables 3.2 and 3.8) than did smaller host species. Greater surface area on larger host species may allow larger populations of ectoparasites to live on a single host. Moreover, larger host individuals may provide opportunities for greater niche partitioning among ectoparasite species, thereby leading to greater ectoparasite richness. The data support these interpretations when comparing ectoparasite assemblages among bat species.

If larger host individuals within a host species harbor greater ectoparasite loads (i.e., greater ectoparasite abundance) by providing more habitat, all significant responses of ectoparasite abundance to host body size should be positive. However, more than half of significant responses were negative (i.e., smaller hosts had significantly greater ectoparasites abundances than did larger hosts). Therefore, within the context of ETIB, increases in host size (i.e., island size) do not lead to increases in ectoparasite abundance that would reduce extinction rates, and may not be the most important host character in determining ectoparasite abundance within a host species. Females were larger in most host species in which larger hosts had greater ectoparasite abundances and were smaller in all host species in which smaller hosts had greater ectoparasite abundance. This suggests that size captures sex-specific differences in host quality or behavior that affect ectoparasite abundance and diversity, and that females are preferred hosts regardless of host body size.

When considering all Paraguayan bats as a group, larger host individuals had greater ectoparasite average richness (MeanS) than did smaller individuals. Four of the

largest common species of bat (i.e., *Noctilio albiventris*, *N. leporinus*, *Artibeus fimbriatus*, and *A. jamaicensis*) were the only taxa to average > 2.0 ectoparasite species per individual. Larger bats provide more surface area (i.e., habitat) for ectoparasites. Increased surface area of host individuals may affect MeanS in two ways. First, increased surface area allows for increased population sizes, thereby reducing the probability of stochastic extinction. Second, greater host body size may relax interspecific competition and allow more ectoparasite species to maintain sufficient population sizes to avoid local extinction.

Within the Vespertilionidae, ectoparasite assemblages of smaller bat species (i.e., *Myotis*) have greater Shannon diversity and lesser Berger-Parker dominance (Table 3.8) than do those of larger vespertilionids (i.e., *Eptesicus* and *Lasiurus*). *Myotis* were captured more often than were other vespertilionids. If capture rates for vespertilionid species are an adequate measure of relative abundance, larger population sizes of *Myotis* may permit smaller host species to harbor more diverse ectoparasite assemblages than do larger host species with similar morphology and ecology.

Effects of Host Ecology on Ectoparasite Biodiversity

Ecology, morphology, life history, and behavior of mammalian hosts interact to influence structure of parasite assemblages (Altizer et al. 2003). Because of their strong correlation, disentangling the effects of host body size, demographics, phylogeny, and social organization is complex. In addition, sampling deficiencies and contamination can confound attempts to understand patterns of ectoparasite abundance and diversity. Verily, a myriad of factors (e.g., host evolutionary age, host roosting ecology) may provide insights regarding patterns of ectoparasite diversity. The effects of habitat area (i.e., patagial area, trunk surface area) as estimated by host mass and forearm length on ectoparasite abundance and diversity were difficult to interpret. In analyses for all bats as a group or for all bats of a particular host family, host specificity obfuscates potential effects of body size. In analyses within host species, host body size is less important than

other host-related characteristics (e.g., sex, age, mating system) that may affect ectoparasite abundance or diversity.

The majority of investigations concerning factors that affect assemblage structure of ectoparasites has focused on birds. A number of studies document the effects of host size on abundance and diversity of ectoparasite assemblages. Although swallow mass had no effect on ectoparasite assemblage biodiversity, group-living species evinced greater mite prevalence compared to solitary species (Poulin 1991). Similarly, swift mass had no effect on lice density or richness (Lee and Clayton 1995), and host mass had no effect on tick densities in birds of New Guinea (Pruett-Jones and Pruett-Jones 1991). In a detailed study of four species of seabirds (Choe and Kim 1987), kittiwakes harbored more diverse ectoparasite assemblages (i.e., greater richness and evenness) than did murres. Kittiwakes are larger than are murres; wings of kittiwakes have 40% more wing surface area than do those of murres. Nonetheless, differences in ectoparasite diversity were more a consequence of host nesting, foraging, and migratory behavior than of host size. For example, kittiwakes build nests whereas murres nest on bare rock. This allows parasites that require nest habitat for part of their life cycle to infest kittiwakes but not murres. In addition, murres are under water feeders that dive to depths of 60 m, whereas kittiwakes feed at the water's surface. Therefore, murre ectoparasites must be adapted to underwater situations. Such demands may affect ectoparasite persistence on murres. Moreover, differences in migratory activity (i.e., black-legged kittiwakes migrate over the Bering Sea whereas red-legged kittiwakes are sedentary) may account for the more diverse ectoparasite fauna on the migratory species. Migration can expose birds to diverse parasite faunal pools, resulting in increased parasite richness. Two salient features characterize all of these studies, including this one. First, the effect of host size on ectoparasite assemblage structure is weak or non-existent. Second, host ecology, life history, demography, and behavior may be more important in structuring ectoparasite assemblages than is host body size. This observation is consistent with those for bat ectoparasites.

Successful species (i.e., those that are common and widespread), whether free-living or parasitic, avail themselves of abundant and reliable resources. For ectoparasites, measuring resource reliability is difficult because the host is not killed and therefore is constantly "available". In addition, the host is longer lived than the ectoparasite, so once a host is located, one need not be found again for a number of ectoparasite generations. However, space on the host is limited. Therefore, location of new resources (i.e., other host individuals or species) for dispersal of offspring is of utmost importance. The social structure and mating system of host species determine the opportunities for horizontal (i.e., interspecific) or vertical (i.e., intraspecific) host transfer. In most bat social systems, all host individuals do not provide equal transfer opportunities. Therefore, ectoparasites should select those hosts with the greatest prospects for reliable host transfer. Many bat ectoparasites require bodily contact of hosts to achieve transfer. However, even those ectoparasites that are vagile (e.g., streblids) can exist without feeding for only several hours. Thus, host transfer that does not involve body contact is risky for all bat ectoparasites. A common social and mating system in Neotropical phyllostomids and noctilionids is the harem, which usually consists of one adult male, several adult females, and their young. Similarly, female *Myotis* form maternity colonies that are nearly devoid of males (Humphrey and Cope, 1976). In Paraguay, *Myotis* and *Eptesicus* have two breeding seasons; therefore, maternity colonies may be maintained much of the year (Myers 1976). Based on transmission opportunities, female bats in harems or maternity colonies should be preferred by ectoparasites; adult male bats should be sub-optimal hosts; and sub-adult male bats (usually solitary) should be least desirable. Analyses showed 11 species of Paraguayan bat to be sexually dimorphic (Table 3.3) with males larger in five cases and females larger in six cases. Nonetheless, while accounting for sex-related differences in body size, females harbored more ectoparasites in 11 of 13 instances where ectoparasite abundance responded significantly to host sex (Table 3.7). The remaining two cases in which males harbored greater ectoparasite abundances than did females may involve interspecific competition among the ectoparasites. In the first case, a tick, *Ornithodoros hasei*, was three times more abundant on male *Noctilio*

albiventris than on females, whereas a bat fly, *Paradyschiria parvula*, was two times more abundant on female *N. albiventris* than on males. In the second case, *Steatonyssus joaquimi* was more abundant on male *Myotis nigricans* than on females, whereas *Macronyssus crosbyi* was more abundant on female *M. nigricans* than on males. These two cases may represent (resource) partitioning of the by ectoparasites to reduce competition.

Results of the FEA analysis for streblids on *N. albiventris* contradict the above scenario (Table 3.5). Male *N. albiventris* are larger than females, and harbor half as many streblids as do females. However, streblids are significantly more abundant on larger than on smaller *N. albiventris*. In addition to being abundant on female *N. albiventris*, streblids are abundant on larger adult males, which likely have harems. This is additional support for the hypothesis that the social status of a host is important to host selection by ectoparasites.

In general, migratory and hibernation activities, as well as mating systems and roosting ecology, are potential factors that affect ectoparasite assemblage structure. For example, bats that hibernate effectively eliminate ectoparasite species incapable of enduring prolonged cold temperatures, thereby reducing ectoparasite diversity. In contrast, migrations may expose bats to a greater diversity of bat species in multispecific roosts, which increases opportunities for invasion by new ectoparasite species. Bats exhibit social systems that can be classified broadly as colonial or solitary. Because colonial bats frequently make physical contact with one another, ectoparasite species that have gone extinct on host individuals may subsequently reestablish populations on those individuals. Therefore, greater ectoparasite richness and abundance should result from rescue effects (Brown and Kodric-Brown 1977) in which continual reestablishment of ectoparasite populations enhance biodiversity of colonial hosts (Altizer et al. 2003). Moreover, colonial bats are more faithful to roosts and use more permanent structures (e.g., buildings, caves, tree cavities) than do solitary bats (Kunz and Lumsden 2003). Reliable use of roosts by bats enhances the likelihood that ectoparasite species that make use of roosts during part of their life cycle successfully find a host. Any aspect of roost

ecology that enhances host availability will result in increased ectoparasite diversity and abundance. Whereas roost type may be responsible for differences in ectoparasite assemblage structure between host species, mating systems can affect host selection of ectoparasites within host species. Individuals that are not part of a harem are usually juvenile or adult bachelor males (Ortega and Arita 1999). Harem members are more roost faithful than are non-harem bats (Kunz et al. 1983, Ortega and Arita 1999). Roost fidelity is important for ectoparasite reproductive success, as well as for host infestation or vertical transmission (i.e., between hosts of the same species). Adult females usually are found in harems, and therefore have desirable host characteristics compared to solitary bats. Consequently, adult females should be preferred to other host individuals of the same species. These arguments may be extended to compare host species with different mating systems. For example, colonial host species may harbor more diverse and abundant ectoparasite assemblages than do solitary bat species (Altizer et al. 2003).

Of those bat species for which ectoparasite abundances varied with host body size, *Sturnira lilium* presents one of the most interesting cases. The three most common species of ectoparasites of *S. lilium* are more abundant on females than on males (Tables 3.4 and 3.6). This implies a difference between males and females that make the latter more desirable hosts. Because male *S. lilium* are significantly larger than females, selective advantages associated with female hosts must be strong enough to overcome potential benefits of greater body size in males. Differences in roosting ecology may make females more reliable hosts. Unfortunately, little is known about the roosting ecology or mating system of *S. lilium* (Gannon et al. 1989, Kunz 1982, Kunz and Lumsden 2003, McCracken and Wilkinson 2000). However, male *S. lilium* have potent scent glands on their shoulders that emit a strong odor (Altringham and Fenton 2003, Gannon et al. 1989). In addition, Altringham and Fenton (2003) reported "wing flapping associated with calling" in males that may serve as a visual cue to females in addition to dispersing glandular secretions. These secretions probably serve as a means for females to evaluate potential mates and for males to evaluate potential competitors. In Paraguay, *S. lilium* use buildings and tree hollows for roosts when caves are not available (Gannon

et al. 1989). Harems could be established in any of these structures. Because harem members are more site-faithful than are solitary bats (Kunz and Lumsden 2003, Kunz and McCracken 1996, Morrison 1979, Ortega and Arita 1999), harems provide ectoparasites with opportunities for dispersal to other host individuals and furnish a reliable source pool for ectoparasite species that are not permanent host residents (e.g., streblids). If male *S. lilium* are effectively solitary, whereas females are colonial, preferential selection of female hosts by ectoparasites explains how smaller hosts (i.e., females) have more ectoparasite species and individuals than do larger hosts (i.e., males).

A similar scenario has been documented for *Desmodus rotundus* in Costa Rica (Wilkinson 1985). Colony size was a significant factor in the number of *Trichobius* found on *Desmodus*. Larger host groups had higher ectoparasite densities and prevalences than did smaller groups.

Species Rich, Species Poor

In general, ectoparasite families are species-rich because most ectoparasite species are monoxenous and close host-parasite associations result in specialization and speciation. In contrast, ectoparasite assemblages on individual bats are species poor with average ectoparasite species richness on Paraguayan bat species ranging from 0.23 to 2.5 species per individual. Reasons are two-fold. First, many obstacles prevent infestation of new host species. Second, ectoparasites may be particularly susceptible to extinction.

Infestation of new host species is difficult for ectoparasites of bats. Bat ectoparasites experience various levels of physical isolation from hosts (see introduction above) that limit opportunities for transient associations that can become, over evolutionary time, primary associations. The effect of physical isolation is amplified because most bat ectoparasites survive less than two days without feeding. When ectoparasites infest a new host species (i.e., horizontal transfer), physical limitations related to specializations for life on their primary host species often result in death by starvation or host predation. Moreover, priority effects (Paine 1977) exist when transient

ectoparasites must compete with established ectoparasite species that likely are better adapted to survive on the newly infested host species.

Particular demographic and life history traits make some species more prone to extinction than others. Species that naturally occur at low abundances, with a high degree of specialization, are large-bodied, have small or fragmented geographic distributions, or occupy high trophic levels are more subject to extinction than common, generalist, wide-ranging, or small-bodied counterparts (Davies et al. 2000, 2004, Fagan et al. 2002). Ectoparasites of bats possess many of the qualities that make them susceptible to extinction (locally or globally). In general, they occur at low abundances, are ultimate specialists, and occupy high trophic levels (i.e., secondary or tertiary consumers). In addition, geographic ranges of ectoparasites are dependent on those of their host (i.e., they may be small or fragmented).

Successful horizontal transfer (i.e., transfers that result in formation of viable ectoparasite populations on newly infested host species), the proverbial "foot in the door", likely is the greatest obstacle to establishing new primary host-parasite associations. Any aspect of host biology that facilitates initial infestation or relaxes the demanding conditions of life on an unfamiliar host could lead to greater ectoparasite diversity on a particular host species. For example, colonial species of hosts, by occurring in large aggregates, may provide more favorable conditions for new infestation than would solitary roosting host species. In addition, large colonies are more roost faithful than are smaller colonies or solitary bats. Hosts that consistently return to the same roost provide ectoparasites that are not highly specialized (i.e., adapted to spend their entire life on the host) a greater opportunity to form new associations, which may lead to adaptation and speciation. To spend their entire life on a host requires extensive specialization by an ectoparasite. Such specialization limits the ability of ectoparasites to infest new host species that are not closely related to their primary host. Indeed, extensive specialization by some ectoparasite species has made hosts that are closely related to their primary host species (i.e., members of the same genus) unsuitable alternatives.

Conclusions

The use of body size as a surrogate for island area in the context of ETIB is practical and seems reasonable. However, the range of body sizes for bats of Paraguay is relatively small, spanning only one order of magnitude, compared to traditional islands which span several orders of magnitude and that have been the subject of biogeographic analysis. The range of body sizes in bats may not be great enough to allow the mechanisms associated with ETIB to operate at a detectible level. If a similar study were conducted with respect to all Paraguayan mammal species, for which the range of body sizes spans five orders of magnitude, body size might emerge as a more important determinant of ectoparasite diversity. Such dependence on scale or hierarchy is common in ecological studies of biodiversity (Scheiner et al. 2000, Willig et al. 2003). Alternatively, sex-related differences in behavior, particularly roosting habits, may be a more important factor for predicting ectoparasite diversity than is host size, *per se*.

Because bats are small and do not provide unlimited space for population growth, opportunities for transfer are important. Therefore, host individuals may not be the most appropriate scale to consider ectoparasite assemblages to be isolated evolutionary units. Nonetheless, ectoparasite assemblages on groups of host individuals (i.e., colonies or populations) may be evolutionarily isolated and better conform to predictions of ETIB. In this context, bat colony size may be a realistic surrogate for island area. Correspondingly, inter-colony distance may be an appropriate measure of distance to a source population. Some patterns (e.g., increased nycteribiid abundance on smaller vespertilionids) observed here are not adequately explained by either host size or social system. These cases may be better explained by investigating differences in host abundances. The effect of host abundance on ectoparasite abundance and diversity is explored in the following chapter.

Ectoparasite assemblages on bats have many qualities that make them attractive systems for study: 1) hosts are easily defined units of study, 2) each host individual harbors an assemblage of ectoparasites, 3) many bat species are common so many

replicate samples are available, and 4) bats are species-rich and differ in morphology, ecology, and behavior, facilitating analysis of the effects of hosts on ectoparasite assemblages. In addition, a host and its ectoparasites appear to constitute a simple system that is ideal for study. However, many ectoparasites of bats are host specific and may respond to variables at multiple scales (e.g., within host species, among host species). Moreover, ectoparasites and hosts often have congruent phylogenies which may complicate interpretation of analyses (Brooks and McLennan 1993). The detailed analyses employed here elucidated responses of ectoparasites to host characters at multiple scales and provided evidence that may explain why some host individuals have more diverse ectoparasite assemblages than do others (e.g., harem members versus non-harem members). In addition, by analyzing ectoparasite assemblages at multiple scales of host taxonomy, it became evident that at one focal scale (i.e., all host species as a group) body size is an important determinant of ectoparasite biodiversity, whereas at another scale (i.e., all host individuals within a particular species) ectoparasite biodiversity may be more affected by elements of host ecology (e.g., roosting behavior) than by host body size.

Literature Cited

Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. P. Dobson, V. Ezenwa, K. E. Jones, A. B. Pedersen, M. Poss, and J. R. C. Pulliam. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. Annual Review of Ecology, Evolution and Systematics 34:417-547.

Altringham, J. D., and M. B. Fenton. 2003. Sensory ecology and communication in the Chiroptera. Pp. 90-127 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham. 1988. Genetic studies of Lasiurus (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University 117:1-15.

Barquez, R. M., M. A. Mares, and J. K. Braun. 1999. The bats of Argentina. Special Publications, The Museum, Texas Tech University 42:1-275.

Barclay, R. M. R., and L. D. Harder. 2003. Life histories of bats: life in the slow lane. Pp. 209-253 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Brennan, J. M., and M. L. Goff. 1977. Keys to the genera of chiggers of the Western Hemisphere (Acarina: Trombiculidae). The Journal of Parasitology 63:554-566.

Brennan, J. M., and J. T. Reed. 1974. The genus *Eutrombicula* in Venezuela (Acarina: Trombiculidae). The Journal of Parasitology 60:699-711.

Brennan, J. M., and J. T. Reed. 1975. A list of Venezuela chiggers, particularly of small mammalian hosts (Acarina: Trombiculidae). Brigham Young University Science Bulletin, Biological Series 20 (1):45-75.

Brennan, J. M., and C. E. Yunker. 1966. The chiggers of Panama (Acarina: Trombiculidae). Pp. 221-266 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Brooks, D. R., and D. A. McLennan. 1993. Parascript: parasites and the language of evolution. Smithsonian Institution Press, Washington, D. C.

Brower, J. E., J. H. Zar, and C. N. von Ende. 1990. Field and laboratory methods for general ecology. Wm. C. Brown Publishers, Dubuque, Iowa.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. The American Naturalist 105:467-478.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.

Bush, M. B., and R. J. Whittaker. 1991. Krakatau: colonization patterns and hierarchies. Journal of Biogeography 18:341-356.

Camargo, J. A. 1993. Must dominance increase with the number of subordinate species in competitive interactions. Journal of Theoretical Biology 161:537-542.

Camargo, J. A. 1995. On measuring species evenness and other associated parameters of community structure. Oikos 74:538-542.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11:265-270.

Choe, J. C., and K. C. Kim. 1987. Community structure of arthropod ectoparasites on Alaskan seabirds. Canadian Journal of Zoology 65:2998-3005.

Coleman, B. D., M. A. Mares, M. R. Willig, and Y.-H. Hsieh. 1982. Randomness, area, and species richness. Ecology 63:1121-1133.

Colwell, R. K., and D. W. Winkler. 1984. A null model for null models. Pp. 344 - 359 in Ecological communities: conceptual issues and the evidence (D. Strong, D. Simberloff, L. Abele, and A. Thistle, eds.). Princeton University Press, Princeton, New Jersey.

Colwell, R. K. 2001. EstimateS: statistical estimation of species richness and shared species from samples for the Macintosh (V 6.0b1). Available online at http://viceroy.eeb.uconn.edu/EstimateS.

Davies, K. F., C. R. Margules, and J. F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450-1461.

Davies, K. F., C. R. Margules, and J. F. Lawrence. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85:265-271.

De Alckmin Marques, E. S., P. W. Price, and N. S. Cobb. 2000. Resource abundance and insect herbivore diversity on woody fabaceous desert plants. Environmental Entomology 29:696-703.

de la Cruz, J. 1969. Nueva espécie de acaro (Acarina: Listrophoridae) parásito de murciélagos cubanos. Poeyana, Seria A 62:1-8.

Dusbábek, F. 1969*a*. To the phylogeny of genera of the family Myobiidae. Acarologia 11:537-574.

Dusbábek, F. 1969*b*. Generic revision of the myobiid mites (Acarina: Myobiidae) parasitic on bats. Folia Parasitologica 16:1-17.

Dusbábek, F., and J. de la Cruz. 1966. Nuevos géneros y espécies de acaros (Acarina: Listrophoridae) parásitos de murciélagos cubanos. Poeyana, Seria A 31:1-20.

Emerson, S. B., H. W. Greene, and E. L. Charnov. 1994. Allometric aspects of predator-prey interactions. Pp. 123-139 in Ecological morphology: integrative organismal biology (P. C. Wainwright and S. M. Reilly, eds.). The University of Chicago Press, Chicago, Illinois.

Fagan, W. F., P. J. Unmack, C. Burgess, and W. L. Minckley. 2002. Rarity, fragmentation, and extinction in desert fishes. Ecology 83:3250-3256.

Fain, A. 1978. Mites of the family Myobiidae (Acarina: Prostigmata) from mammals in the collection of the British Museum (Natural History). Bulletin of the British Museum of Natural History, Zoological Series 33:193-229.

Fairchild, G. B., G. M. Kohls, and V. J. Tipton. 1966. The ticks of Panama (Acarina: Ixodoidea). Pp. 167-220 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Ferris, G. F., and R. L. Usinger. 1939. The family Polyctenidae (Hemiptera: Heteroptera). Microentomology 4:1-50.

Ferris, G. F., and R. L. Usinger. 1945. Notes and descriptions of American Polyctenidae (Hemiptera). Pan Pacific Entomologist 21:121-124.

Frenzel, M., and R. Brandl. 1998. Diversity and composition of phytophagous insect guilds on Brassicaceae. Oecologia 113:391-399.

Gannon, M. R., and M. R. Willig. 1997. The effect of lunar illumination on movement and activity of the red fig-eating bat (*Stenoderma rufum*). Biotropica 29:525-529.

Gannon, M. R., M. R. Willig, and J. K. Jones, Jr. 1989. Sturnira lilium. Mammalian Species 333:1-5.

Gilbert, F. S. 1980. The equilibrium theory of island biogeography, fact or fiction? Journal of Biogeography 7:209-235.

Guimarães, L. R. 1966. Nycteribiid bat flies from Panama (Diptera: Nycteribiidae). Pp. 393-404 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Guimarães, L. R. 1972. Venezuelan nycteribiid batflies (Diptera: Nycteribiidae). Brigham Young University Science Bulletin, Biological Series 17 (1):1-11.

Haila, Y., and O. Järvinen. 1982. The role of theoretical concepts in understanding the ecological theatre: a case study on island biogeography. Pp. 261-278 in Conceptual issues in ecology (E. Saarinen, ed.). D. Reidel, Dordrecht, The Netherlands.

Handley, C. O., Jr. 1987. New species of mammals from northern South America: fruit-eating bats, genus *Artibeus* Leach. Pp. 163-172 in Studies in neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana, Zoology (New Series) 39:1-506.

Humphrey, S. R., and J. B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and North-central Kentucky. The American Society of Mammalogists, Special Publications 4:1-81.

Herrin, C. S., and V. J. Tipton. 1975. Spinturnicid mites of Venezuela. Brigham Young University Science Bulletin, Biological Series 20 (2):1-72.

Hurlbert, S. H. 2003. Design and analysis: uncertain intent, uncertain result. Ecology 84:810-812.

Johnson, M. P., and D. S. Simberloff. 1974. Environmental determinants of island species numbers in the British Isles. Journal of Biogeography 1:149-154.

Jones, E. K, C. M. Clifford, J. E. Keirans, and G. M. Kohls. 1972. Ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of *Amblyomma* in the Western Hemisphere. Brigham Young University Science Bulletin, Biological Series 17 (4):1-40.

Kennedy, C. R. 1978*a*. An analysis of the metazoan parasitocoenoses of brown trout *Salmo trutta* from British lakes. Journal of Fish Biology 13:255-263.

Kennedy, C. R. 1978*b*. The parasite fauna of resident char *Salvelinus alpinus* from Arctic islands, with special reference to Bear Island. Journal of Fish Biology 13:457-466.

Koopman, K. F. 1993. Order Chiroptera. Pp. 137-241 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D. C.

Kunz, T. H. 1982. Roosting ecology. Pp. 1-56 in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, New York.

Kunz, T. H., P. V. August, and C. D. Burnett. 1983. Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Biotropica 15:133-138.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3-89 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Kunz, T. H., and G. F. McCracken. 1996. Tents and harems: apparent defence of foliage roosts by tent-making bats. Journal of Tropical Ecology 12:121-137.

Kuris, A. M., A. R. Blaustein, and J. J. Alió. 1980. Hosts as islands. The American Naturalist 116:570-586.

Lee, P. L. M., and D. H. Clayton. 1995. Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. Ecological Entomology 20:43-50.

Lewinsohn, T. M. 1991. Insects in flower heads of Asteraceae in southeast Brazil: a case study of tropical species richness. Pp. 525-559 in Plant-Animal interactions: evolutionary ecology in tropical and temperate regions (P. Price, T. Lewinsohn, G Fernandes, and W. Benson, eds.). Wiley & Sons, New York, New York.

López-González, C. 1998. Systematics and zoogeography of the bats of Paraguay. Ph.D. dissertation, Texas Tech University, Lubbock.

López-González, C. 2005. Los murciélagos de Paraguay. Publicaciones Comité Español MAB y Red Ibero MAB (in press).

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

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

McCracken, G. F., and G. S. Wilkinson. 2000. Bat mating systems. Pp. 321-362 in Reproductive biology of bats (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, New York, New York.

McDaniel, B. 1970. The labidocarpid batmites of Nicaragua (Listrophoroidea : Labidocarpidae). Acarologia 12:803-823.

McDaniel, B. 1973. Labidocarpid bat-mites of Venezuela (Listophoroidea: Labidocarpidae). Brigham Young University Science Bulletin, Biological Series 17 (2):15-32.

Machado-Allison, C. E. 1965. Las espécies Venezolanas del género *Periglischrus* Kolenati 1857. Acta Biología Venezuelica 4:259-348.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

Marshall, A. G. 1971. The ecology of *Basilia hispida* (Diptera: Nycteribiidae) in Malaysia. Journal of Animal Ecology 40:141-154.

Marshall, A. G. 1982. Ecology of insects ectoparasitic on bats. Pp. 369-401 in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, New York.

The Math Works, Inc. 1994. Matlab for Macintosh, ver. 4.2c.1. Prentice Hall, Englewood Cliffs, New Jersey.

May, R. M. 1975. Patterns of species abundance and diversity. Pp. 81-120 in Ecolgy and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap Press of Harvard University, Cambridge, Massachusetts.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403-405.

Morrison, D. W. 1979. Apparent male defense of tree hollows in the fruit bat, *Artibeus jamaicensis*. Journal of Mammalogy 60:11-15.

Myers, P. 1976. Patterns of reproduction of four species of vespertilionid bats in Paraguay. University of California Publications in Zoology 107:1-41.

Myers, P. 1982. Origins and affinities of the mammal fauna of Paraguay. Pp. 85-93 in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications, Pymatuning Laboratory of Ecology 6:1-539.

Newbound, D. R., and B. Knott. 1999. Parasitic copepods from pelagic sharks in western Australia. Bulletin of Marine Science 65:715-724.

Ortega, J., and H. T. Arita. 1999. Structure and social dynamics of harem groups in *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Journal of Mammalogy 80:1173-1185.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Special Publications of the Academy of Natural Sciences, Philadelphia 12:245-270.

Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. American Zoologist 34:134-144.

Peet, R. K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5:285-307.

Pinichpongse, S. 1963*a*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (1st series). Acarologia 5:81-91.

Pinichpongse, S. 1963*b*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part Two). Acarologia 5:266-278.

Pinichpongse, S. 1963*c*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part three). Acarologia 5:397-404.

Pinichpongse, S. 1963*d*. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part four). Acarologia 5:620-627.

Poulin, R. 1991. Group-living and infestation by ectoparasites in passerines. The Condor 93:418-423.

Pruett-Jones, M., and S. Pruett-Jones. 1991. Analysis and ecological correlates of tick burdens in a New Guinea avifauna. Pp. 154-176 in Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M. Zuk, eds.). Oxford University Press, Oxford, England.

Radovsky, F. J. 1967. The Macronyssidae and Laelapidae (Acarina: Mesostigmata) parasitic on bats. University of California Publications in Entomology 46:1-288.

Reed, J. T., and J. M. Brennan. 1975. The subfamily Leeuwenhoekinae in the Neotropics (Acarina: Trombiculidae). Brigham Young University Science Bulletin, Biological Series 20 (1):1-42.

Ronderos, R. A. 1959. Polycténidae americanos. I. (Hemiptera). Actas y Trabajos del Primer Congreso Sudamericano de Zoologia 3:173-180.

Ronderos, R. A. 1962. Polycténidae americanos. II. (Hemiptera). Acta Zoologica Lilloana 18:259-262.

Rudnick, A. 1960. A revision of the mites of the family Spinturnicidae (Acarina). University of California Publications in Entomology 17: 157-283.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, England.

Saunders, R. C. 1975. Venezuelan Macronyssidae (Acarina: Mesostigmata). Brigham Young University Science Bulletin, Biological Series 20 (2):75-90.

Scheiner, S. M. 2003. Six types of species-area curves. Global Ecology & Biogeography 12:441-447.

Scheiner, S. M., S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari. 2000. Species density, species-area curves and Simpson's paradox. Evolutionary Ecology Research 2:791-802.

Schrader-Frechette, K. S., and E. D. McCoy. 1993. Method in ecology: strategies for conservation. Cambridge University Press, Cambridge, England.

Shoener, A. 1988. Experimental island biogeography. Pp. 485-512 in Analytical biogeography: an integrated approach to the study of animal and plant distributions (A. Myers and P. Giller, eds.). Chapman and Hall, New York, New York.

Simberloff, D. S. 1976. Species turnover and equilibrium island biogeography. Science 194:572-578.

Simberloff, D. S. 1983. When is an island community in equilibrium? Science 220:1275-1277.

Simberloff, D. S., and E. O. Wilson. 1970. Experimental zoogeography of islands. A two-year record of colonization. Ecology 51:934-937.

Simmons, N. B., and R. S. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 1. Bats. Bulletin of the American Museum of Natural History 237:1-219.

Sismondo, S. 2000. Island biogeography and the multiple domains of models. Biology and Philosophy 15:239-258.

Southwood, T. R. E. 1978. Ecological Methods. Chapman and Hall, London, Great Britain.

SPSS, Inc. 1990. The SPSS base system user's guide. SPSS, Inc., Chicago, Illinois.

Ueshima, N. 1972. New World Polyctenidae (Hemiptera), with special reference to Venezuelan species. Brigham Young University Science Bulletin, Biological Series 17 (1):13-21.

Wenzel, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin, Biological Series 20 (4):1-177.

Wenzel, R. L., and V. J. Tipton. 1966. Some relationships between mammal hosts and their ectoparasites. Pp. 677-723 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Wenzel, R. L., V. J. Tipton, and A. Kiewlicz. 1966. The streblid batflies of Panama (Diptera: Streblidae). Pp. 405-675 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Whittaker, R. H. 1960. Vegetation of the Kiskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Whitaker, R. J. 1998. Island biogeography: ecology, evolution and conservation. Oxford University Press, Oxford, England.

Wilkinson, G. S. 1985. The social organization of the common vampire bat. I. Pattern and cause of association. Behavioral Ecology and Sociobiology 17:111-121.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution and Systematics 34: 273-309.

Willig, M. R., S. J. Presley, R. D. Owen, and C. López-González. 2000. Composition and structure of bat assemblages in Paraguay: a subtropical – temperate interface. Journal of Mammalogy 81:386-401.

Table 3.1. For the 22 common host species, the average forearm length (FA) in millimeters, mass (MA) in grams, and sample size (N), as well as the total number of collected ectoparasites (EN) and 9 measures of ectoparasite biodiversity. See text for abbreviations.

Host family	Host characteristics		
Host species	FA	MA	N
Noctilionidae			
Noctilio albiventris	62.6	31.5	133
Noctilio leporinus	86.1	55.0	30
Phyllostomidae			
Glossophaga soricina	35.3	8.9	104
Carollia perspicillata	40.9	16.7	89
Desmodus rotundus	63.4	40.9	61
Artibeus fimbriatus	66.3	52.6	87
Artibeus jamaicensis	60.5	43.4	45
Artibeus lituratus	71.3	65.8	498
Platyrrhinus lineatus	47.0	22.4	103
Pygoderma bilabiatum	39.8	18.1	55
Sturnira lilium	42.4	19.3	556
Family Vespertilionidae			
Eptesicus furinalis	38.5	8.0	75
Lasiurus ega	46.7	12.2	75
Myotis albescens	34.2	6.0	116
Myotis nigricans	32.7	4.7	137
Family Molossidae			
Eumops glaucinus	60.4	33.9	57
Eumops patagonicus	43.9	12.9	1102
Molossops temminckii	30.6	5.4	178
Molossus ater	48.3	28.7	112
Molossus currentium	42.8	17.8	37
Molossus molossus	38.6	12.1	313
Nyctinomops laticaudatus	44.1	10.9	47

Table 3.1. Continued

Host family		Richness of ectoparasites			
Host species	EN	MeanS	AccumS	Chao1	LogS
Noctilionidae					
Noctilio albiventris	1460	2.5	11.0	13.3	17.4
Noctilio leporinus	553	2.4	8.0	0.0	8.4
Phyllostomidae					
Glossophaga soricina	64	0.5	10.0	11.7	12.3
Carollia perspicillata	124	1.0	14.0	1.8	17.5
Desmodus rotundus	407	1.0	8.0	9.0	20.9
Artibeus fimbriatus	561	2.3	12.0	18.3	23.7
Artibeus jamaicensis	306	2.0	12.0	3.7	14.2
Artibeus lituratus	1123	1.2	17.0	21.2	25.4
Platyrrhinus lineatus	394	1.2	14.0	18.0	19.1
Pygoderma bilabiatum	13	0.2	7.0	7.5	8.2
Sturnira lilium	2023	1.9	23.0	55.0	59.1
Family Vespertilionidae					
Eptesicus furinalis	812	1.3	16.0	16.5	21.6
Lasiurus ega	411	0.7	5.0	4.0	5.6
Myotis albescens	1550	1.7	15.0	0.0	17.5
Myotis nigricans	557	1.0	16.0	16.2	18.1
Family Molossidae					
Eumops glaucinus	335	1.2	8.0	8.5	9.6
Eumops patagonicus	1693	0.8	17.0	21.0	29.5
Molossops temminckii	541	0.9	15.0	19.3	25.2
Molossus ater	911	1.3	16.0	19.1	27.9
Molossus currentium	64	1.0	4.0	4.0	5.0
Molossus molossus	2427	1.3	15.0	18.0	23.3
Nyctinomops laticaudatus	182	1.0	9.0	0.0	12.0

Table 3.1. Continued

Host family / Host species	Biodiversity of ectoparasites				
	Shannon	Even	Dom	Rare	Betadiv
Noctilionidae					
Noctilio albiventris	0.5	0.5	0.5	8	14.9
Noctilio leporinus	0.6	0.7	0.4	4	6.1
Phyllostomidae					
Glossophaga soricina	0.8	0.8	0.4	5	11.8
Carollia perspicillata	0.7	0.6	0.5	11	16.5
Desmodus rotundus	0.5	0.5	0.5	5	19.9
Artibeus fimbriatus	0.6	0.5	0.5	9	21.5
Artibeus jamaicensis	0.7	0.7	0.4	8	12.2
Artibeus lituratus	0.5	0.4	0.6	14	24.2
Platyrrhinus lineatus	0.6	0.5	0.4	11	17.9
Pygoderma bilabiatum	0.8	1.0	0.2	0	8.0
Sturnira lilium	0.7	0.5	0.4	19	57.2
Family Vespertilionidae					
Eptesicus furinalis	0.3	0.2	0.9	15	20.3
Lasiurus ega	0.1	0.1	1.0	3	5.0
Myotis albescens	0.5	0.4	0.5	13	15.8
Myotis nigricans	0.7	0.6	0.4	13	17.1
Family Molossidae					
Eumops glaucinus	0.5	0.6	0.5	5	8.4
Eumops patagonicus	0.3	0.3	0.8	15	28.7
Molossops temminckii	0.5	0.4	0.7	9	24.4
Molossus ater	0.5	0.4	0.6	13	26.6
Molossus currentium	0.3	0.4	0.8	2	3.9
Molossus molossus	0.5	0.5	0.5	11	22.0
Nyctinomops laticaudatus	0.3	0.3	0.9	7	11.0

Table 3.2. Results of simple regression analyses determining the effect of host body size (FA and MA) on total ectoparasite abundance (TEA) for all hosts as a group, for each host family, and for each host species. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Host family	FA			MA		
Host species	r^2	p-value	B_1	r^2	p-value	B_1
All bats	0.001	0.053		0.000	0.693	
Noctilionidae	0.008	0.406		0.006	0.458	
Noctilio albiventris	0.006	0.537		0.016	0.307	
Noctilio leporinus	0.000	0.995		0.132	0.058	
Phyllostomidae	**0.004**	**0.026**	**0.06**	0.001	0.425	
Glossophaginae						
Glossophaga soricina	0.005	0.614		0.004	0.668	
Carollinae						
Carollia perspicillata	0.002	0.741		0.012	0.355	
Desmodontinae						
Desmodus rotundus	0.001	0.806		0.013	0.428	
Stenodermatinae						
Artibeus fimbriatus	0.000	0.928		**0.051**	**0.045**	**0.23**
Artibeus jamaicensis	0.002	0.756		0.015	0.445	
Artibeus lituratus	0.002	0.406		0.000	0.784	
Platyrrhinus lineatus	0.000	0.956		0.001	0.831	
Pygoderma bilabiatum	0.022	0.293		0.002	0.773	
Sturnirinae						
Sturnira lilium	0.002	0.351		**0.055**	**< 0.001**	**-0.23**

Table 3.2. Continued

Host family	FA			MA		
Host species	r^2	p-value	B_1	r^2	p-value	B_1
Vespertilionidae	0.000	0.789		0.000	0.853	
Eptesicus furinalis	0.009	0.443		0.000	0.875	
Lasiurus ega	0.005	0.565		0.017	0.272	
Myotis albescens	**0.050**	**0.038**	**0.22**	**0.046**	**0.045**	**0.22**
Myotis nigricans	0.000	0.834		0.017	0.137	
Molossidae	0.000	0.569		0.003	0.061	
Eumops glaucinus	0.008	0.507		0.019	0.309	
Eumops patagonicus	0.000	0.707		0.002	0.330	
Molossops temminckii	0.024	0.054		**0.031**	**0.026**	**0.18**
Molossus ater	0.013	0.262		**0.042**	**0.042**	**-0.20**
Molossus currentium	0.006	0.696		0.033	0.368	
Molossus molossus	0.000	0.819		0.014	0.073	
Nyctinomops laticaudatus	0.047	0.173		0.006	0.612	

Table 3.3. Significance of multivariate (MANOVA) and univariate (ANOVA) analyses of sexual size dimorphism for each of 19 common host species. Significant results in bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Host family	MANOVA	ANOVA		Larger
Host species		FA	MA	sex
Noctilionidae				
Noctilio albiventris	**0.009**	0.967	**0.013**	Males
Noctilio leporinus	**0.037**	0.439	**0.014**	Males
Phyllostomidae				
Carollia perspicillata	**0.042**	0.892	**0.024**	Females
Artibeus fimbriatus	0.426	0.515	0.414	
Artibeus jamaicensis	0.493	0.245	0.996	
Artibeus lituratus	**< 0.001**	**0.029**	**< 0.001**	Females
Platyrrhinus lineatus	**0.018**	0.590	**0.005**	Females
Sturnira lilium	**< 0.001**	0.052	**< 0.001**	Males
Vespertilionidae				
Eptesicus furinalis	0.101	0.118	0.471	
Lasiurus ega	**< 0.001**	**< 0.001**	**< 0.001**	Females
Myotis albescens	**0.001**	**0.004**	**0.002**	Females
Myotis nigricans	**0.001**	0.208	**< 0.001**	Females
Molossidae				
Eumops glaucinus	0.302	0.088	0.095	
Eumops patagonicus	0.641	0.709	0.448	
Molossops temminckii	0.334	0.168	0.973	
Molossus ater	**0.021**	0.466	**0.011**	Males
Molossus currentium	0.077	0.217	**0.031**	Males
Molossus molossus	**< 0.001**	**0.031**	**< 0.001**	Males
Nyctinomops laticaudatus	0.289	0.700	0.133	

Table 3.4. Results of simple regression analyses determining the effect of host body size (FA and MA) on familial ectoparasite abundance (FEA) for all hosts as a group, for each primary host family and each primary host species Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Host family / Host species / Ectoparasite family	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
All bats						
Streblidae	**0.055**	**< 0.001**	**0.23**	**0.024**	**< 0.001**	**0.16**
Polyctenidae	0.000	0.993		0.000	0.648	
Nycteribiidae	**0.019**	**< 0.001**	**-0.14**	**0.016**	**< 0.001**	**-0.12**
Spinturnicidae	**0.067**	**< 0.001**	**0.26**	**0.094**	**< 0.001**	**0.31**
Macronyssids	**0.013**	**< 0.001**	**-0.11**	**0.015**	**< 0.001**	**-0.12**
Argasidae	**0.013**	**< 0.001**	**0.11**	**0.002**	**0.007**	**0.05**
Trombiculidae	0.001	0.055		**0.001**	**0.050**	**0.04**
Chirodiscidae	0.035	0.064		**0.001**	**0.040**	**-0.04**
Noctilionidae						
Streblidae	0.009	0.368		**0.056**	**0.020**	**0.24**
Argasidae	0.031	0.089		0.008	0.401	
Noctilio albiventris						
Streblidae	**0.088**	**0.015**	**0.30**	0.056	0.052	
Argasidae	0.040	0.107		0.001	0.774	
Noctilio leporinus						
Streblidae	0.051	0.257		0.137	0.052	
Phyllostomidae						
Streblidae	0.000	0.555		**0.003**	**0.045**	**-0.60**
Spinturnicidae	**0.036**	**< 0.001**	**0.19**	**0.028**	**< 0.001**	**0.17**

Table 3.4. Continued

Host family Host species Ectoparasite family	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Macronyssidae	0.000	0.686		0.000	0.617	
Carollinae						
Carollia perspicillata						
Streblidae	0.000	0.964		0.012	0.354	
Stenodermatinae						
Artibeus fimbriatus						
Streblidae	0.012	0.339		0.022	0.191	
Spinturnicidae	0.002	0.692		0.017	0.249	
Macronyssidae	0.002	0.725		0.024	0.177	
Artibeus jamaicensis						
Spinturnicidae	0.010	0.519		0.001	0.820	
Artibeus lituratus						
Streblidae	0.000	0.764		**0.038**	**< 0.001**	**0.19**
Spinturnicidae	0.003	0.275		0.008	0.088	
Macronyssidae	0.000	0.947		0.000	0.925	
Platyrrhinus lineatus						
Spinturnicidae	0.007	0.443		0.037	0.072	
Macronyssidae	0.002	0.694		0.007	0.427	
Sturnirinae						
Sturnira lilium						
Streblidae	0.006	0.126		**0.023**	**0.002**	**-0.15**
Spinturnicidae	0.001	0.665		**0.076**	**< 0.001**	**-0.28**
Macronyssidae	**0.021**	**0.004**	**0.14**	**0.015**	**0.014**	**-0.12**

Table 3.4. Continued

Host family / Host species / Ectoparasite family	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Family Vespertilionidae						
Nycteribiidae	**0.032**	**< 0.001**	**-0.18**	**0.024**	**0.002**	**-0.16**
Spinturnicidae	0.008	0.081		0.005	0.153	
Macronyssidae	0.000	0.906		0.001	0.590	
Eptesicus furinalis						
Macronyssidae	0.022	0.233		0.003	0.675	
Lasiurus ega						
Macronyssidae	0.006	0.522		0.014	0.327	
Myotis albescens						
Nycteribiidae	**0.086**	**0.006**	**-0.29**	0.031	0.103	
Macronyssidae	**0.057**	**0.027**	**0.24**	0.040	0.062	
Myotis nigricans						
Nycteribiidae	0.027	0.065		**0.078**	**< 0.001**	**0.28**
Macronyssidae	0.000	0.762		0.004	0.455	
Family Molossidae						
Streblidae	0.002	0.126		**0.006**	**0.008**	**0.08**
Polyctenidae	**0.013**	**< 0.001**	**0.11**	**0.021**	**< 0.001**	**0.15**
Macronyssidae	0.001	0.410		0.002	0.102	
Argasidae	0.001	0.350		0.002	0.119	
Trombiculidae	0.002	0.163		0.003	0.055	
Chirodiscidae	0.001	0.437		0.000	0.801	
Eumops glaucinus						
Polyctenidae	0.009	0.482		0.062	0.064	
Macronyssidae	0.015	0.374		0.001	0.832	

Table 3.4. Continued

Host family Host species Ectoparasite family	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Eumops patagonicus						
Streblidae	0.003	0.248		0.000	0.830	
Polyctenidae	0.000	0.742		0.000	0.995	
Macronyssidae	0.002	0.367		0.003	0.209	
Argasidae	0.000	0.995		**0.014**	**0.006**	**-0.12**
Molossops temminckii						
Polyctenidae	0.014	0.134		0.001	0.734	
Macronyssidae	**0.045**	**0.008**	**0.21**	**0.031**	**0.027**	**0.18**
Molossus ater						
Macronyssidae	0.000	0.838		0.038	0.051	
Molossus currentium						
Macronyssidae	0.004	0.754		0.040	0.316	
Molossus molossus						
Polyctenidae	**0.020**	**0.036**	**-0.140**	**0.068**	**< 0.001**	**-0.260**
Macronyssidae	0.000	0.971		0.007	0.194	
Chirodiscidae	0.001	0.660		0.009	0.161	
Nyctinomops laticaudatus						
Macronyssidae	0.056	0.137		0.006	0.624	

Table 3.5. Significance levels for analyses of covariance determining the effect of host sex on familial ectoparasite abundance while removing the effect of host size (FA and MA). Correlation coefficients and p-values are provided for separate correlation analyses of the association between body size (FA and MA) and familial ectoparasite abundances. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Host family			Pearson product-moment correlation analysis			
Host species	p-value		FA		MA	
Ectoparasite family	Covariates	Sex	r	p-value	r	p-value
Noctilionidae						
Noctilio albiventris						
Streblidae	**0.003**	**< 0.001**	0.778	0.384	**0.969**	**0.029**
Argasidae	0.212	**0.032**	-0.958	0.099	-0.344	0.612
Noctilio leporinus						
Streblidae	0.318	0.764	0.703	0.800	0.986	0.281
Phyllostomidae						
Carollia perspicillata						
Streblidae	0.918	0.078	-0.131	0.827	0.847	0.683
Artibeus fimbriatus						
Streblidae	0.500	0.134	0.487	0.883	0.992	0.305
Spinturnicidae	0.617	0.958	0.074	0.764	0.952	0.329
Macronyssidae	0.099	**0.022**	-0.240	0.204	**0.810**	**0.037**
Artibeus jamaicensis						
Spinturnicidae	0.895	0.339	0.963	0.683	0.485	0.899
Artibeus lituratus						
Streblidae	**0.006**	0.474	0.198	0.543	0.982	**0.002**
Spinturnicidae	**0.012**	**0.015**	0.291	0.058	**-0.775**	**0.004**
Macronyssidae	0.839	0.308	-0.272	0.947	-0.994	0.569

Table 3.5. Continued

Host family			Pearson product-moment correlation analysis			
Host species	p-value		FA		MA	
Ectoparasite family	Covariates	Sex	r	p-value	r	p-value
Platyrrhinus lineatus						
Spinturnicidae	0.252	0.988	-0.459	0.714	-0.976	0.141
Macronyssidae	0.958	0.158	0.450	0.951	0.978	0.795
Sturnira lilium						
Streblidae	**0.006**	0.780	-0.175	0.994	**-1.000**	**0.002**
Spinturnicidae	< **0.001**	0.154	-0.260	0.659	**-0.996**	< **0.001**
Macronyssidae	**0.001**	0.585	**0.699**	**0.002**	**-0.581**	**0.005**
Vespertilionidae						
Eptesicus furinalis						
Macronyssidae	0.471	0.118	0.824	0.450	0.788	0.487
Lasiurus ega						
Macronyssidae	0.103	**0.042**	-0.715	0.249	-0.844	0.134
Myotis albescens						
Nycteribiidae	**0.010**	0.573	**-0.740**	**0.009**	**0.508**	**0.038**
Macronyssidae	**0.036**	0.603	0.846	0.062	0.694	0.165
Myotis nigricans						
Nycteribiidae	**0.020**	0.471	0.453	0.814	**0.997**	**0.012**
Macronyssidae	0.282	0.798	-0.706	0.143	0.388	0.260
Molossidae						
Eumops glaucinus						
Polyctenidae	0.095	0.088	0.494	0.234	0.840	0.059
Macronyssidae	0.743	0.481	-0.930	0.466	-0.318	0.777

Table 3.5. Continued

Host family			Pearson product-moment correlation analysis			
Host species	p-value		FA		MA	
Ectoparasite family	Covariates	Sex	r	p-value	r	p-value
Eumops patagonicus						
Streblidae	0.276	0.093	0.925	0.114	-0.167	0.542
Polyctenidae	0.138	0.691	**-0.956**	**0.047**	0.076	0.558
Macronyssidae	0.361	0.568	0.275	0.493	-0.877	0.170
Argasidae	**0.020**	0.280	-0.423	0.550	**-0.977**	**0.011**
Molossops temminckii						
Polyctenidae	0.321	0.801	-0.988	0.140	-0.203	0.812
Macronyssidae	**0.010**	0.312	**0.879**	**0.044**	0.754	0.143
Molossus ater						
Macronyssidae	0.083	0.246	0.121	0.511	**0.956**	**0.027**
Molossus currentium						
Macronyssidae	0.596	0.733	-0.471	0.522	0.775	0.373
Molossus molossus						
Polyctenidae	< **0.001**	0.202	-0.095	0.520	**-0.987**	< **0.001**
Macronyssidae	0.111	0.596	-0.582	0.106	0.640	0.088
Chirodiscidae	0.806	0.318	0.462	0.561	0.975	0.884
Nyctinomops laticaudatus						
Macronyssidae	0.321	0.599	0.951	0.148	0.259	0.640

Table 3.6. Results of simple regression analyses determining the effect of host body size (FA and MA) on specific ectoparasite abundance (SEA) for all hosts as a group, for each primary host family, and for each primary host species. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Host family / Host species / Ectoparasite species	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
All bats						
Aspidoptera falcata	**0.004**	**< 0.001**	**-0.06**	**0.001**	**0.040**	**-0.04**
Megistopoda aranea	**0.024**	**< 0.001**	**0.16**	**0.023**	**< 0.001**	**0.15**
Megistopoda proxima	**0.007**	**< 0.001**	**-0.08**	**0.002**	**0.013**	**-0.05**
Noctiliostrebla maai	**0.016**	**< 0.001**	**0.12**	**0.002**	**0.023**	**0.42**
Paradyschiria fusca	**0.030**	**< 0.001**	**0.17**	**0.012**	**< 0.001**	**0.11**
Paradyschiria parvula	**0.014**	**< 0.001**	**0.12**	**0.002**	**0.008**	**0.05**
Paratrichobius longicrus	**0.072**	**< 0.001**	**0.27**	**0.113**	**< 0.001**	**0.34**
Trichobius joblingi	**0.002**	**0.025**	**-0.04**	0.001	0.125	
Trichobius jubatus	0.001	0.103		0.001	0.068	
Trichobius parasiticus	**0.005**	**< 0.001**	**0.07**	**0.002**	**0.018**	**0.04**
Hesperoctenes fumarius	**0.004**	**< 0.001**	**-0.06**	**0.002**	**0.010**	**-0.05**
Hesperoctenes longiceps	**0.001**	**0.046**	**-0.04**	**0.006**	**< 0.001**	**-0.08**
Hesperoctenes parvulus	**0.008**	**< 0.001**	**-0.09**	**0.004**	**< 0.001**	**-0.06**
Hesperoctenes n. sp. 1	**0.002**	**0.036**	**0.04**	0.001	0.110	
Periglischrus iheringi	**0.136**	**< 0.001**	**0.37**	**0.167**	**< 0.001**	**0.41**
Periglischrus ojasti	**0.005**	**< 0.001**	**-0.07**	**0.003**	**0.007**	**-0.05**
Chiroptonyssus haematophagus	**0.003**	**0.002**	**-0.06**	**0.008**	**< 0.001**	**-0.09**
Chiroptonyssus robustipes	0.000	0.673		0.001	0.119	
Chiroptonyssus venezolanus	**0.011**	**< 0.001**	**-0.10**	**0.008**	**< 0.001**	**-0.09**
Macronyssoides conciliatus	0.000	0.920		0.000	0.933	
Macronyssoides kochi	**0.046**	**< 0.001**	**0.21**	**0.061**	**< 0.001**	**0.25**
Macronyssus crosbyi	**0.015**	**< 0.001**	**-0.12**	**0.011**	**< 0.001**	**-0.10**

Table 3.6. Continued

Host family / Host species / Ectoparasite species	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Parichoronyssus euthysternum	**0.003**	**0.004**	**-0.05**	**0.002**	**0.037**	**-0.04**
Steatonyssus furmani	0.000	0.622		**0.003**	**0.004**	**-0.05**
Steatonyssus joaquimi	**0.008**	**< 0.001**	**-0.09**	**0.010**	**< 0.001**	**-0.10**
Ornithodoros hasei	**0.013**	**< 0.001**	**0.12**	**0.003**	**0.007**	**0.05**
Parkosa maxima	**0.002**	**0.034**	**-0.04**	**0.001**	**0.045**	**-0.04**
Parkosa tadarida	0.001	0.136		0.001	0.097	
Noctilionidae						
Noctiliostrebla maai	**0.123**	**< 0.001**	**-0.35**	**0.104**	**< 0.001**	**-0.34**
Paradyschiria fusca	**0.286**	**< 0.001**	**0.53**	**0.304**	**< 0.001**	**0.55**
Paradyschiria parvula	**0.113**	**0.001**	**-0.34**	**0.050**	**0.028**	**-0.22**
Ornithodoros hasei	0.031	0.089		0.008	0.401	
Noctilio albiventris						
Noctiliostrebla maai	**0.077**	**0.023**	**0.28**	0.001	0.785	
Paradyschiria parvula	0.041	0.102		**0.063**	**0.040**	**0.25**
Ornithodoros hasei	0.040	0.103		0.001	0.774	
Noctilio leporinus						
Paradyschiria fusca	0.080	0.153		0.117	0.075	
Phyllostomidae						
Aspidoptera falcata	**0.044**	**< 0.001**	**-0.21**	**0.041**	**< 0.001**	**-0.20**
Megistopoda aranea	**0.020**	**< 0.001**	**0.14**	**0.010**	**< 0.001**	**0.10**
Megistopoda proxima	**0.082**	**< 0.001**	**-0.29**	**0.074**	**< 0.001**	**-0.27**
Paratrichobius longicrus	**0.080**	**< 0.001**	**0.28**	**0.112**	**< 0.001**	**0.33**
Trichobius joblingi	**0.016**	**< 0.001**	**-0.13**	**0.015**	**< 0.001**	**-0.12**
Trichobius parasiticus	**0.004**	**0.029**	**0.06**	0.000	0.750	

Table 3.6. Continued

Host family / Host species / Ectoparasite species	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Periglischrus iheringi	**0.132**	**< 0.001**	**0.36**	**0.117**	**< 0.001**	**0.34**
Periglischrus ojasti	**0.064**	**< 0.001**	**-0.25**	**0.066**	**< 0.001**	**-0.26**
Macronyssoides conciliatus	0.002	0.112		**0.003**	**0.048**	**-0.46**
Macronyssoides kochi	**0.041**	**< 0.001**	**0.20**	**0.041**	**< 0.001**	**0.20**
Parichoronyssus euthysternum	**0.036**	**< 0.001**	**-0.19**	**0.039**	**< 0.001**	**-0.20**
Carollinae						
Carollia perspicillata						
Trichobius joblingi	0.002	0.719		0.006	0.517	
Stenodermatinae						
Artibeus fimbriatus						
Megistopoda aranea	0.013	0.334		0.005	0.556	
Periglischrus iheringi	0.002	0.670		0.018	0.234	
Macronyssoides kochi	0.002	0.734		0.024	0.17	
Artibeus jamaicensis						
Periglischrus iheringi	0.010	0.520		0.001	0.820	
Artibeus lituratus						
Paratrichobius longicrus	0.000	0.763		**0.038**	**< 0.001**	**0.20**
Periglischrus iheringi	0.003	0.340		0.006	0.134	
Macronyssoides kochi	0.000	0.929		0.000	0.965	
Platyrrhinus lineatus						
Periglischrus iheringi	0.009	0.384		0.037	0.069	
Macronyssoides conciliatus	0.001	0.762		0.006	0.467	
Sturnirinae						
Sturnira lilium						
Aspidoptera falcata	0.005	0.175		**0.021**	**0.003**	**-0.15**
Megistopoda proxima	0.003	0.310		0.008	0.076	

Table 3.6. Continued

Host family / Host species / Ectoparasite species	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Periglischrus ojasti	0.000	0.669		**0.077**	**< 0.001**	**-0.28**
Parichoronyssus euthysternum	**0.020**	**0.005**	**0.14**	**0.013**	**0.022**	**-0.11**
Vespertilionidae						
Macronyssus crosbyi	**0.039**	**< 0.001**	**-0.20**	**0.013**	**0.020**	**-0.12**
Steatonyssus furmani	**0.142**	**< 0.001**	**0.38**	**0.138**	**< 0.001**	**0.37**
Steatonyssus joaquimi	0.000	0.874		0.000	0.825	
Eptesicus furinalis						
Steatonyssus joaquimi	0.024	0.208		0.002	0.687	
Lasiurus ega						
Steatonyssus furmani	0.006	0.512		0.014	0.327	
Myotis albescens						
Macronyssus crosbyi	0.006	0.485		**0.097**	**0.003**	**0.31**
Steatonyssus joaquimi	0.045	0.051		0.000	0.961	
Myotis nigricans						
Macronyssus crosbyi	0.003	0.535		0.014	0.169	
Steatonyssus joaquimi	0.000	0.973		0.001	0.781	
Molossidae						
Trichobius jubatus	0.002	0.132		**0.006**	**0.007**	**0.08**
Hesperoctenes fumarius	0.002	0.107		0.001	0.278	
Hesperoctenes longiceps	0.002	0.107		0.002	0.100	
Hesperoctenes parvulus	**0.032**	**< 0.001**	**-0.18**	**0.013**	**< 0.001**	**-0.11**
Hesperoctenes n. sp. 1	**0.021**	**< 0.001**	**0.14**	**0.025**	**< 0.001**	**0.16**
Chiroptonyssus haematophagus	0.001	0.248		0.000	0.804	
Chiroptonyssus robustipes	**0.011**	**< 0.001**	**0.10**	**0.056**	**< 0.001**	**0.24**

Table 3.6. Continued

Host family / Host species / Ectoparasite species	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Chiroptonyssus venezolanus	**0.028**	**< 0.001**	**-0.17**	**0.016**	**< 0.001**	**-0.13**
Ornithodoros hasei	0.001	0.374		0.002	0.107	
Parkosa maxima	0.003	0.084		0.002	0.167	
Parkosa tadarida	0.000	0.614		0.000	0.969	
Eumops glaucinus						
Hesperoctenes n. sp. 1	0.009	0.482		0.062	0.064	
Chiroptonyssus haematophagus	0.013	0.404		0.003	0.681	
Eumops patagonicus						
Trichobius jubatus	0.002	0.292		0.000	0.818	
Hesperoctenes longiceps	0.000	0.742		0.000	0.995	
Chiroptonyssus haematophagus	0.002	0.354		0.003	0.203	
Ornithodoros hasei	0.000	0.989		**0.015**	**0.005**	**-0.12**
Molossops temminckii						
Hesperoctenes parvulus	0.014	0.134		0.001	0.734	
Chiroptonyssus venezolanus	0.003	0.490		0.000	0.785	
Molossus ater						
Chiroptonyssus robustipes	0.000	0.911		0.035	0.064	
Molossus currentium						
Chiroptonyssus haematophagus	0.000	0.946		0.066	0.196	
Molossus molossus						
Hesperoctenes fumarius	**0.020**	**0.036**	**-0.14**	**0.071**	**< 0.001**	**-0.27**
Chiroptonyssus haematophagus	0.000	0.994		0.007	0.206	
Parkosa maxima	0.000	0.945		**0.019**	**0.035**	**-0.14**
Parkosa tadarida	0.001	0.668		0.016	0.060	
Nyctinomops laticaudatus						
Chiroptonyssus venezolanus	0.044	0.186		0.010	0.522	

Table 3.7. Significance levels for analyses of covariance determining the effect of host sex on specific ectoparasite abundance while removing the effect of host size (FA and MA). Correlation coefficients and p-values are provided for separate correlation analyses of the association between body size (FA and MA) and familial ectoparasite abundances. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Host family			Pearson product-moment correlation analysis			
Host species	p-value		FA		MA	
Ectoparasite species	Covariates	Sex	r	p-value	r	p-value
Noctilionidae						
Noctilio albiventris						
Noctiliostrebla maai	0.058	0.091	**0.938**	**0.022**	0.284	0.402
Paradyschiria parvula	**0.006**	**< 0.001**	0.539	0.813	**0.997**	**0.007**
Ornithodoros hasei	0.212	**0.032**	-0.958	0.099	-0.344	0.612
Noctilio leporinus						
Paradyschiria fusca	0.246	0.576	0.836	0.532	0.93	0.353
Phyllostomidae						
Carollia perspicillata						
Trichobius joblingi	0.910	**0.045**	-0.766	0.677	0.266	0.781
Artibeus fimbriatus						
Megistopoda aranea	0.434	0.458	0.694	0.239	-0.408	0.352
Periglischrus iheringi	0.615	0.976	0.434	0.948	0.998	0.376
Macronyssoides kochi	0.096	**0.023**	-0.233	0.206	**0.815**	**0.036**
Artibeus jamaicensis						
Periglischrus iheringi	0.895	0.339	0.963	0.683	0.485	0.899
Artibeus lituratus						
Paratrichobius longicrus	**0.002**	0.718	0.031	0.217	**0.936**	**< 0.001**
Periglischrus iheringi	**0.005**	**< 0.001**	0.184	0.078	**-0.839**	**0.002**
Macronyssoides kochi	0.781	0.094	-0.129	0.857	-0.967	0.486

Table 3.7. Continued

Host family			Pearson product-moment correlation analysis			
Host species	p-value		FA		MA	
Ectoparasite species	Covariates	Sex	r	p-value	r	p-value
Platyrrhinus lineatus						
Periglischrus iheringi	0.231	0.970	-0.492	0.659	-0.967	0.137
Macronyssoides conciliatus	0.980	**0.013**	0.792	0.853	-0.390	0.902
Sturnira lilium						
Aspidoptera falcata	**0.022**	0.224	-0.418	0.486	**-0.968**	**0.012**
Megistopoda proxima	0.368	0.079	-0.583	0.542	-0.903	0.251
Periglischrus ojasti	**< 0.001**	**0.029**	-0.118	0.767	**-0.998**	**< 0.001**
Parichoronyssus euthysternum	**0.001**	0.214	**0.761**	**0.001**	**-0.504**	**0.014**
Vespertilionidae						
Eptesicus furinalis						
Steatonyssus joaquimi	0.395	0.126	0.933	0.285	0.619	0.624
Lasiurus ega						
Steatonyssus furmani	0.103	**0.042**	-0.715	0.249	-0.844	0.134
Myotis albescens						
Macronyssus crosbyi	0.063	0.164	0.019	0.658	**0.983**	**0.019**
Steatonyssus joaquimi	0.074	0.231	**0.991**	**0.023**	0.071	0.758
Myotis nigricans						
Macronyssus crosbyi	0.387	**0.020**	-0.685	0.211	0.415	0.316
Steatonyssus joaquimi	0.899	**0.028**	0.611	0.902	0.964	0.716
Molossidae						
Eumops glaucinus						
Hesperoctenes n. Sp.1	0.095	0.088	0.494	0.234	0.840	0.059
Chiroptonyssus haematophagus	0.762	0.179	-0.734	0.571	-0.637	0.618

Table 3.7. Continued

Host family			Pearson product-moment correlation analysis			
Host species	p-value		FA		MA	
Ectoparasite species	Covariates	Sex	r	p-value	r	p-value
Eumops patagonicus						
Trichobius jubatus	0.479	**0.033**	0.891	0.240	-0.246	0.582
Hesperoctenes longiceps	0.927	**0.004**	0.918	0.701	-0.185	0.877
Chiroptonyssus haematophagus	0.181	**0.012**	0.517	0.200	-0.721	0.113
Ornithodoros hasei	**0.012**	0.764	-0.007	0.526	**-0.977**	**0.003**
Molossops temminckii						
Hesperoctenes parvulus	0.338	0.938	-0.991	0.151	-0.215	0.843
Chiroptonyssus venezolanus	0.730	0.093	-0.954	0.429	-0.047	0.812
Molossus ater						
Chiroptonyssus robustipes	0.115	0.280	0.073	0.607	**0.970**	**0.038**
Molossus currentium						
Chiroptonyssus haematophagus	0.507	0.800	-0.210	0.645	0.919	0.259
Molossus molossus						
Hesperoctenes fumarius	**0.004**	0.790	-0.552	0.275	**-0.946**	**0.005**
Chiroptonyssus haematophagus	0.757	0.478	-0.243	0.720	0.877	0.469
Parkosa maxima	0.079	0.392	0.053	0.491	**-0.953**	**0.025**
Parkosa tadarida	0.077	0.194	0.198	0.896	**0.998**	**0.026**
Nyctinomops laticaudatus						
Chiroptonyssus venezolanus	0.438	0.564	0.986	0.241	0.397	0.831

Table 3.8. Results of simple regression analyses determining the effect of host body size (FA and MA) on ectoparasite biodiversity for all hosts as a group and for each host family. Significant results are bold. No analyses were significant after Bonferroni sequential adjustment. See text for abbreviations.

Taxon	FA			MA		
Biodiversity	r^2	p-value	B_1	r^2	p-value	B_1
All Bats						
Average richness	**0.149**	**0.015**	**0.39**	**0.127**	**0.026**	**0.36**
Accumulative richness	0.015	0.459		0.001	0.893	
Log richness	0.008	0.596		0.000	0.999	
Chao1 richness	0.002	0.765		0.003	0.762	
Shannon diversity	0.002	0.770		0.039	0.226	
Shannon evenness	0.020	0.394		0.045	0.196	
Berger-Parker dominance	0.023	0.353		0.088	0.068	
Rare species	0.019	0.492		0.002	0.799	
Beta diversity	0.012	0.513		0.000	0.910	
Phyllostomidae						
Average richness	0.126	0.234		0.085	0.333	
Accumulative richness	0.014	0.700		0.002	0.898	
Log richness	0.008	0.777		0.002	0.885	
Chao1 richness	0.010	0.742		0.003	0.869	
Shannon diversity	0.083	0.339		0.045	0.489	
Shannon evenness	0.001	0.902		0.001	0.930	
Berger-Parker dominance	0.000	0.958		0.004	0.846	
Rare species	0.002	0.875		0.000	0.943	
Beta diversity	0.011	0.737		0.003	0.852	

Table 3.8. Continued

Taxon / Biodiversity	FA r^2	FA p-value	FA B_1	MA r^2	MA p-value	MA B_1
Vespertilionidae						
Average richness	0.200	0.195		0.272	0.122	
Accumulative richness	0.265	0.128		0.098	0.377	
Log richness	0.218	0.174		0.084	0.418	
Chao1 richness	0.045	0.558		0.004	0.862	
Shannon diversity	**0.666**	**0.004**	**-0.82**	**0.581**	**0.010**	**-0.76**
Shannon evenness	0.149	0.271		0.225	0.166	
Berger-Parker dominance	**0.515**	**0.020**	**0.72**	**0.451**	**0.033**	**0.67**
Rare species	0.181	0.220		0.049	0.540	
Beta diversity	0.190	0.209		0.064	0.482	
Molossidae						
Average richness	**0.336**	**0.038**	**0.58**	**0.557**	**0.003**	**0.75**
Accumulative richness	0.153	0.186		0.112	0.263	
Log richness	0.160	0.176		0.123	0.241	
Chao1 richness	0.075	0.364		0.039	0.516	
Shannon diversity	0.011	0.736		0.019	0.651	
Shannon evenness	0.094	0.308		0.171	0.160	
Berger-Parker dominance	0.003	0.861		0.028	0.582	
Rare species	0.110	0.269		0.110	0.269	
Beta diversity	0.177	0.153		0.142	0.205	

CHAPTER IV

FLYING ISLANDS II: THE EFFECT OF HOST ABUNDANCE ON ECTOPARASITE ASSEMBLAGE BIODIVERSITY

Introduction

Biogeography is an integrated discipline that requires understanding of ecological and evolutionary elements to define patterns and identify causal mechanisms at regional, continental, and global scales. Biogeographic processes *per se* may not exist; rather, large-scale geoclimatic (e.g., tectonic plate movements, changes in sea level, climate, and oceanic circulation), evolutionary (e.g., adaptation, speciation, extinction), and ecological (e.g., predation, competition) processes operate in concert to produce biogeographic patterns. These processes do not operate in isolation. For example, as geoclimatic characteristics change overtime, species must adapt (i.e., evolve) to remain competitive or avoid predation. These interactions may result in extinction or speciation. Consequently, the dynamic nature of interactions at large scales of space and time make it difficult to determine which mechanisms are dominant driving forces in structuring communities.

Islands possess many tractable qualities that make them attractive foci for biogeographic study (Shoener 1988). An island is a more feasible study unit than is a continent or ocean, and is visibly discreet so that resident populations may be distinguished more easily along natural boundaries. In addition, islands are abundant and differ in shape, size, degree of isolation, history, and ecology; consequently they provide the replication necessary to conduct non-manipulative experiments. Low primary diversity on islands (i.e., species richness due to immigration) promotes *in situ* diversification, with the most isolated islands evincing the largest adaptive radiations (Paulay, 1994). Whether intra-island or inter-island speciation is more important depends on the dispersal ability of the taxon and opportunities for isolation from parent populations (Paulay, 1994). The small size and isolation of islands results in relatively small populations, which makes island species especially vulnerable to local extinction.

Therefore, islands provide biotas with opportunities for larger radiations and more frequent *in situ* diversification than occur on mainlands, while simultaneously subjecting them to higher extinction rates. Because of these phenomena, islands provide insight into assemblage rules.

In the 1960s, MacArthur and Wilson (1963, 1967) proposed the equilibrium theory of island biogeography (ETIB) in an attempt to explain patterns of species richness on islands. The primary predictions of ETIB are two fold: 1) larger islands maintain greater species richness than do smaller islands, and 2) islands more distant from a source of colonization support fewer species than do closer islands. Distance from a source population primarily affects richness by molding immigration rates, whereas island size primarily affects richness by molding extinction rates.

The ETIB has been much debated (for review see Whitaker 1998). Despite executing one of the more successful tests of ETIB (Simberloff and Wilson 1970), Simberloff (1976) was foremost among the critics claiming that ETIB gained paradigm status despite numerous studies that failed to conform to its predictions. These failures often are explained by faulting deductive logic or by "willful suspension of belief in the experimental result" (Simberloff 1976). Early work (Simberloff 1983) with development and application of null models attempted to discount the dynamic equilibrium facet of ETIB (i.e., that extinction and immigration rates converge to form a stable equilibrium). Unfortunately, the design of Simberloff's model predisposes a finding of randomness and is not an unbiased test of dynamic equilibria (Colwell and Winkler 1984). Many (Gilbert 1980, Schrader-Frechette and McCoy 1993, Simberloff 1976) remain frustrated by the continued application of ETIB to various types of islands (e.g., habitat patches, lakes, parasite hosts) in diverse theoretical and applied situations. Nonetheless, prominent biologists have endorsed it as being useful and insightful despite simplifying assumptions (Brown 1971, Rosenzweig 1995). Contention has lasted for decades because of the different ways that researchers employ ETIB. Detractors often test predictions of ETIB based on natural history data (e.g., Gilbert 1980, Johnson and Simberloff 1974, Bush and Whittaker 1991) and discredit the theory because data fail to conform to predictions.

However, the failure of these tests should not be surprising given the simplicity of the theory and the complexity of natural systems (Sismondo 2000). A different perspective (Haila and Järvinen 1982) views ETIB as a heuristic model that provides opportunities to explore patterns rather than as a suite of hypotheses to falsify.

Although the ETIB has been applied to a multitude of taxa, few investigations have focused on ectoparasite assemblages. In evolutionary studies, the focus often is on a single ectoparasite species and its co-evolutionary relationship with a host and not the community or assemblage. I use ETIB as a model for understanding host characteristics that determine community structure of arthropod ectoparasite assemblages on chiropteran hosts.

Bats and Their Ectoparasites as Model Systems

Generally, bats come in contact with few non-bats, thereby isolating bat ectoparasites from potential non-bat hosts. In addition, bat species rarely come into contact with each other, except in multispecific colonies, which usually contain species from the same family (Kunz 1982), restricting potential inter-specific host transfer of ectoparasites to members of the same host family. Finally, with the exception of colonial species, individual bats may be in contact with conspecifics only during periods of mating and rearing, reducing opportunities for ectoparasite transfer among individuals. Prolonged periods of host isolation in solitary bat species may increase the likelihood of local extinction of ectoparasites on the host.

Four host characteristics affect parasite species richness within the context of ETIB (Kuris et al. 1980): 1) host size, 2) host age, 3) habitat complexity (often correlated with host age or size), and 4) distance to potential sources of infestation. Host size, and its relationship to habitat complexity, is evaluated in this chapter, whereas host population density is considered in chapter IV. Because bats essentially reach adult size in a few (4 – 7) months (Barclay and Harder 2003), which is only a small fraction of average life expectancy of bats (11 – 15 years), the effect of size and age can be de-coupled. This is not possible in work on ectoparasites of fishes (Kennedy 1978*a*, 1978*b*,

Newbound and Knott 1999), because these hosts exhibit indeterminate growth. Moreover, bats have long life expectancies compared to animals of similar size (Barclay and Harder 2003). Such long life may provide ectoparasite assemblages on individual hosts with opportunities to experience processes similar to those on habitat or oceanic islands (e.g., local extinction, colonization, rescue effect).

When considering individuals as islands, five aspects of host biology must be addressed to accommodate traditional interpretations of ETIB (Kuris et al. 1980). First, inter-island distances fluctuate over time. These fluctuations may occur over short time frames for vagile hosts such as bats and may create only sporadic opportunities for infestation. Although host individuals and species are like islands in being discrete and easily identifiable units, they are not like islands in that the level of isolation is dynamic. Indeed, considering hosts as islands is complicated because the distances among islands are changing continually and some islands even make temporary physical contact. Moreover, physical contact differs in frequency, regularity, and duration depending on season, as well as host species identity, age, sex, and mating and social systems.

Second, seasonal changes in behavior or physiology may affect the presence of parasites. Host behavior could have a significant effect on distance to source populations for bat species that form maternity colonies as well as for those that hibernate individually or in colonies. Conversely, physiological peculiarities of bats may expose ectoparasites to phenomena similar to those experienced by inhabitants of temperate islands. For example, daily changes in bat body temperature (from torpor to activity) are analogous to daily fluctuations in ambient temperature. Similarly, seasonal changes in bat body temperature related to hibernation in temperate species or to extended periods of torpor in sub-tropical or tropical species are analogous to seasonal changes in climate that are characteristic of temperate islands. Seasonal or daily changes in bat behavior do not require modification of theory applied to oceanic islands.

Third, quality of the host island changes over ecological time as a result of growth and aging. Host islands may change over much shorter time frames than do those that characterize true islands; however, the effects of these changes with respect to invading

species are similar. Indeed, fewer complications arise due to age of hosts than due to successional changes related to the age of islands On true islands, early colonizers may facilitate invasion by other species, leading to a more predictable order of invasion and community structure than may occur on host islands. Because all hosts, from birth to death, are inhabitable islands for potential parasites, evaluations of ETIB for host-parasite systems are not complicated by host (i.e., island) age.

Fourth, presence of certain parasites may affect characteristics of host islands, including survival. Characteristics of true islands change with the presence of every species, either enhancing or diminishing the chance of other species establishing populations on the island. Still, it is difficult to imagine a scenario where an invading species would cause the "death" of an island. Furthermore, it is unlikely that the presence of ectoparasite species commonly facilitates the infestation of others. Fortunately, little evidence suggests that species ectoparasitic on bats have deleterious effects on their hosts as to commonly cause death of an otherwise healthy individual. Indeed, bat host survival is affected marginally by ectoparasite load, although energy demands may be significantly increased by heavy ectoparasite loads (Marshall 1982). Nonetheless, all hosts die. How death of an island affects evaluations of ETIB in host-parasite systems is unclear.

Finally, Kuris et al. (1980) consider hosts to be sufficiently ephemeral to prevent parasite assemblages from reaching equilibrium. Nonetheless, bats have remarkably long life spans, with species documented to live 20 years or longer (Barclay and Harder 2003). Because the life-span of most ectoparasite species is only a few months, bat hosts may be sufficiently long-lived as to support equilibrial assemblages.

In summary, the only characteristic of bats that may require significant modification of ETIB for application to ectoparasite assemblages is the potential for distance from sources to fluctuate quickly and with varying frequency and regularity. Whereas ectoparasite residency was considered the host individual from which it was collected, it is possible that individuals residing on one host communicate with other hosts via direct invasion or the dispersal of offspring, especially species that are vagile

and regularly leave the host (e.g., streblids). As such, extinction (i.e., no ectoparasites on a host individual) and extinction rates, which are fundamental to the equilibrium theory of island biogeography, may be difficult to define. This is also true of highly interactive islands (Coleman et al. 1982), such as archipelagos in which mobile members of biotas move among islands on a daily or monthly basis.

A Host Is an Island, Entire of Itself

Islands have large adaptive radiations of species and high levels of *in situ* diversification compared to mainland communities (Paulay 1994). Bat ectoparasite assemblages exhibit both of these island characteristics, implying that they may have evolved as isolated evolutionary units. Ectoparasite faunas of mammalian hosts contain relatively few species, many of which are monoxenous (i.e., occur on only one host species), indicating evolution of ectoparasite species on the host island (i.e., *in situ* diversification). In addition, many ectoparasite families contain hundreds of species, but all are restricted to a single family of host, indicating relatively recent and large adaptive radiations. Together, these observations are evidence, albeit circumstantial, that ectoparasite faunas on bat hosts experience similar ecological and evolutionary mechanisms to those of biotas on true islands.

Limiting Factors

The most important factor inhibiting ectoparasites from interspecific host transfer is physical isolation (Kuris et al. 1980, Marshall 1971, 1982, Wenzel and Tipton 1966). Indeed, many ectoparasite species have virtually no chance to move to another host species because direct body contact likely is rare between host species. Moreover, survival away from the host is brief (< 1 day for most bat ectoparasites). Hence, even ectoparasites that do not require direct body contact of hosts for transfer would have only brief windows of opportunity to infest alternative host species. When opportunities for infestation do exist, many factors inhibit successful infestation (i.e., survival and reproduction) of new host species. In experimental transfers of ectoparasitic insects to

non-primary bat host species, nycteribiids starved and bat flies fell victim to predation by hosts (Marshall 1971, 1982). Often, ectoparasites even find potential host species that are closely related to their typical host to be unsuitable. Two sets of ideas account for these observations. First, ectoparasites have specialized adaptations for life on their host and these may be unsuitable on other host species. More specifically, claws may be unsuitable for attachment, or body form, setae, and combs may be inappropriate for movement through hair. Failure to match proper morphological adaptations to the microhabitat will enhance exposure to predation. Second, parasites may starve because their mouthparts are unsuitable for feeding or the host's blood may be inadequate nutritionally (Marshall 1982).

Within the context of ETIB, host abundance may be analogous to distance to a source population. Rare host species represent more distant islands because intraspecific contact should be less frequent for rare species than common species. Bat ectoparasites usually maintain relatively low population densities on individual bats (Marshall, 1982). Therefore, in situations where host individuals experience infrequent intraspecific contact, ectoparasite populations that locally have gone extinct have a lower probability of re-establishing (i.e., reduced rescue effect) than do those on more common host species, resulting in an overall reduction in ectoparasite species diversity. Thus, rare host taxa may be effectively more distant from ectoparasites source populations.

However, the effect of host abundance, *per se*, may be overshadowed by effects of social group size. Bats that are solitary may represent very small islands, with harems or colonies comprising more individuals equivalent to larger islands. Therefore, the effects of host abundance, as measured by number of captured individuals, on ectoparasite assemblage diversity may be difficult to determine without consideration of host social organization.

In simplest terms, there are four possible combinations of host abundance and social organization. Host species that are rare and solitary represent islands that are small and far from a source population. Ectoparasite assemblages on such host species should be among the most species poor, suffering negative effects from increased extinction

rates related to small population sizes and reduced immigration rates related to source population distance. Host species that are abundant and colonial represent islands that are large and near a source population. Ectoparasite assemblages on such host species should be among the most species rich because of reduced extinction rates related to larger population sizes and increased immigration rates related to the proximity of source populations. Ectoparasite assemblages on rare, colonial host species or common, solitary host species should have moderate levels of species richness, as responses to abundance and social system may neutralize each other.

Host abundance (i.e., number of captured individuals) probably is a poor estimate of host group size. Although some bats were captured while exiting day roosts, no reliable estimates of host group size in Paraguay are available. Even in instances where nets were placed at roost exits, many bats were observed avoiding capture. Moreover, captures are not an accurate estimate of bat abundance. The flight characteristics (i.e., speed, height, directness) of all bat species are not the same. Differences in flight affect the ability to capture bats; for example, species that fly close to the ground (e.g., frugivorous phyllostomids) are more susceptible to capture than those that fly at higher altitudes (e.g., molossids). In addition, some bats (e.g., vespertilionids) display greater awareness and subsequent avoidance of nets than do other bats (e.g., phyllostomids). Therefore, the relative abundances of bat species may be affected greatly. Nonetheless, number of captures is the best estimate available for bat abundances.

I used host (i.e., bat) capture numbers as an estimate of abundance to explore questions about ectoparasite assemblage diversity within the framework of the equilibrium theory of island biogeography. A suite of analyses was designed to determine the effect of host abundance on ectoparasite assemblage diversity at multiple levels of host taxonomy as well as at local and regional spatial scales. Although information about host group size for bats of Paraguay is not available, the roosting habits of some Paraguayan bat species are documented from other locales and this knowledge of natural history may help interpret ectoparasite assemblage diversity responses to host abundance (i.e., number of captures).

Materials and Methods

Field Methods

Mammals and their associated ectoparasites were collected from July 1995 to June 1997, and again from July to August in 1998, as part of a scientific expedition entitled “Paraguayan Mammals and Their Ectoparasites: an Intensive Survey in a Temperate-Subtropical Interface” (Willig et al. 2000). Bats were surveyed at 28 sites (Table A.1), representing all major biomes, including many protected areas, and spanning gradients of moisture and temperature in Paraguay (Figure 2.1). Because of the potential importance of the Río Paraguay as a biogeographic barrier (Myers 1982), approximately one-half of the sites were on each side (east or west) of the river. In general, mist nets were erected in all habitats at a site and were monitored from dusk until 0100 h. Much of the time, nets were monitored until dawn. Rates of capture for bats in the field depend on a variety of factors including net characteristics (e.g., mesh size, length, condition, placement, configuration), temporal factors (e.g., length of time, particular hours of the night, period in the lunar cycle; Gannon and Willig 1997), local weather conditions (especially with respect to temperature and precipitation), and history (i.e., number of consecutive nights at a site; Simmons and Voss 1998). Captured bats were sacrificed and prepared as standard museum specimens. Specific bat identification was initiated in the field but verified after comparison with systematic reference materials by C. López-González (López-González 1998, 2005).

Host and Parasite Systematics

The systematic recommendations of López-González (1998, 2005) were followed for bat taxa in Paraguay. Ectoparasites were identified using the most recent, comprehensive information about South American representatives for each family including Wenzel (1976) and Wenzel et al. (1966) for the Streblidae; Guimarães (1966, 1972) for the Nycteribiidae; Ueshima (1972), Ferris and Usinger (1939, 1945), and

Ronderos (1959, 1962) for the Polyctenidae; Rudnick (1960), Machado-Allison (1965), and Herrin and Tipton (1975) for the Spinturnicidae; Radovsky (1967) and Saunders (1975) for the Macronyssidae; Dusbábek (1969*a*, 1969*b*) and Fain (1978) for the Myobiidae; Jones et al. (1972) and Fairchild et al. (1966) for the Ixodidae and Argasidae; Reed and Brennan (1975), Brennan and Reed (1974, 1975), Brennan and Yunker (1966), and Brennan and Goff (1977) for the Trombiculidae; McDaniel (1970, 1973), Pinichpongse (1963a, 1963b, 1963c, 1963d), de la Cruz (1969) and Dusbábek and de la Cruz (1966) for the Chirodiscidae. Details about field and laboratory methods appear in chapter II.

Statistical Methods

Mean ectoparasite abundance (MEA) per host individual was calculated in addition to nine metrics of different aspects of biodiversity (e.g., richness, evenness, diversity, dominance). Four indices estimated richness. MeanS was defined as the average ectoparasite richness on host individuals of a particular host species. Accumulative S (AccumS) was defined as the total number of ectoparasite species found on all individuals of a particular host species. Chao1 is an abundance-based estimate of cumulative species richness (Chao 1984) calculated using EstimateS (Colwell 2001). LogS was calculated using Matlab ver. 4.2c.1 for the Macintosh (The Math Works, Inc. 1994; script files available from the author, Appendix E) as an alternative abundance-based cumulative estimate of richness. This function used a jackknife sampling regime to produce a mean species-accumulation curve from 1000 random permutations of individuals based on the ectoparasite species-abundance distribution (SAD) from a particular host species. In each iteration, individuals were ordered randomly and sampled without replacement. An iterative process was used to determine the best-fit logistic curve to the mean species-accumulation curve. The asymptote of that curve is the number of species predicted to occur in an assemblage after infinite sampling (= LogS). Preliminary investigations of this metric revealed that it was overly sensitive to rare species, especially those that occur only once (i.e., singletons), likely leading to

overestimates of richness. To diminish the effect of singletons, one individual was added to each species in the SAD at the beginning of the simulation. This modification better predicted richness for known universes (Presley, unpublished data) than did the original incarnation.

Five additional indices (Table 3.1) measured other aspects of ectoparasite SADs. Shannon Diversity (Shannon), Shannon Evenness (Even), and Berger-Parker Dominance (Dom) were calculated using Matlab. Following Whitaker (1960), beta diversity (Betadiv) was calculated as the difference between gamma diversity, as estimated by LogS (i.e., LogS is the cumulative species richness estimate previously discussed, not Log[S]), and alpha diversity as estimated by MeanS. Rare ectoparasite species were defined separately for each ectoparasite taxon (i.e., species, family, or class). Rare species richness (Rare) was equal to the number of ectoparasite species whose separate proportional abundances < 0.05. A common definition of rarity (e.g. Chalcraft et al. 2004, Stevens and Willig 2000, Willig et al. 2003) considers a species to be rare if its abundance is < 1/S of the total individuals of a community or assemblage, where S = species richness (Camargo 1992). However, problems characterize this definition of rarity. First, use of 1/S for a species-poor assemblage, like those of ectoparasites on host individuals, could result in the assignment of relatively abundant species as rare. For example, in an assemblage with S = 5, a species that comprises 19% of the assemblage is rare although it represents a large portion of the assemblage. Second, because all assemblages do not have equal species richness, 1/S defines rareness at different relative abundances for assemblages with different species richness. Third, 1/S requires at least one species be rare in all but the most even of assemblages. Defining rareness using the 5% criterion eliminates these problems. Regardless of the employed definition of rare, species of ectoparasites defined as rare may represent transients or contamination in addition to identifying species of ectoparasite that are naturally rare on their primary host.

Transient ectoparasite species were defined as those species that were not members of primary host-ectoparasite associations (i.e., all associations with and incidence of < 0.05). An exception to this rule was made for small mite taxa (e.g.,

Myobiidae, Chirodiscidae, Trombiculidae) that were rare on all host species. The host on which these parasites most often were found was considered to be the primary association. The definitions of rareness and transience use 5% rules, however they are not congruent. Rare species comprise < 5% of the ectoparasite individuals of an assemblage, whereas transients occur on < 5% of host individuals, regardless of total number of individuals. Because host-ectoparasite associations were included in defining transient species, transient species need not be rare and rare species need not be transient. Nonetheless, in general, transient species were rare.

Simple linear regressions determined the effect of regional host abundance on ectoparasite assemblage diversity, with measures of ectoparasite diversity as dependent variables and regional host species abundances as independent variables. Ectoparasite diversity measures for these analyses were calculated for each host species using all ectoparasite collections across Paraguay. Because phylogenetic processes influence the available ectoparasite species pool for each host species, analyses were conducted separately for families of phyllostomid, vespertilionid, and molossid bats, as well as for all bat species.

Simple linear regressions evaluated the effect of local host species abundance on diversity of local ectoparasite assemblages. Regressions were conducted separately for each of 13 common and wide-spread host species (i.e., those with at least five individuals inspected for ectoparasites at three or more collection sites). For each host species, measures of ectoparasite diversity were calculated separately for each site.

Analyses to determine the effect of abundance of local host families (i.e., total number of host individuals from a given host family at a given site) and abundance of local host assemblages (i.e., total number of host individuals at a given site) were similar in design to those evaluating the effect of abundance of local host species. However, measures of ectoparasite assemblage diversity were calculated after pooling either all host individuals, or all host individuals of a particular host family, at each site. Analyses of host-assemblage abundance included all sites. Analyses of host-family abundance were conducted separately for each family and included only those sites where five or

more individuals of that family were inspected for ectoparasites. All regression analyses were executed using SPSS 4.0 for the Macintosh (SPSS, Inc. 1990).

An ongoing debate characterizes the ecological literature on the use of methods to maintain type I error rate at a reasonable level for suites of analyses (Hurlbert 2003, Moran 2003). Chief among the misconceptions that lead to the idea of a need to account for multiple tests is the view that every test increases overall likelihood of a Type I error. In actuality, the likelihood of such an error only increases in instances for which the null hypothesis is rejected (Hurlbert 2003). The Bonferroni sequential adjustment (BSA) is a common method used to maintain experiment-wise error rate (EWER) at a predetermined, albeit arbitrary, rate (i.e., alpha). However, this method is conservative and leads to elevated type II error rates (i.e., failure to reject a null hypothesis that is false). An alternate approach to the use of BSA is to present exact p-values and make "reasonable" interpretations of results based on experimental design, differences in treatment responses, and logic based on experience and scientific understanding (Moran 2003). Hurlbert (2003) stated, "Without knowing how many, if any, of the null hypotheses being tested are true, it is not possible to calculate the probability of making one or more Type I errors. For most investigations that probability is likely to be zero." Nonetheless, most statisticians and ecologists prefer to maintain EWER at a predetermined level (i.e., alpha). Therefore, I applied BSA separately to each independent variable (e.g., host forearm length and mass) in each suite of analyses (i.e., table of analyses) and included those results in each table. I was more concerned about the consequences of ignoring results that could have biological implications than about the potential for type I errors. Because of the exploratory nature of analyses, I interpreted results before application of the BSA, with the understanding that a few significant results contributing to the overall pattern in each discussion may represent type I errors. In most cases, general patterns are the same, just not as strong, when EWER is maintained at alpha (i.e., 0.05).

Results

Regional Host Abundance. Country-wide host abundance does not significantly affect biodiversity of ectoparasite assemblages on host species. Although many measures of biodiversity (Table 4.1) responded to regional host abundance (RHA), all significant results are associated with increased opportunities to observe contamination, transients, or rare ectoparasite species as a consequence of larger sample sizes (i.e., passive sampling). Accumulative richness is a direct measure of this phenomenon and was always significantly and positively affected by RHA. In addition, number of rare species had a highly significant, positive relationship with RHA in analyses of bat species as a group and within each of the three species-rich bat families of Paraguay. LogS and Chao1 are richness estimators that are sensitive to number of rare species; both responded significantly to RHA. Beta diversity was defined as the difference between LogS and MeanS. Because MeanS was unaffected by RHA, but LogS was positively affected by RHA, beta diversity exhibited a positive, significant response to RHA in all analyses. Because rare species increase with host sample size, Shannon evenness exhibited significant, negative responses to RHA. All measures insensitive to rare species (i.e., MEA, MeanS, Shannon, and Dom) were unaffected by RHA (Table 4.1).

Local Host Abundance. Analyses of the effect of local host abundance (LHA) on ectoparasite assemblage biodiversity within 13 common, wide-spread host species yielded similar conclusions to those at the regional scale (Tables 4.2 – 4.4). Significant, positive responses were associated with the number of rare species or transients, or with contamination associated with larger ectoparasite sample sizes. The effect of passive sampling (i.e., the addition of rare species) was strong enough to evince significant, negative responses in Shannon evenness for ectoparasite assemblages from *Sturnira lilium* and *Myotis nigricans*, as well as a significant, positive response in Shannon diversity for the ectoparasite assemblage from *Sturnira lilium*. Analyses of host species (e.g., *Platyrrhinus lineatus*, *Lasiurus ega*) with sufficient collections (i.e., 5 or more inspected hosts) at fewer sites had less power and fewer statistically significant responses

than did analyses of host species occurring at a greater number of sites (e.g., *Sturnira lilium*, *Artibeus lituratus*).

Analyses that combined ectoparasite assemblages collected from common host families and all host species at each site produced similar patterns to analyses of ectoparasite assembles from particular host species (Table 4.5). Ectoparasite assemblages from more abundant hosts had significantly more ectoparasite species that are rare. Moreover, only diversity indices that are sensitive to number of rare species (i.e., AccumS, LogS, Chao1, beta diversity) consistently evinced significant and positive responses to host abundance. However, because these ectoparasite assemblages are from host assemblages instead of host populations, alternative explanations should be explored.

In addition to the potential effect of passive sampling on number of transient or rare ectoparasite species, the effect of host abundance on ectoparasite biodiversity could be caused by differences in host SADs. Host species richness and number of rare species increase with host sample size. Moreover, increases in host species richness occur with increased number of rare species. To explore the effects of host SADs on ectoparasite biodiversity, simple linear regressions quantified the effects of host sample size on host species richness and number of rare host species (Table 4.6). In general, as host sample sizes increased, so did host richness and number of rare host species. Moreover, increases in host richness resulted from the addition of rare species, and not the addition of host species of high or moderate abundances. Host and ectoparasite SADs respond similarly to increases in sample size. Changes in host SADs with increased sample size may contribute to the effects of host sample size on ectoparasite biodiversity.

Discussion

Host Species Abundance and Ectoparasite Biodiversity

The effects of host abundance (i.e., sample size) on ectoparasite biodiversity were predictable. The opportunity for contamination or to observe transients, rare species, or species that are difficult to collect increases as sample size increases. Therefore,

measures of biodiversity that are sensitive to the number of rare species should respond positively to sample size, as was observed. However, responses of Shannon diversity and evenness did not meet expectations. Because ectoparasite richness increased with host sample size, Shannon diversity was expected to increase as well. Shannon evenness was expected to decrease because rare species were added to ectoparasite assemblages. The statistical response of these metrics to sample size did not correspond to expectations. Most host species were collected in sufficient number (i.e., ≥ 5 individuals) at only a few (i.e., ≤ 6) sites, resulting in low statistical power. In addition, some host species (e.g., *Molossops temminckii*) that occurred in sufficient numbers at many sites evinced little variation in host sample size, which reduced statistical power. Only *Artibeus lituratus*, *Sturnira lilium*, and *Eumops patagonicus* occurred in sufficient numbers at 10 or more sites, and only the ectoparasite assemblages from *S. lilium* responded as expected (i.e., Shannon diversity increased with host sample size and Shannon evenness decreased with sample size). In general, *Eumops* are colonial (Best et al. 1996, 1997, 2002, Kiser 1995, Redford and Eisenberg 1992) and colonies of *E. patagonicus* colonies commonly occur in human dwellings in Paraguay (López-González 1998). Frequent body contact among such host individuals provides ectoparasites with opportunities to move among host individuals. This may serve to homogenize ectoparasite richness and composition among host individuals, which could obviate the effects of increased host sample sizes. Available natural history information does not suggest any behavioral differences between *A. lituratus* and *S. lilium* that would account for the lack of effect of host abundance on ectoparasite evenness and diversity for ectoparasite assemblages from *A. lituratus*. Nonetheless, the ectoparasite fauna of *A. lituratus* differs from those of closely related host species. *A. lituratus* had the fewest ectoparasites per individual of any common stenodermatine in Paraguay and less than half those occurring on congeners. Moreover, *A. lituratus* does not have primary associations with the same genera of streblids that occur on other species of *Artibeus* in Paraguay (Tables 2.15 – 2.17, Appendix B).

Parallels may be drawn between the effect of host abundance on ectoparasite species richness and species-area relationships. Two primary factors account for species-area relationships (Rosenzweig 1995, Williamson 1988). First, larger habitats have more species than do smaller habitats. In general, assemblages are characterized by few common species, few species of intermediate abundance, and many rare species (i.e., specialists). Species richness in larger habitats increases because there are more rare species than in smaller habitats; the number of non-rare species changes little. Larger habitats support larger populations that reduce the risk of stochastic extinction and allow a greater number of rare species to persist. Therefore, as habitat size increases, SADs should change by the addition of rare species.

Second, in general, as area increases the number of habitats increases, and areas with more types of habitat have more species than do areas with fewer types of habitats (Williamson 1988). Each habitat type should have distinct species that are abundant, of intermediate abundance, and rare. Assuming that habitats are sampled equally, as the number of habitats increases with area, the richness of species of all abundance levels should increase.

If host abundance is analogous to area for ectoparasites, then host species that are more abundant (i.e., those that represent larger areas) should have greater ectoparasite richness than would host species that are less abundant. The ectoparasite assemblage data from the bats of Paraguay are consistent with this prediction. Alternatively, abundant host species do not provide a greater number of habitats. Therefore, as host species abundance increases, ectoparasite species abundance distributions should change by addition of rare species, which is exactly what is observed here.

The More Individuals Hypothesis (Srivastava and Lawton 1998) was developed by Preston (1962*a*, 1962*b*) and posits that as the number of individuals in an area (or sampled) increases, so does species richness. Three mechanisms have been invoked to explain this pattern: speciation, random placement (also called passive sampling), and local extinction rates (Scheiner and Willig 2004).

Speciation rates are thought to increase with the number of individuals (VanderMeulen et al. 2001); more individuals provide greater opportunity for chance mutations that lead to speciation. This mechanism is most suited for patterns at large scales and provides the richness necessary to explain patterns at smaller scales that sample from larger regional pools of individuals (Scheiner and Willig 2004).

At smaller scales, random placement of individuals (i.e., passive sampling) creates positive relationships between number of individuals and number of species if local richness is determined by random sampling from a species pool (Coleman 1981; Coleman et al. 1982); more individuals increases the likelihood of including rare species due to chance alone. Moreover, as the number of individuals increases, the number of species that maintain populations above some minimum viable size increases, resulting in reduced extinction rates.

Ectoparasite assemblages from more abundant Paraguayan bat species or families have greater cumulative ectoparasite abundances and are more species-rich. Passive sampling and reduced extinction rates are the most appropriate mechanism to consider for patterns observed on ectoparasite assemblages of bats of Paraguay. Larger samples of inspected hosts provide more opportunities to observe rare or transient species (passive sampling) from the regional species pool. In addition, larger host population sizes provide a greater resource base (i.e., greater productivity) that may allow more species of ectoparasite to maintain viable population sizes and reduce extinction rates that result in greater assemblage richness.

Host Family Abundance and Ectoparasite Biodiversity

The effects of host abundance on ectoparasite biodiversity at the host family level were unexpected. In general, if more individuals of a host family occur at a site, more species from that family are present. Because of host specificity, increases in host species richness should increase ectoparasite species richness. In addition, transient species usually are primary ectoparasites of host species from the same family. Because ectoparasites were pooled from all members of each host family, fewer rare species

should emerge as ectoparasites that are rare (i.e., transient) on one host species should be more common on other host species. Therefore, I expected ectoparasite assemblages pooled from larger groups of host individuals to be more species-rich and even, with relatively fewer rare species, than would characterize assemblages pooled from smaller groups of host individuals. This was not the case. Indices of biodiversity that are sensitive to number of rare species responded significantly to host abundance (Table 4.5), indicating an increase in number of rare species. Alternatively, indices that are sensitive to evenness and richness (i.e., Shannon diversity and evenness) did not respond significantly to host abundance.

Expectations concerning the effect of host abundance on ectoparasite biodiversity were not realized. As host sample size increases, host SADs change by increasing the number of rare species, which results in greater species richness (Table 4.6). From the ectoparasites perspective, each host species is a distinct type of habitat. Addition of rare host species increases the number of "rare habitats" to the landscape. Abundant species restricted to rare habitats will be rare from a landscape perspective. As the number of rare host species increases, the number of rare ectoparasites increases because monoxenous ectoparasites from rare or uncommon host species continue to augment the ectoparasite assemblage.

Host Abundance and ETIB

Hosts may be considered "islands" at multiple scales (i.e., host individuals or host populations) within the context of ETIB. Consequently, host abundance may be analogous to island area or distance to a source population depending on the scale of analysis. If host individuals are considered to be islands, host abundance may be a measure of distance to a source population for ectoparasite assemblages. However, if host populations or assemblages are considered to be islands, host abundance may be a measure of island area for ectoparasite assemblages. Although this distinction does not affect the analytical design of this study, interpretation of results within the context of ETIB is problematic.

For example, if individuals of host species X have greater ectoparasite species richness from areas of higher host abundance than from areas of lower host abundance, multiple interpretations exist for the same pattern. If individuals of species X are considered islands and host abundance is a measure of distance to a source population, the interpretation within the context of ETIB is that host individuals (i.e., islands) for which host abundance is higher (i.e., those that are closer to a source population) have greater ectoparasite richness because of increased immigration rates. Alternatively, if host populations of species X are considered islands and host abundance is a measure of island area, the interpretation is that host populations (i.e., islands) that are larger have greater ectoparasite richness because of reduced extinction rates. Consequently, two mechanisms may operate to produce the same patterns. Disentangling the influence of each mechanism is difficult.

Herbivorous insects that live and feed on plants represent a similar system to that of ectoparasites on bats. A body of literature explores the effect of host plant distribution, host plant density, host plant size, and resource (i.e., leaf and flower abundance) abundance (de Alckmin Marques et al. 2000, Frenzel and Brandl 1998, Lewinsohn 1991) on herbivorous insect richness. Host plant geographic range size affects richness of generalist herbivores across the entire range of the species, but does not affect specialist richness or local herbivore richness. Only resource abundance (i.e., leaf and flower mass) is correlated positively with local herbivore richness. The limiting resource for ectoparasites of bats is space on the host. Resource abundance on individual bats has little variation and is unimportant in determining ectoparasite richness. However, if host resources are viewed at the population level, considerable variation characterizes resource abundance. If resource abundance determines ectoparasite richness, bat species abundance is a more important factor in determining ectoparasite assemblage richness than is bat body size. Therefore, within the context of ETIB, host populations and not host individuals should be viewed as islands. This inference is consistent with the conclusions from chapter III. Individual bats do not provide sufficient

space for ectoparasite population growth and ectoparasite assemblages on groups of host individuals are more likely to conform to predictions of ETIB.

Evolution of Specificity Versus Maintenance of Transience.

Current theory concerning the evolution of host specificity (ter Hofstede et al. 2004) states that ectoparasites of common host species should become host specific (i.e., monoxenous). If a host is an abundant and reliable resource, then an ectoparasite species that evolves specializations for life on that host species (i.e., becomes more host specific) should persist because its resource base allows for large populations and reduced probability of stochastic extinction. Alternatively, ectoparasites whose primary host is uncommon that evolve specializations for that host have a higher probability of experiencing a chance extinction because they specialize on a rare resource. Therefore, ectoparasites on uncommon host species should remain generalists with good colonization abilities (ter Hofstede et al. 2004). This framework results in host specific, specialists with poor colonization abilities on common host species and non-host specific, generalists with good colonization abilities on rare host species. In addition, on their primary hosts, ectoparasites should be competitively dominant to transient ectoparasite species.

A logical problem exists with this scenario. When a rare host species population declines or goes extinct the resident ectoparasites should colonize alternate host species. Ideally, a more common host species should be colonized. However, common host species should already be infested by monoxenous ectoparasites that are competitively dominant to transients, which would result in failed colonization. Alternatively, other uncommon or rare host species could be colonized; however, moving from one rare host species to another does not improve the chances of persistence of the ectoparasites species. Moreover, alternate rare host species may be difficult to locate because they are rare. This suggests that ectoparasite species on rare host species may be prone to extinction whether they become specialized or not.

Data from Paraguay do not support the theoretical suppositions of ter Hofstede et al. (2004). Host species abundance did not significantly affect the number of monoxenous ectoparasites on a host species ($p = 0.28$, $r^2 = 0.03$). The six most abundant host species harbored 1, 5, 1, 0, 1, and 0 monoxenous ectoparasite species. Host species with the most monoxenous ectoparasites were *Sturnira lilium*, *Desmodus rotundus*, and *Noctilio albiventris*, which harbored 5, 4, and 4 monoxenous ectoparasite species, respectively. The genus *Sturnira* is basal within, and a sister taxon to the rest of, the Stenodermatinae (Baker et al. 2003, Jones et al. 2002, Owen 1987). The distinctive nature of *Sturnira* resulted in placing it in its own subfamily (i.e., Sturnirinae; Miller 1907). *Desmodus* is monospecific and a member of a subfamily with only three species. *Noctilio* comprises two species and is the only genus in the Noctilionidae. Phylogenetic isolation of host species rather than host abundance appears to be a factor that more likely determines the number of highly host specific ectoparasites.

Conclusions

Biodiversity of ectoparasite assemblages increased with host abundance. Although, these results may be an artifact of collection or passive sampling, parallels exist between the effect of host abundance on ectoparasite species richness and species-area relationships. Larger habitats harbor more rare species than do smaller habitats. Similarly, more abundant bat species harbor a greater number of rare ectoparasite species than do less abundant bat species. Transient ectoparasites do not prefer common host species, and occur on all host species at similar levels of incidence regardless of host abundance.

Biodiversity of ectoparasites increased with host abundance when ectoparasites were combined for all host species within each host family or for all host species as a group. This parallels results obtained in analyses at the level of host species. However, the cause of this pattern was not related to occurrence of transients, but reflected changes in host SADs. As the number of host individuals increased, so did the number of rare host species. Because bat ectoparasites are highly host-specific, additional rare host

species result in additional rare ectoparasite species. Consequently, different mechanisms influence the same pattern of ectoparasite biodiversity at multiple levels of host phylogeny.

Within the context of ETIB, hosts may be considered “islands” at multiple scales (i.e., host individuals or host populations). As a result, host abundance may be a measure of distance to a source population or a measure of island area for ectoparasite assemblages. Disentangling the influence of each mechanism is difficult. Regardless of scale, ETIB predicts that more abundant hosts should support more species-rich ectoparasite faunas, which was observed for ectoparasite assemblages on bats of Paraguay.

Literature Cited

Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche. 2003. Diversification among New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:1-32.

Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham. 1988. Genetic studies of *Lasiurus* (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University 117:1-15.

Barclay, R. M. R., and L. D. Harder. 2003. Life histories of bats: life in the slow lane. Pp. 209-253 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Barquez, R. M., M. A. Mares, and J. K. Braun. 1999. The bats of Argentina. Special Publications, The Museum, Texas Tech University 42:1-275.

Best, T. L., J. L. Hunt, L. A. McWilliams, and K. G. Smith. 2002. Eumops auripendulus. Mammalian Species 708:1-5.

Best, T. L., W. M. Kiser, and J. C. Rainey. 1997. Eumops glaucinus. Mammalian Species 551:1-6.

Best, T. L., W. M. Kiser, and P. W. Freeman. 1996. Eumops perotis. Mammalian Species 534:1-8.

Brennan, J. M., and M. L. Goff. 1977. Keys to the genera of chiggers of the Western Hemisphere (Acarina: Trombiculidae). The Journal of Parasitology 63:554-566.

Brennan, J. M., and J. T. Reed. 1974. The genus *Eutrombicula* in Venezuela (Acarina: Trombiculidae). The Journal of Parasitology 60:699-711.

Brennan, J. M., and J. T. Reed. 1975. A list of Venezuela chiggers, particularly of small mammalian hosts (Acarina: Trombiculidae). Brigham Young University Science Bulletin, Biological Series 20 (1):45-75.

Brennan, J. M., and C. E. Yunker. 1966. The chiggers of Panama (Acarina: Trombiculidae). Pp. 221-266 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. The American Naturalist 105:467-478.

Bush, M. B., and R. J. Whittaker. 1991. Krakatau: colonization patterns and hierarchies. Journal of Biogeography 18:341-356.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11:265-270.

Coleman, B. D. 1981. On random placement and species-area relationships. Mathematical Biosciences 54:191-215.

Coleman, B. D., M. A. Mares, M. R. Willig, and Y.-H. Hsieh. 1982. Randomness, area, and species richness. Ecology 63:1121-1133.

Colwell, R. K., and D. W. Winkler. 1984. A null model for null models. Pp. 344-359 in Ecological communities: conceptual issues and the evidence (D. Strong, D. Simberloff, L. Abele, and A. Thistle, eds.). Princeton University Press, Princeton, New Jersey.

Colwell, R. K. 2001. EstimateS: statistical estimation of species richness and shared species from samples for the Macintosh (V 6.0b1). Available online at http://viceroy.eeb.uconn.edu/EstimateS.

de la Cruz, J. 1969. Nueva espécie de ácaro (Acarina: Listrophoridae) parásito de murciélagos cubanos. Poeyana, Seria A 62:1-8.

Dusbábek, F. 1969*a*. To the phylogeny of genera of the family Myobiidae. Acarologia 11:537-574.

Dusbábek, F. 1969*b*. Generic revision of the myobiid mites (Acarina: Myobiidae) parasitic on bats. Folia Parasitologica 16:1-17.

Dusbábek, F., and J. de la Cruz. 1966. Nuevos géneros y espécies de acaros (Acarina: Listrophoridae) parásitos de murciélagos cubanos. Poeyana, Seria A 31:1-20.

Fain, A. 1978. Mites of the family Myobiidae (Acarina: Prostigmata) from mammals in the collection of the British Museum (Natural History). Bulletin of the British Museum of Natural History, Zoological Series 33:193-229.

Fairchild, G. B., G. M. Kohls, and V. J. Tipton. 1966. The ticks of Panama (Acarina: Ixodoidea). Pp. 167-220 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Ferris, G. F., and R. L. Usinger. 1939. The family Polyctenidae (Hemiptera: Heteroptera). Microentomology 4:1-50.

Ferris, G. F., and R. L. Usinger. 1945. Notes and descriptions of American Polyctenidae (Hemiptera). Pan Pacific Entomologist 21:121-124.

Gannon, M.R., and M.R. Willig. 1997. The effect of lunar illumination on movement and activity of the red fig-eating bat (*Stenoderma rufum*). Biotropica 29:525-529.

Gilbert, F. S. 1980. The equilibrium theory of island biogeography, fact or fiction? Journal of Biogeography 7:209-235.

Graciolli, G., and C. W. Dick. 2004. *Metelasmus wenzeli* new species (Diptera: Streblidae: Streblinae) from southern South America. Zootaxa (submitted).

Guimarães, L. R. 1966. Nycteribiid bat flies from Panama (Diptera: Nycteribiidae). Pp. 393-404 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Guimarães, L. R. 1972. Venezuelan nycteribiid batflies (Diptera: Nycteribiidae). Brigham Young University Science Bulletin, Biological Series 17 (1):1-11.

Haila, Y., and O. Järvinen. 1982. The role of theoretical concepts in understanding the ecological theatre: a case study on island biogeography. Pp. 261-278 in Conceptual issues in ecology (E. Saarinen, ed.). D. Reidel, Dordrecht, The Netherlands.

Handley, C. O., Jr. 1987. New species of mammals from northern South America: fruit-eating bats, genus *Artibeus* Leach. Pp. 163-172 in Studies in neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana, Zoology (New Series) 39:1-506.

Herrin, C. S., and V. J. Tipton. 1975. Spinturnicid mites of Venezuela. Brigham Young University Science Bulletin, Biological Series 20 (2):1-72.

Hurlbert, S. H. 2003. Design and analysis: uncertain intent, uncertain result. Ecology 84:810-812.

Johnson, M. P., and D. S. Simberloff. 1974. Environmental determinants of island species numbers in the British Isles. Journal of Biogeography 1:149-154.

Jones, E. K, C. M. Clifford, J. E. Keirans, and G. M. Kohls. 1972. Ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of Amblyomma in the Western Hemisphere. Brigham Young University Science Bulletin, Biological Series 17 (4):1-40.

Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biological Review 77:223-259.

Kennedy, C. R. 1978*a*. An analysis of the metazoan parasitocoenoses of brown trout *Salmo trutta* from British lakes. Journal of Fish Biology 13:255-263.

Kennedy, C. R. 1978*b*. The parasite fauna of resident char *Salvelinus alpinus* from Arctic islands, with special reference to Bear Island. Journal of Fish Biology 13:457-466.

Kiser, W. M. 1995. Eumops underwoodi. Mammalian Species 516:1-4.

Koopman, K. F. 1993. Order Chiroptera. Pp. 137-241 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D. C.

Kunz, T. H. 1982. Roosting ecology. Pp. 1-56 in Ecology of bats. (T. H. Kunz, ed.). Plenum Press, New York, New York.

Kuris, A. M., A. R. Blaustein, and J. J. Alió. 1980. Hosts as islands. The American Naturalist 116:570-586.

López-González, C. 1998. Systematics and zoogeography of the bats of Paraguay. Ph.D. dissertation, Texas Tech University, Lubbock, Texas.

López-González, C. 2005. Los murciélagos de Paraguay. Publicaciones Comité Español MAB y Red Ibero MAB (in press).

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

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

McDaniel, B. 1970. The labidocarpid batmites of Nicaragua (Listrophoroidea : Labidocarpidae). Acarologia 12:803-823.

McDaniel, B. 1973. Labidocarpid bat-mites of Venezuela (Listophoroidea: Labidocarpidae). Brigham Young University Science Bulletin, Biological Series 17 (2):15-32.

Machado-Allison, C. E. 1965. Las espécies Venezolanas del género *Periglischrus* Kolenati 1857. Acta Biología Venezuelica 4:259-348.

Marshall, A. G. 1971. The ecology of *Basilia hispida* (Diptera: Nycteribiidae) in Malaysia. Journal of Animal Ecology 40:141-154.

Marshall, A. G. 1982. Ecology of insects ectoparasitic on bats. Pp. 369-401 in Ecology of bats. (T. H. Kunz, ed.). Plenum Press, New York, New York.

The Math Works, Inc. 1994. Matlab for Macintosh, ver. 4.2c.1. Prentice Hall, Englewood Cliffs, New Jersey.

Miller, G. S., Jr. 1907. The families and genera of bats. Bulletin of the Unites States National Museum 57:1-65.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403-405.

Myers, P. 1982. Origins and affinities of the mammal fauna of Paraguay. Pp. 85-93 in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications, Pymatuning Laboratory of Ecology 6:1-539.

Newbound, D. R., and B. Knott. 1999. Parasitic copepods from pelagic sharks in western Australia. Bulletin of Marine Science 65:715-724.

Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 10:99-109.

Owen, R. D. 1987. Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Special Publications, Museum of Texas Tech University 26:1-65.

Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. American Zoologist, 34:134-144.

Pik, A. J., I. Oliver, and A. J. Beattie. 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Australian Journal of Ecology 24:555-562.

Pinichpongse, S. 1963a. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (1st series). Acarologia 5:81-91.

Pinichpongse, S. 1963b. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part Two). Acarologia 5:266-278.

Pinichpongse, S. 1963c. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part three). Acarologia 5:397-404.

Pinichpongse, S. 1963d. A review of the Chirodiscinae with descriptions of new taxa (Acarina : Listrophoridae) (Part four). Acarologia 5:620-627.

Preston, F. W. 1962*a*. The canonical distribution of commonness and rarity: part I. Ecology 43:185-215.

Preston, F. W. 1962*b*. The canonical distribution of commonness and rarity: part II. Ecology 43:410-432.

Radovsky, F. J. 1967. The Macronyssidae and Laelapidae (Acarina: Mesostigmata) parasitic on bats. University of California Publications in Entomology 46:1-288.

Redford, K. H., and J. F. Eisenberg. 1992. Mammals of the Neotropics: the southern cone. Volume 2, Chile, Argentina, Uruguay, Paraguay. The University of Chicago Press, Chicago, Illinois.

Reed, J. T., and J. M. Brennan. 1975. The subfamily Leeuwenhoekinae in the Neotropics (Acarina: Trombiculidae). Brigham Young University Science Bulletin, Biological Series 20 (1):1-42.

Ronderos, R. A. 1959. Polycténidae americanos. I. (Hemiptera). Actas y Trabajos del Primer Congreso Sudamericano de Zoologia 3:173-180.

Ronderos, R. A. 1962. Polycténidae americanos. II. (Hemiptera). Acta Zoológica Lilloana 18:259-262.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, England.

Rudnick, A. 1960. A revision of the mites of the family Spinturnicidae (Acarina). University of California Publications in Entomology 17: 157-283.

Saunders, R. C. 1975. Venezuelan Macronyssidae (Acarina: Mesostigmata). Brigham Young University Science Bulletin, Biological Series 20 (2):75-90.

Scheiner, S. M., and M. R. Willig. 2004. Toward a unified theory of diversity gradients. The American Naturalist. (submitted).

Schrader-Frechette, K. S., and E. D. McCoy (Eds.). 1993. Method in ecology: strategies for conservation. Cambridge University Press, Cambridge, England.

Shoener, A. 1988. Experimental island biogeography. Pp. 485-512 in Analytical biogeography: an integrated approach to the study of animal and plant

distributions (A. Myers and P. Giller, eds.). Chapman and Hall, New York, New York.

Simberloff, D. S. 1976. Species turnover and equilibrium island biogeography. Science 194:572-578.

Simberloff, D. S. 1983. When is an island community in equilibrium? Science 220:1275-1277.

Simberloff, D. S., and E. O. Wilson. 1970. Experimental zoogeography of islands. A two-year record of colonization. Ecology 51:934-937.

Simmons, N. B., and R. S. Voss. 1998. The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna. Part 1. Bats. Bulletin of the American Museum of Natural History 237:1-219.

Sismondo, S. 2000. Island biogeography and the multiple domains of models. Biology and Philosophy 15:239-258.

SPSS, Inc. 1990. The SPSS base system user's guide. SPSS, Inc., Chicago, Illinois.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. The American Naturalist 152:510-529.

ter Hofstede, H. M., M. B. Fenton, and J. O. Whitaker, Jr. 2004. Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) of Neotropical bats (Chiroptera). Canadian Journal of Zoology 82:616-626.

Ueshima N. 1972. New World Polyctenidae (Hemiptera), with special reference to Venezuelan species. Brigham Young University Science Bulletin, Biological Series 17 (1):13-21.

VanderMeulen, M. A., A. J. Hudson, and S. M. Scheiner. 2001. Three evolutionary hypotheses for the hump-shaped productivity-diversity curve. Evolutionary Ecology Research 3:379-392.

Wenzel, R. L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin, Biological Series 20 (4):1-177.

Wenzel, R. L., V. J. Tipton, and A. Kiewlicz. 1966. The streblid batflies of Panama (Diptera: Streblidae). Pp. 405-675 in Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.). Field Museum of Natural History, Chicago, Illinois.

Whittaker, R. H. 1960. Vegetation of the Kiskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Whitaker, R. J. 1998. Island biogeography: ecology, evolution and conservation. Oxford University Press, Oxford, England.

Williamson. M. 1988. Relationships of species number to area, distance and other variables. Pp. 91-115 in Analytical biogeography: an integrated approach to the study of animal and plant distributions (A. Myers and P. Giller, eds.). Chapman and Hall, New York, New York.

Willig, M. R., S. J. Presley, R. D. Owen, and C. López-González. 2000. Composition and structure of bat assemblages in Paraguay: a subtropical – temperate interface. Journal of Mammalogy 81:386-401.

Table 4.1. Results of simple regression analyses determining the effect of regional (i.e., country-wide) host abundance on the biodiversity of ectoparasite assemblages from all hosts as a group and for each host family. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Bioiversity measure Bat group	r^2	p-value	B_1
Mean ectoparasite abundance			
All bats	0.061	0.130	
Phyllostomidae	0.106	0.277	
Vespertilionidae	0.055	0.514	
Molossidae	0.055	0.442	
Average richness			
All bats	0.012	0.507	
Phyllostomidae	0.004	0.841	
Vespertilionidae	0.239	0.670	
Molossidae	0.021	0.635	
Accumulative richness			
All bats	**0.428**	**< 0.001**	**0.65**
Phyllostomidae	**0.700**	**< 0.001**	**0.84**
Vespertilionidae	**0.772**	**< 0.001**	**0.88**
Molossidae	**0.449**	**0.012**	**0.67**
Log richness			
All bats	**0.474**	**< 0.001**	**0.69**
Phyllostomidae	**0.719**	**< 0.001**	**0.85**
Vespertilionidae	**0.660**	**0.004**	**0.81**
Molossidae	**0.479**	**0.009**	**0.69**
Chao1 richness			
All bats	**0.432**	**< 0.001**	**0.66**
Phyllostomidae	**0.739**	**< 0.001**	**0.86**
Vespertilionidae	0.363	0.065	
Molossidae	**0.449**	**0.012**	**0.67**
Shannon diversity			
All bats	0.019	0.399	
Phyllostomidae	0.061	0.415	
Vespertilionidae	0.212	0.180	
Molossidae	0.001	0.906	

Table 4.1. Continued

Bioiversity measure Bat group	r^2	p-value	B_1
Shannon evenness			
All bats	**0.139**	**0.019**	**-0.370**
Phyllostomidae	0.178	0.152	
Vespertilionidae	0.145	0.278	
Molossidae	**0.331**	**0.040**	**-0.570**
Berger-Parker dominance			
All bats	0.000	0.908	
Phyllostomidae	0.033	0.551	
Vespertilionidae	0.093	0.391	
Molossidae	0.049	0.469	
Rare species			
All bats	**0.438**	**< 0.001**	**0.66**
Phyllostomidae	**0.683**	**< 0.001**	**0.83**
Vespertilionidae	**0.751**	**0.001**	**0.87**
Molossidae	**0.527**	**0.005**	**0.73**
Beta diversity			
All bats	**0.483**	**< 0.001**	**0.70**
Phyllostomidae	**0.725**	**< 0.001**	**0.85**
Vespertilionidae	**0.679**	**0.003**	**0.82**
Molossidae	**0.487**	**0.008**	**0.70**

Table 4.2. Results of simple regression analyses determining the effect of local host abundance on the biodiversity of ectoparasite assemblages from common, wide-spread species of phyllostomid bat. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Biodiversity measure Bat species	r^2	p-value	B_1
Mean ectoparasite abundance			
Artibeus fimbriatus	0.217	0.534	
Artibeus lituratus	0.015	0.713	
Platyrrhinus lineatus	0.952	0.140	
Sturnira lilium	0.005	0.813	
Average richness			
Artibeus fimbriatus	0.039	0.802	
Artibeus lituratus	0.028	0.622	
Platyrrhinus lineatus	0.989	0.066	
Sturnira lilium	0.007	0.786	
Accumulative richness			
Artibeus fimbriatus	0.872	0.066	
Artibeus lituratus	**0.652**	**0.003**	**0.81**
Platyrrhinus lineatus	0.988	0.070	
Sturnira lilium	**0.547**	**0.004**	**0.74**
Log richness			
Artibeus fimbriatus	0.845	0.081	
Artibeus lituratus	**0.565**	**0.008**	**0.75**
Platyrrhinus lineatus	**0.996**	**0.042**	**1.00**
Sturnira lilium	**0.645**	**0.001**	**0.80**
Chao1 richness			
Artibeus fimbriatus	**0.933**	**0.034**	**0.97**
Artibeus lituratus	0.315	0.072	
Platyrrhinus lineatus	0.986	0.075	
Sturnira lilium	**0.617**	**0.002**	**0.79**
Shannon diversity			
Artibeus fimbriatus	0.590	0.232	
Artibeus lituratus	0.042	0.548	
Platyrrhinus lineatus	0.642	0.409	
Sturnira lilium	**0.318**	**0.045**	**0.56**

Table 4.2. Continued

Biodiversity measure Bat species	r^2	p-value	B_1
Shannon evenness			
Artibeus fimbriatus	0.241	0.509	
Artibeus lituratus	0.225	0.140	
Platyrrhinus lineatus	0.552	0.467	
Sturnira lilium	**0.431**	**0.015**	**-0.66**
Berger-Parker dominance			
Artibeus fimbriatus	0.658	0.189	
Artibeus lituratus	0.002	0.887	
Platyrrhinus lineatus	0.508	0.495	
Sturnira lilium	0.175	0.155	
Rare species			
Artibeus fimbriatus	**0.915**	**0.044**	**0.96**
Artibeus lituratus	**0.583**	**0.006**	**0.76**
Platyrrhinus lineatus	**0.998**	**0.030**	**1.00**
Sturnira lilium	**0.607**	**0.002**	**0.78**
Beta diversity			
Artibeus fimbriatus	0.847	0.080	
Artibeus lituratus	**0.569**	**0.007**	**0.75**
Platyrrhinus lineatus	**0.995**	**0.047**	**1.00**
Sturnira lilium	**0.654**	**0.001**	**0.81**

Table 4.3. Results of simple regression analyses determining the effect of local host abundance on the biodiversity of ectoparasite assemblages from common, wide-spread species of vespertilionid bat. Significant results are bold. No analyses were significant after Bonferroni sequential adjustment. Four diversity measures of ectoparasite assemblage diversity were constants for Lasiurus ega. See text for abbreviations.

Biodiversity measure Bat species	r^2	p-value	B_1
Mean ectoparasite abundance			
Eptesicus furinalis	0.019	0.795	
Lasiurus ega	**0.997**	**0.036**	**-1.00**
Myotis abescens	0.023	0.776	
Myotis nigricans	0.067	0.536	
Average richness			
Eptesicus furinalis	0.490	0.121	
Lasiurus ega	0.993	0.052	
Myotis abescens	0.249	0.314	
Myotis nigricans	0.001	0.957	
Accumulative richness			
Eptesicus furinalis	0.384	0.189	
Lasiurus ega	--	--	
Myotis abescens	**0.829**	**0.012**	**0.91**
Myotis nigricans	**0.556**	**0.034**	**0.75**
Log richness			
Eptesicus furinalis	0.038	0.711	
Lasiurus ega	--	--	
Myotis abescens	**0.851**	**0.009**	**0.92**
Myotis nigricans	0.495	0.052	
Chao1 richness			
Eptesicus furinalis	0.419	0.165	
Lasiurus ega	--	--	
Myotis abescens	**0.872**	**0.007**	**0.93**
Myotis nigricans	0.198	0.270	
Shannon diversity			
Eptesicus furinalis	0.493	0.120	
Lasiurus ega	0.983	0.082	
Myotis abescens	0.439	0.152	
Myotis nigricans	0.010	0.446	

Table 4.3. Continued

Biodiversity measure Bat species	r^2	p-value	B_1
Shannon evenness			
Eptesicus furinalis	0.193	0.384	
Lasiurus ega	0.980	0.091	
Myotis abescens	0.108	0.525	
Myotis nigricans	**0.719**	**0.008**	**-0.85**
Berger-Parker dominance			
Eptesicus furinalis	0.028	0.753	
Lasiurus ega	0.983	0.082	
Myotis abescens	0.336	0.228	
Myotis nigricans	0.326	0.140	
Rare species			
Eptesicus furinalis	0.005	0.890	
Lasiurus ega	0.993	0.052	
Myotis abescens	**0.790**	**0.018**	**0.89**
Myotis nigricans	**0.732**	**0.007**	**0.86**
Beta diversity			
Eptesicus furinalis	0.012	0.838	
Lasiurus ega	--	--	
Myotis abescens	**0.886**	**0.005**	**0.94**
Myotis nigricans	**0.538**	**0.038**	**0.73**

Table 4.4. Results of simple regression analyses determining the effect of local host abundance on the biodiversity of ectoparasite assemblages from common, wide-spread species of molossid bat. Significant results are bold. No analyses were significant after Bonferroni sequential adjustment. See text for abbreviations.

Biodiversity measure Bat species	r^2	p-value	B_1
Mean ectoparasite abundance			
Eumops glaucinus	0.254	0.496	
Eumops patagonicus	0.252	0.139	
Molossops temminckii	0.043	0.591	
Molossus ater	0.040	0.746	
Molossus molossus	0.030	0.745	
Average richness			
Eumops glaucinus	**0.954**	**0.023**	**0.98**
Eumops patagonicus	0.000	0.961	
Molossops temminckii	0.038	0.615	
Molossus ater	0.259	0.381	
Molossus molossus	0.001	0.941	
Accumulative richness			
Eumops glaucinus	0.156	0.605	
Eumops patagonicus	0.118	0.332	
Molossops temminckii	0.298	0.129	
Molossus ater	0.101	0.602	
Molossus molossus	0.069	0.615	
Log richness			
Eumops glaucinus	0.077	0.722	
Eumops patagonicus	0.062	0.489	
Molossops temminckii	**0.479**	**0.039**	**0.69**
Molossus ater	0.159	0.506	
Molossus molossus	0.015	0.820	
Chao1 richness			
Eumops glaucinus	0.068	0.739	
Eumops patagonicus	0.032	0.623	
Molossops temminckii	0.289	0.136	
Molossus ater	0.085	0.634	
Molossus molossus	0.041	0.700	

Table 4.4. Continued

Biodiversity measure Bat species	r^2	p-value	B_1
Shannon diversity			
Eumops glaucinus	0.017	0.869	
Eumops patagonicus	0.003	0.881	
Molossops temminckii	0.000	0.964	
Molossus ater	0.638	0.105	
Molossus molossus	0.017	0.806	
Shannon evenness			
Eumops glaucinus	0.113	0.665	
Eumops patagonicus	0.041	0.573	
Molossops temminckii	0.294	0.131	
Molossus ater	0.196	0.455	
Molossus molossus	0.137	0.471	
Berger-Parker dominance			
Eumops glaucinus	0.655	0.191	
Eumops patagonicus	0.042	0.572	
Molossops temminckii	0.009	0.811	
Molossus ater	0.650	0.099	
Molossus molossus	0.001	0.948	
Rare species			
Eumops glaucinus	0.367	0.395	
Eumops patagonicus	0.184	0.217	
Molossops temminckii	**0.576**	**0.018**	**0.76**
Molossus ater	0.137	0.539	
Molossus molossus	0.274	0.287	
Beta diversity			
Eumops glaucinus	0.041	0.798	
Eumops patagonicus	0.058	0.502	
Molossops temminckii	**0.507**	**0.032**	**0.71**
Molossus ater	0.074	0.657	
Molossus molossus	0.016	0.814	

Table 4.5. Results of simple regression analyses determining the effect of local host abundance on the biodiversity of ectoparasite assemblages from the entire host assemblage and for each common host family. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Biodiversity measure Bat group	r^2	p-value	B_1
Mean ectoparasite abundance			
All bats	0.051	0.250	
Phyllostomidae	0.102	0.211	
Vespertilionidae	0.012	0.678	
Molossidae	0.018	0.569	
Average richness			
All bats	0.008	0.642	
Phyllostomidae	0.008	0.725	
Vespertilionidae	0.030	0.505	
Molossidae	0.002	0.848	
Accumulative richness			
All bats	**0.375**	**< 0.001**	**0.61**
Phyllostomidae	**0.753**	**< 0.001**	**0.87**
Vespertilionidae	**0.601**	**< 0.001**	**0.78**
Molossidae	**0.305**	**0.012**	**0.55**
Log richness			
All bats	**0.355**	**< 0.001**	**0.60**
Phyllostomidae	**0.653**	**< 0.001**	**0.81**
Vespertilionidae	**0.456**	**0.003**	**0.68**
Molossidae	**0.269**	**0.019**	**0.52**
Chao1 richness			
All bats	**0.272**	**0.004**	**0.52**
Phyllostomidae	**0.678**	**< 0.001**	**0.82**
Vespertilionidae	**0.239**	**0.046**	**0.49**
Molossidae	0.161	0.080	
Shannon diversity			
All bats	0.126	0.063	
Phyllostomidae	**0.573**	**< 0.001**	**0.76**
Vespertilionidae	0.181	0.088	
Molossidae	0.010	0.681	

Table 4.5. Continued

Biodiversity measure Bat group	r^2	p-value	B_1
Shannon evenness			
All bats	0.022	0.447	
Phyllostomidae	0.006	0.766	
Vespertilionidae	0.024	0.550	
Molossidae	0.090	0.198	
Berger-Parker dominance			
All bats	0.049	0.255	
Phyllostomidae	0.197	0.074	
Vespertilionidae	0.097	0.225	
Molossidae	0.006	0.751	
Rare species			
All bats	**0.381**	**< 0.001**	**0.62**
Phyllostomidae	**0.718**	**< 0.001**	**0.85**
Vespertilionidae	**0.600**	**< 0.001**	**0.77**
Molossidae	**0.384**	**0.004**	**0.62**
Beta diversity			
All bats	**0.358**	**< 0.001**	**0.60**
Phyllostomidae	**0.661**	**< 0.001**	**0.81**
Vespertilionidae	**0.476**	**0.002**	**0.69**
Molossidae	**0.277**	**0.017**	**0.53**

Table 4.6. Results of simple regression analyses determining the relationships between host abundance, host species richness, and number of rare host species from the entire host assemblage and for each common host family. Significant results are bold. Significant results after Bonferroni sequential adjustment are underlined. See text for abbreviations.

Independent variable Dependent variable Host group	r^2	p-value	B_1
Host abundance			
Host species richness			
All bats	**0.317**	**0.002**	**0.56**
Phyllostomidae	**0.319**	**0.044**	**0.56**
Vespertilionidae	0.020	0.633	0.14
Molossidae	0.188	0.106	0.44
Host abundance			
Number of rare host species			
All bats	**0.355**	**< 0.001**	**0.60**
Phyllostomidae	0.195	0.131	0.44
Vespertilionidae	0.003	0.848	-0.06
Molossidae	0.252	0.057	0.50
Host species richness			
Number of rare host species			
All bats	**0.885**	**< 0.001**	**0.94**
Phyllostomidae	**0.880**	**< 0.001**	**0.94**
Vespertilionidae	0.000	0.959	-0.02
Molossidae	**0.621**	**< 0.001**	**0.79**

CHAPTER V
CONCLUSIONS

Ectoparasites were collected from 2,909 of the 4,143 bats captured during the study, representing 44 species and five families of hosts. Bat assemblages were defined for each of 28 sites, distributed throughout all major biomes of Paraguay. Over 17,500 ectoparasites were collected, representing 104 species and 11 families (Appendix C). In abundance, five families (Insecta: Streblidae; Arachnida: Spinturnicidae, Macronyssidae, Chirodiscidae, and Argasidae) accounted for 94.5% of all ectoparasites.

The employed method of ectoparasite collection was developed recently (Sheeler-Gordon and Owen 1999) and likely results in less cross-host contamination than in previous studies (e.g., Herrin and Tipton 1975). In general, host-parasite associations in Paraguay corroborate previously reported associations. Analysis of the species abundance distributions (SADs) of ectoparasite assemblages (restricted to primary associations) revealed that limiting resources for ectoparasites (i.e., space on the host) are relatively evenly divided among component taxa, within the context of commonly used models of SADs such as the broken stick, geometric series, log normal, and log series models. Ectoparasite SADs are not consistent with a model (i.e., geometric series) based on niche preemption. Observations of insects ectoparasitic on bats suggest that competition may be reduced by specializations for locomotion on particular parts of the host (i.e., microhabitats). Co-existence of multiple fly species on individual hosts often is attained by microhabitat specialization in this taxon.

The use of body size as a surrogate for island area in the context of ETIB is practical and seems reasonable. However, the range of body sizes for bats of Paraguay is relatively small, spanning only one order of magnitude, compared to traditional islands which span several orders of magnitude and that have been the subject of biogeographic analysis. The range of body sizes in bats may not be sufficiently great to allow mechanisms associated with ETIB to operate at a detectible level. If a similar study were conducted with respect to all Paraguayan mammal species for which the range of body

sizes spans five orders of magnitude, then body size might emerge as a more important determinant of ectoparasite diversity. Such dependence on scale or heirarchy is common in ecological studies of biodiversity (Scheiner et al. 2000, Willig et al. 2003). Alternatively, sex-related differences in behavior, specifically roosting habits, may be a more important factor for predicting ectoparasite diversity than is host size, *per se*.

Because bats are small and do not provide unlimited space for population growth, opportunities for transfer are important. Therefore, host individuals may not be the most appropriate scale to consider ectoparasite assemblages to be isolated evolutionary units. Ectoparasite assemblages on groups of host individuals (i.e., colonies or populations) may be evolutionarily isolated and better conform to predictions of ETIB than do assemblages on individual hosts. In this context, bat colony size may be a realistic surrogate for island area. Correspondingly, inter-colony distance may be an appropriate measure of distance to a source population. Some patterns (such as increased nycteribiid abundance on smaller vespertilionids in Paraguay) are not explained adequately by either host size or social system, and may be better explained by investigating the effect of host abundance on ectoparasite biodiversity.

Biodiversity of ectoparasite assemblages increased with host abundance. These results may be an artifact of collection or passive sampling. Nonetheless, parallels exist between the effect of host abundance on ectoparasite species richness and species-area relationships. Larger habitats harbor more rare species than do smaller habitats. Similarly, more abundant bat species harbor more rare species of ectoparasites than do less abundant bat species.

Biodiversity of ectoparasites also increased with host abundance after ectoparasites were combined for all host species within each host family or for all host species as a group. However, the cause of the pattern at these levels was not occurrence of transients, but reflected changes in host SADs. As the number of host individuals increases, so does the number of rare host species. Because bat ectoparasites are highly host-specific, additional rare host species result in additional rare ectoparasite species.

Consequently, different mechanisms influence the same pattern of ectoparasite biodiversity at multiple levels of host phylogeny.

Within the context of ETIB, hosts may be considered to be islands at multiple scales (i.e., host individuals, host populations, or host families). As a result, host abundance may be a measure of distance to a source population (at the host individual level) or a measure of island area (at the host species level). Disentangling the influence of each mechanism is difficult. Regardless of scale, ETIB predicts that larger host populations should support more species-rich ectoparasite faunas and this does occur at multiple scales for ectoparasite assemblages of bats in Paraguay.

Because bats are small and safe spaces for ectoparasites are limited, opportunities for vertical transfer are important in maintaining large enough populations to avoid stochastic extinction. Consequently, location of new resources (i.e., additional host individuals) is paramount. Bats that have colonial roosting habits, harem mating systems, or form maternity colonies should support more diverse ectoparasite assemblages than do solitary bat species. In addition, common bat species should provide more transfer opportunities than do rare bat species. Group size was not measured during the study; however, there is evidence that ectoparasite assemblages of bats with gregarious behaviors (e.g., female *Sturnira lilium* and *Noctilio albiventris* that are members of harems) are more species-rich than are those of more solitary bats (e.g., sub-adult male *S. lilium* and *N. albiventris* that are solitary). Moreover, ectoparasite assemblages on common bat species (e.g., *Artibeus lituratus*, *S. lilium*, *Eumops patagonicus*, *Molossus molossus*) are more species-rich than are those on rare bat species (e.g., *Chiroderma doriae*, *Pygoderma bilabiatum*, *Eumops auripendulus*, *Molossops planirostris*).

The application of ETIB to ectoparasite assemblages at multiple scales has provided insights into mechanisms that may structure these assemblages in space and time. Host body size was analyzed at two extents, within host species and among host species. Within a species, host body size did not affect the biodiversity of ectoparasite assemblages on most host species, as smaller host individuals harbored more diverse ectoparasite assemblages as often as did larger host individuals. Nonetheless, the use of

ETIB as a heuristic model was crucial in discovering the importance that host social organization may play in host selection by ectoparasites. Moreover, variation in host body size among species did significantly affect ectoparasite biodiversity. Larger species of bats had more common and abundant ectoparasites than did smaller species of bats. One factor that accounts for species-area relationships is that larger areas have more habitats than do smaller areas and habitat diversity leads to species diversity (Rosenzweig 1995, Williamson 1988). Similarly, larger host individuals may have more microhabitats that provide sufficient space to support viable populations of more species of ectoparasite than do smaller host individuals.

The effect of host abundance was analyzed at threes hierarchical levels; for all bats as a group, for all bats within each host family, and separately for each host species. At all levels, host abundance positively affected ectoparasite biodiversity; however, the mechanisms invoked to explain this phenomenon differed with hierarchy. At the host species level, two mechanisms associated with the More Individuals Hypothesis explain increases in ectoparasite biodiversity with increases in host species abundance (Scheiner and Willig 2004). From the perspective of ectoparasites, an increase in number of host individuals can be interpreted as either an increase in habitat area or an increase in productivity. At local scales, an increase in area or productivity positively affects number of individuals in two ways (Srivastava and Lawton 1998). First, more ectoparasite individuals provide more opportunities to observe rare or transient ectoparasite species (i.e., passive sampling; Coleman 1981; Coleman et al. 1982). Second, more ectoparasite individuals can increase the number of species that maintain viable population sizes, which reduces extinction rates.

At the levels of host family and of all host species, an aspect of species-area relationships, number of habitats, explains changes in ectoparasite biodiversity. More host individuals from a group of host species (family or all bat species) increase host species richness through passive sampling. Each host species is a unique habitat. Therefore, more species-rich host assemblages provide more habitats for ectoparasites. As predicted by species-area relationships, more types of habitat increase ectoparasite

biodiversity. Failure to investigate host-parasite systems at multiple levels would paint an incomplete picture of the mechanisms that structure ectoparasite assemblages.

Literature Cited

Coleman, B. D. 1981. On random placement and species-area relationships. Mathematical Biosciences 54:191-215.

Coleman, B. D., M. A. Mares, M. R. Willig, and Y.-H. Hsieh. 1982. Randomness, area, and species richness. Ecology 63:1121-1133.

Herrin, C. S., and V. J. Tipton. 1975. Spinturnicid mites of Venezuela. Brigham Young University Science Bulletin, Biological Series 20(2):1-72.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, England.

Scheiner, S. M., S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari. 2000. Species density, species-area curves and Simpson's paradox. Evolutionary Ecology Research 2:791-802.

Scheiner, S. M., and M. R. Willig. 2004. Toward a unified theory of diversity gradients. The American Naturalist. (submitted).

Sheeler-Gordon, L. L., and R. D. Owen. 1999. Host tracking or resource tracking? The case of *Periglischrus* wing mites (Acarina: Spinturnicidae) of leaf-nosed bats (Chiroptera: Phyllostomidae) from Michoacan, Mexico. Acta Zoológica Mexicana (nueva serie) 76:85-102.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. The American Naturalist 152:510-529.

Williamson, M. 1988. Relationships of species number to area, distance and other variables. Pp. 91-115 in Analytical biogeography: an integrated approach to the study of animal and plant distributions (A. Myers and P. Giller, eds.). Chapman and Hall, New York, New York.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution and Systematics 34: 273-309.

APPENDIX A

SITE DESCRIPTIONS FOR 28 COLLECTION LOCALITIES IN PARAGUAY

Table A.1. Description of 28 sites (Figure 2.1) at which bats were collected from Paraguay (July 1995 to May 1997; July to August 1998). Biome codes appear in Table 2.1; sampling regime includes year, season (wet, W; dry, D), and number of net nights. Wet seasons = October to March. Dry season = April to September.

Site code	Site name	Biome code	Departamento	Latitude (S)	Longitude (W)	Elevation	Sampling regime
1	Estancia La Victoria	BC	Presidente Hayes	23°39.03'	58°34.79'	120	95D20
2	Estancia San Jorge	AC	Boquerón	22°02.11'	60°19.93'	160	95D20
3	Cerro León	AC	Alto Paraguay	20°26.25'	60°19.19'	250	95D10
4	Estancia Sombrero	CP	Cordillera	25°04.26'	56°36.08'	100	95W37, 97W70
5	Lago Ypoá	NE	Paraguari	25°56.71'	57°26.80'	120	95W30
6	Estancia Cerrito	CC	Concepción	23°15.14'	57°29.57'	120	95W36
7	Fuerte Olimpo	MG	Alto Paraguay	21°02.37'	57°52.29'	120	95W22
8	Ayolas	NE	Misiones	27°23.42'	56°50.15'	70	96W39
9	Parque Nacional San Rafael	AP	Itapúa	26°45.46'	55°51.67'	170	96W43
10	Bahía Negra	MG	Alto Paraguay	20°10.98'	58°09.42'	90	96W25
11	Yaguareté Forest	CP	San Pedro	23°48.50'	56°07.68'	250	96W47
12	Parque Nacional Cerro Corá	CC	Amambay	22°37.90'	56°01.43'	280	96W86
13	Parque Nacional Serranía San Luis	CC	Concepción	22°37.91'	57°21.35'	270	96D75, 96W137
14	Estacia Yacaré	NE	Ñeembucú	26°37.94'	58°07.46'	60	96D107, 97W97
15	Reserva Natural del Bosque Mbaracayú	CP	Canindeyú	24°07.69'	55°30.34'	250	96D143, 96W202
16	Estancia Loma Porá	BC	Presidente Hayes	23°29.92'	57°32.92'	80	96D63, 97W75
17	Estancia Tres Marias	AC	Alto Paraguay	21°16.72'	59°33.13'	70	96D139, 97D99
18	Estancia Samaklay	AC	Presidente Hayes	23°28.81'	59°48.43'	120	96D111, 97W87

Table A.1. Continued

Site code	Site name	Biome code	Departamento	Latitude (S)	Longitude (W)	Elevation	Sampling regime
19	Dr. Pedro P. Peña	AC	Boquerón	22°27.16'	62°20.65'	240	96D148
20	Destacamento Militar Gabino Mendoza	AC	Alto Paraguay and Boquerón	20°05.30'	61°47.22'	390	96D71, 97D27
21	Estancia Rivas	AP	Canindeyú	24°30.43'	54°38.25'	300	96D136, 97W63
22	Estancia Golondrina	AP	Caazapá	25°32.30'	55°29.02'	300	96W87
23	Parque Nacional Ybycuí	CP	Paraguari	26°04.64'	56°50.98'	150	96W64
24	Parque Nacional Teniente Enciso	AC	Boquerón	21°11.40'	61°41.81'	250	97W57, 98D87
25	Palmar de las Islas	AC	Alto Paraguay	19°32.91'	60°31.64'	150	97D108
26	Ape Aimé	AP	Itapúa	26° 32.13'	54° 50.44'	150	98D145
27	Estancia San José	NE	Ñeembucú	27° 12.08'	58° 26.89'	50	98D116
28	Estancia Parabel	AP	Itapúa	26° 20.85'	55° 30.95'	440	98D153

APPENDIX B

HOST-PARASITE LIST

Ectoparasite species followed by an asterisk (*) indicate that this is probably a non-primary host species association that represents a transitory relationship or the result of contamination. In general, these relationships were defined by an incidence < 5%. For very small mites of the Trombiculidae, Chirodiscidae, and Myobiidae that rarely were collected in our samples, no judgment could be rendered with respect to primary host associations. Therefore, none of these taxa were labeled with asterisks. Number of host individuals of each host family and species (in bold) inspected for ectoparasites are in parentheses.

Noctilionidae (96)

***Noctilio albiventris* (68)**

Chiroptonyssus haematophagus *

Chiroptonyssus robustipes

Macronyssus crosbyi *

Steatonyssus sp. 1 *

Steatonyssus sp. 2 *

Unknown macronyssid *

Ornithodoros hasei

Lawrenceocarpus sp.

Noctiliostrebla maai

Paradyschiria parvula

Xenotrichobius noctilionis

***Noctilio leporinus* (28)**

Chiroptonyssus haematophagus

Steatonyssus sp. 1

Parkosa tadarida

Unknown mite

Noctiliostrebla aitkeni

Noctiliostrebla dubia

Paradyschiria fusca

Ornithodoros hasei

Phyllostomidae (1220)

Phyllostominae

***Chrotopterus auritus* (3)**

Unknown macronyssid

Trombicula sp. 1

Strebla chrotopteri

***Tonatia bidens* (3)**

Parichoronyssus crassipes

Periglischrus tonatii

Trichobius joblingi

***Tonatia brasiliense* (1)**

Parichoronyssus sclerus

Mastoptera minuta

Glossophaginae

***Glossophaga soricina* (54)**

Chiroptonyssus venezolanus *

Unknown macronyssid *

Periglischrus caligus

Periglischrus ojasti *

Speiseria ambigua

Pseudolabidocarpus sp.

Unknown mite

Strebla guajiro

Trichobius dugesii

Trichobius uniformis

Carollinae

***Carollia perspicillata* (75)**

Macronyssoides conciliatus *

Macronyssoides kochi *

Macronyssus sp. 3 *

Parichoronyssus crassipes

Parichoronyssus euthysternum *

Unknown macronyssid *

Periglischrus iheringi *

Periglischrus ojasti *

Unknown spinturnicid *

Unknown ixodid *

Pseudolabidocarpus sp.

Megistopoda proxima *

Strebla guajiro

Trichobius joblingi

Desmodontinae

***Desmodus rotundus* (51)**

Parichoronyssus euthysternum *

Parichoronyssus sclerus *

Radfordiella desmodi

Periglischrus herrerai

Unknown spinturnicid *

Ornithodoros hasei *

Strebla weidemanni

Trichobius parasiticus

***Diaemus youngi* (11)**

Macronyssus crosbyi *

Radfordiella desmodi *

Radfordiella oudemansi

Strebla diaemi

Trichobius diaemi

Stenodermatinae

***Artibeus fimbriatus* (79)**

Macronyssoides kochi

Parichoronyssus euthysternum *

Periglischrus iheringi

Periglischrus ojasti *

Beamerella acutascuta

Eudusbabekia viguerasi

Aspidoptera falcata *

Aspidoptera phyllostomatis

Megistopoda aranea

Megistopoda proxima *

Metelasmus pseudopterus

Strebla guajiro *

***Artibeus jamaicensis* (42)**

Chiroptonyssus haematophagus *

Macronyssoides kochi

Periglischrus iheringi

Ornithodoros hasei

Beamerella acutascuta

Trombicula dicrura

Trombicula sp.

Parkosa maxima

Eudusbabekia viguerasi

Aspidoptera phyllostomatis

Megistopoda aranea

Metelasmus pseudopterus *

***Artibeus lituratus* (351)**

Chiroptonyssus haematophagus *

Chiroptonyssus venezolanus *

Macronyssoides kochi

Parichoronyssus euthysternum *

Steatonyssus joaquimi *

Periglischrus iheringi

Periglischrus ojasti *

Euschoengastia megastyrax

Parkosa maxima

Eudusbabekia viguerasi

Unknown mite

Aspidoptera falcata *

Aspidoptera phyllostomatis *

Megistopoda aranea *

Megistopoda proxima *

Metelasmus pseudopterus *

Paratrichobius longicrus

***Chiroderma doriae* (3)**

Periglischrus iheringi

***Platyrrhinus lineatus* (90)**

Chiroptonyssus haematophagus *

Macronyssoides conciliatus

Macronyssoides kochi

Macronyssus crosbyi *

Parichoronyssus crassipes *

Steatonyssus furmani *

Steatonyssus joaquimi *

Periglischrus iheringi

Periglischrus ojasti *

Spinturnix orri *

Aspidoptera falcata *

Megistopoda proxima *

Paratrichobius longicrus *

Trichobius angulatus

***Pygoderma bilabiatum* (53)**

Periglischrus iheringi *

Unknown spinturnicid *

Chiroptonyssus haematophagus *

Macronyssoides kochi *

Macronyssoides sp. *

Parichoronyssus euthysternum *

Eudusbabekia sp.

***Sturnira lilium* (404)**

Chiroptonyssus haematophagus *

Macronyssoides kochi *

Parichoronyssus crassipes *

Parichoronyssus euthysternum

Steatonyssus joaquimi *

Unknown macronyssid *

Periglischrus iheringi *

Periglischrus ojasti

Ornithodoros hasei *

Rhipicephalus sp. *

Beamerella acutascuta

Eutrombicula sp.

Hooperella vesperuginus

Perisopalla precaria

Trombicula dicrura

Trombicula sp.

Eudusbabekia lepidoseta

Aspidoptera falcata

Megistopoda aranea *

Megistopoda proxima

Metelasmus paucisetus

Noctiliostrebla aitkeni *

Paratrichobius longicrus *

Natalidae (1)

***Natalus stramineus* (1)**

Periglischrus natali

Trichobius galei

Vespertilionidae (401)

***Eptesicus brasiliensis* (12)**

Chiroptonyssus venezolanus

Steatonyssus joaquimi

Ornithodoros hasei

Basilia sp. 5

Basilia spp. (males only)

***Eptesicus diminutus* (2)**

Steatonyssus joaquimi

Amblyomma sp. *

Basilia sp. (males only)

***Eptesicus furinalis* (69)**

Chiroptonyssus haematophagus *

Chiroptonyssus venezolanus *

Macronyssus crosbyi *

Parichoronyssus cyrtosternum *

Steatonyssus furmani *

Steatonyssus joaquimi

Periglischrus iheringi *

Spinturnix orri

Spinturnix surinamensis

Ornithodoros hasei

Beamerella acutascuta

Basilia sp. 1 *****

Basilia sp. 3 *

Basilia sp. 4

Basilia sp. 5

Basilia spp. (males only)

***Histiotus macrotus* (6)**

Chiroptonyssus haematophagus

Steatonyssus joaquimi

Basilia spp. (males only)

***Lasiurus blossevillii* (11)**

Chiroptonyssus haematophagus

Steatonyssus furmani

Steatonyssus joaquimi

***Lasiurus cinereus* (2)**

Macronyssus meridionalis

***Lasiurus ega* (72)**

Steatonyssus furmani

Labidocarpus sp.

Parkosa tadarida

Unknown mite

***Myotis albescens* (87)**

Chiroptonyssus haematophagus *

Macronyssus crosbyi

Parichoronyssus euthysternum *

Steatonyssus joaquimi

Steatonyssus sp. 2 *

Spinturnix americanus

Spinturnix banksi

Ornithodoros hasei *

Unknown mite *

Basilia sp. 1

Basilia sp. 2 *

Basilia sp. 3

Basilia sp. 6

Basilia spp. (males only)

Myodopsylla wolffsohni *

***Myotis nigricans* (128)**

Chiroptonyssus haematophagus *

Chiroptonyssus robustipes *

Macronyssus crosbyi

Macronyssus meridionalis *

Macronyssus sp. 2*

Steatonyssus furmani *

Steatonyssus joaquimi

Steatonyssus sp. 2*

Unknown macronyssid *

Periglischrus ojasti *

Spinturnix americanus

Ornithodoros hasei *

Basilia sp. 2

Basilia sp. 3

Basilia sp. (males only)

Myodopsylla wolffsohni *

***Myotis riparius* (11)**

Macronyssus crosbyi *

Macronyssus meridionalis

Steatonyssus joaquimi *

Spinturnix americanus *

Basilia sp. 2 *

Basilia sp. 3

***Myotis simus* (1)**

Macronyssus sp. 1

Spinturnix americanus

Molossidae (1192)

***Eumops auripendulus* (2)**

None

***Eumops bonariensis* (5)**

Chiroptonyssus haematophagus

Parichoronyssus euthysternum

Labidocarpus sp.

***Eumops dabbenei* (4)**

Chiroptonyssus haematophagus

Chiroptonyssus venezolanus

Ornithodoros hasei

Parkosa tadarida

Hesperoctenes n. sp. 1

***Eumops glaucinus* (56)**

Chiroptonyssus haematophagus

Chiroptonyssus robustipes *

Periglischrus iheringi *

Ornithodoros hasei *

Beamerella acutascuta

Parkosa tadarida

Hesperoctenes n. sp. 1

Trichobius jubatus *

***Eumops patagonicus* (526)**

Chiroptonyssus haematophagus

Chiroptonyssus venezolanus *

Macronyssus crosbyi *

Macronyssus sp. 3 *

Periglischrus herrerai *

Periglischrus iheringi *

Ornithodoros hasei *

Rhipicephalus sp. *

Beamerella acutascuta

Trombicula dicrura

Trombicula sp.

Ewingana sp. 1

Parkosa maxima

Parkosa tadarida

Hesperoctenes longiceps

Strebla diaemi *

Trichobius jubatus *

***Eumops perotis* (3)**

Chiroptonyssus haematophagus

Hesperoctenes n. sp. 2

***Molossops abrasus* (14)**

Chiroptonyssus robustipes

Chiroptonyssus venezolanus

Steatonyssus joaquimi

Ornithodoros hasei

Hesperoctenes cartus

***Molossops planirostris* (12)**

Chiroptonyssus venezolanus

Chiroptonyssus sp. 1

Ornithodoros hasei

Hesperoctenes minor

***Molossops temminckii* (160)**

Chiroptonyssus haematophagus *

Chiroptonyssus robustipes *

Chiroptonyssus venezolanus

Macronyssus crosbyi *

Macronyssus meridionalis *

Steatonyssus joaquimi *

Spinturnix americanus *

Ornithodoros hasei *

Amblyomma sp. *

Trombicula sp.

Unknown mite

Hesperoctenes parvulus

Trichobius jubatus *

***Molossus ater* (100)**

Chiroptonyssus robustipes

Chiroptonyssus venezolanus *

Chiroptonyssus sp. 1 *

Macronyssus crosbyi *

Unknown macronyssid *

Periglischrus iheringi *

Ornithodoros hasei

Hooperella vesperuginus

Trombicula sp.

Lawrenceocarpus sp.

Parkosa maxima

Parkosa tadarida

Unknown mite

Hesperoctenes fumarius

Hesperoctenes n. sp. 3 *

Basilia sp. (males only) *

Trichobius jubatus

***Molossus currentium* (27)**

Chiroptonyssus haematophagus

Steatonyssus joaquimi *

Ornithodoros hasei

Hesperoctenes fumarius

***Molossus molossus* (228)**

Chiroptonyssus haematophagus

Macronyssoides conciliatus *

Macronyssus crosbyi *

Macronyssus sp. 3 *

Steatonyssus furmani *

Ornithodoros hasei *

Beamerella acutascuta

Parkosa maxima

Parkosa tadarida

Unknown mite

Hesperoctenes fumarius

Hesperoctenes n. sp. 3 *

Trichobius jubatus

***Nyctinomops laticaudatus* (42)**

Chiroptonyssus haematophagus

Chiroptonyssus venezolanus

Ornithodoros hasei

Amblyomma sp. *

Trombicula sp.

Ewingana sp. 1

Hesperoctenes setosus

Hormopsylla fosteri

Rothschildopsylla noctilionis

***Promops centralis* (4)**

Chiroptonyssus haematophagus

Hesperoctenes angustatus

***Promops nasutus* (8)**

Chiroptonyssus haematophagus

APPENDIX C

PARASITE-HOST LIST

Host species followed by an asterisk (*) indicate that this is probably a non-primary host species association that represents a transitory relationship or the result of contamination. In general, these relationships were defined by an incidence < 5%. For very small mites of the Trombiculidae, Chirodiscidae, and Myobiidae that rarely were collected in our samples, no judgment could be rendered with respect to primary host associations. Therefore, none of these taxa were labeled with asterisks. Total number of individuals of each ectoparasite family and species (in bold) collected over the course of the project are in parentheses.

Macronyssidae (9766)

***Chiroptonyssus haematophagus* (3272)**

*Noctilio albiventris **

Noctilio leporinus

*Artibeus jamaicensis **

*Artibeus lituratus **

*Platyrrhinus lineatus **

*Pygoderma bilabiatum **

*Sturnira lilium **

*Eptesicus furinalis **

Histiotus macrotus

Lasiurus blossevillii

*Myotis albescens **

*Myotis nigricans **

Eumops bonariensis

Eumops dabbenei

Eumops glaucinus

Eumops patagonicus

Eumops perotis

*Molossops temminckii **

Molossus currentium

Molossus molossus

Nyctinomops laticaudatus

Promops centralis

Promops nasutus

***Chiroptonyssus robustipes* (560)**

Noctilio albiventris

*Myotis nigricans **

*Eumops glaucinus **

Molossops abrasus

*Molossops temminckii **

Molossus ater

***Chiroptonyssus venezolanus* (580)**

*Glossophaga soricina **

*Artibeus lituratus **

Eptesicus brasiliensis

*Eptesicus furinalis **

Eumops dabbenei

*Eumops patagonicus **

Molossops abrasus

Molossops planirostris

Molossops temminckii

*Molossus ater **

Nyctinomops laticaudatus

***Chiroptonyssus* sp. 1 (2)**

Molossops planirostris

*Molossus ater **

***Macronyssoides conciliatus* (140)**

Carollia perspicillata *

Platyrrhinus lineatus

Molossus molossus *

***Macronyssoides kochi* (711)**

Carollia perspicillata *

Artibeus fimbriatus

Artibeus jamaicensis

Artibeus lituratus

Platyrrhinus lineatus

Pygoderma bilabiatum *

Sturnira lilium *

***Macronyssoides* sp. 1 (1)**

Pygoderma bilabiatum *

***Macronyssus crosbyi* (1091)**

Noctilio albiventris *

Diaemus youngi *

Platyrrhinus lineatus *

Eptesicus furinalis *

Myotis albescens

Myotis nigricans

Myotis riparius

Eumops patagonicus *

Molossops temminckii *

Molossus ater *

Molossus molossus *

***Macronyssus meridionalis* (48)**

Lasiurus cinereus

Myotis nigricans *

Myotis riparius

Molossops temminckii *

***Macronyssus* sp. 1 (8)**

Myotis simus

***Macronyssus* sp. 2 (3)**

Myotis nigricans *

***Macronyssus* sp. 3 (6)**

Carollia perspicillata *

Eumops patagonicus *

Molossus molossus *

***Parichoronyssus crassipes* (47)**

Tonatia bidens

Carollia perspicillata

Platyrrhinus lineatus *

Sturnira lilium *

***Parichoronyssus cyrtosternum* (2)**

Eptesicus furinalis *

***Parichoronyssus euthysternum* (862)**

Carollia perspicillata *

Desmodus rotundus *

Artibeus fimbriatus *

Artibeus lituratus *

Pygoderma bilabiatum *

Sturnira lilium

Myotis albescens *

Eumops bonariensis *

***Parichoronyssus sclerus* (3)**

Tonatia brasiliense

Desmodus rotundus *

***Radfordiella desmodi* (105)**

Desmodus rotundus

*Diaemus youngi **

***Radfordiella oudemansi* (68)**

Diaemus youngi

***Steatonyssus furmani* (422)**

*Platyrrhinus lineatus **

*Eptesicus furinalis **

Lasiurus blossevillii

Lasiurus ega

*Myotis nigricans **

*Molossus molossus **

***Steatonyssus joaquimi* (1719)**

*Artibeus lituratus **

*Platyrrhinus lineatus **

*Sturnira lilium **

Eptesicus brasiliensis

Eptesicus diminutus

Eptesicus furinalis

Histiotus macrotus

Lasiurus blossevillii

Myotis albescens

Myotis nigricans

Myotis riparius

*Molossops abrasus **

*Molossops temminckii **

*Molossus currentium **

***Steatonyssus* sp. 1 (11)**

*Noctilio albiventris **

Noctilio leporinus *

***Steatonyssus* sp. 2 (26)**

Noctilio albiventris

Myotis albescens *

Myotis nigricans *

Unknown macronyssid (79)

Noctilio albiventris *

Chrotopterus auritus

Glossophaga soricina *

Carollia perspicillata *

Sturnira lilium *

Myotis nigricans *

Molossus ater *

Spinturnicidae (1763)

***Periglischrus caligus* (10)**

Glossophaga soricina

***Periglischrus herrerai* (5)**

Desmodus rotundus

Eumops patagonicus *

***Periglischrus iheringi* (1122)**

Carollia perspicillata *

Artibeus fimbriatus

Artibeus jamaicensis

Artibeus lituratus

Chiroderma doriae

Platyrrhinus lineatus

Pygoderma bilabiatum *

Sturnira lilium *

Eptesicus furinalis *

Eumops glaucinus *

Eumops patagonicus *

Molossus ater *

***Periglischrus natali* (1)**

Natalus stramineus

***Periglischrus ojasti* (504)**

Glossophaga soricina *

Carollia perspicillata *

Artibeus fimbriatus *

Artibeus lituratus *

Platyrrhinus lineatus *

Sturnira lilium

Myotis nigricans *

***Periglischrus tonatii* (6)**

Tonatia bidens

***Spinturnix americanus* (63)**

Myotis albescens

Myotis nigricans

Myotis riparius

Myotis simus

Molossops temminckii *

***Spinturnix banksi* (6)**

Myotis albescens

***Spinturnix orri* (15)**

Platyrrhinus lineatus *

Eptesicus furinalis

***Spinturnix surinamensis* (28)**

Eptesicus furinalis

Unknown spinturnicid (3)

Carollia perspicillata *

Desmodus rotundus *

Pygoderma bilabiatum *

Argasidae (1195)

***Amblyomma* sp. (3)**

Eptesicus diminutus *

Molossops temminckii *

Nyctinomops laticaudatus *

***Ornithodoros hasei* (1192)**

Noctilio albiventris

Noctilio leporinus

Desmodus rotundus *

Artibeus jamaicensis

Sturnira lilium *

Eptesicus brasiliensis

Eptesicus furinalis

Myotis albescens *

Myotis nigricans *

Eumops dabbenei *

Eumops glaucinus *

Eumops patagonicus *

Molossops abrasus

Molossops planirostris

Molossops temminckii *

Molossus ater

Molossus currentium

Molossus molossus *

Nyctinomops laticaudatus

Ixodidae (3)

***Rhipicephalus* sp. (2)**

Sturnira lilium *

Eumops patagonicus *

Unknown ixodid (1)

Carollia perspicillata *

Trombiculidae (200)

***Beamerella acutascuta* (27)**

Artibeus fimbriatus

Artibeus jamaicensis

Sturnira lilium

Eptesicus furinalis

Eumops glaucinus

Eumops patagonicus

Molossus molossus

***Euschoengastia megastyrax* (1)**

Artibeus lituratus

***Eutrombicula* sp. (1)**

Sturnira lilium

***Hooperella vesperuginus* (4)**

Sturnira lilium

Molossus ater

***Perisopalla precaria* (1)**

Sturnira lilium

***Trombicula dicrura* (70)**

Artibeus jamaicensis

Sturnira lilium

Eumops patagonicus

***Trombicula* sp. 1 (69)**

Chrotopterus auritus

***Trombicula* sp. (27)**

Artibeus jamaicensis

Sturnira lilium

Eumops patagonicus

Molossops temminckii

Molossus ater

Nyctinomops laticaudatus

Myobiidae (12)

***Eudusbabekia lepidoseta* (3)**

Sturnira lilium

***Eudusbabekia viguerasi* (4)**

Artibeus fimbriatus

Artibeus jamaicensis

Artibeus lituratus

***Eudusbabekia* sp. (2)**

Pygoderma bilabiatum

***Ewingana* sp. 1 (2)**

Eumops patagonicus

***Ewingana* sp. 2 (1)**

Nyctinomops laticaudatus

Chirodiscidae (1387)

***Labidocarpus* sp. (13)**

Lasiurus ega

Eumops bonariensis

***Lawrenceocarpus* sp. (19)**

Noctilio albiventris

Molossus ater

***Parkosa maxima* (185)**

Artibeus jamaicensis *

Artibeus lituratus *

Eumops patagonicus

Molossus ater

Molossus molossus

***Parkosa tadarida* (1140)**

Noctilio leporinus

Lasiurus ega

Eumops dabbenei

Eumops glaucinus

Eumops patagonicus

Molossus ater

Molossus molossus

***Pseudolabidocarpus* sp. (30)**

Glossophaga soricina

Carollia perspicillata

Unknown mites (13)

Noctilio leporinus

Glossophaga soricina

Artibeus lituratus

Lasiurus ega

Myotis albescens

Molossops temminckii

Molossus ater

Molossus molossus

Polyctenidae (561)

***Hesperoctenes angustatus* (3)**

Promops centralis

***Hesperoctenes cartus* (7)**

Molossops abrasus

***Hesperoctenes fumarius* (163)**

Molossus ater

Molossus currentium

Molossus molossus

***Hesperoctenes longiceps* (147)**

Eumops patagonicus

***Hesperoctenes minor* (9)**

Molossops planirostris

***Hesperoctenes parvulus* (53)**

Molossops temminckii

***Hesperoctenes setosus* (4)**

Nyctinomops laticaudatus

***Hesperoctenes* n. sp. 1 (167)**

Eumops dabbenei

Eumops glaucinus

***Hesperoctenes* n. sp. 2 (5)**

Eumops perotis

***Hesperoctenes* n. sp. 3 (3)**

Molossus ater

Molossus molossus

Nycteribiidae (155)

***Basilia* sp. 1 (5)**

Eptesicus furinalis *

Myotis albescens

***Basilia* sp. 2 (22)**

Myotis albescens *

Myotis nigricans

Myotis riparius

***Basilia* sp. 3 (62)**

Myotis albescens

Myotis nigricans

Myotis riparius

Eptesicus furinalis *

***Basilia* sp. 4 (12)**

Eptesicus furinalis

***Basilia* sp. 5 (11)**

Eptesicus brasiliensis

Eptesicus furinalis *

Basilia sp. 6 (1)

Myotis albescens

***Basilia* spp. (males only) (42)**

Eptesicus brasiliensis

Eptesicus diminutus

Eptesicus furinalis

Histiotus macrotus

Myotis albescens

Myotis nigricans

Molossus molossus *

Streblidae (2469)

***Aspidoptera falcata* (233)**

Artibeus fimbriatus *

Artibeus lituratus *

Platyrrhinus lineatus *

Sturnira lilium

***Aspidoptera phyllostomatis* (29)**

Artibeus fimbriatus

Artibeus jamaicensis

Artibeus lituratus *

***Mastoptera minuta* (11)**

Tonatia brasiliense

***Megistopoda aranea* (107)**

Artibeus fimbriatus

Artibeus jamaicensis

*Artibeus lituratus **

*Sturnira lilium **

***Megistopoda proxima* (364)**

*Artibeus fimbriatus **

*Artibeus lituratus **

*Carollia perspicillata **

*Platyrrhinus lineatus **

Sturnira lilium

***Metelasmus pseudopterus* (21)**

Artibeus fimbriatus

*Artibeus jamaicensis **

*Artibeus lituratus **

***Metelasmus paucisetus* (5)**

Sturnira lilium

***Noctiliostrebla aitkeni* (80)**

Noctilio leporinus

*Sturnira lilium **

***Noctiliostrebla dubia* (16)**

Noctilio leporinus

***Noctiliostrebla maai* (213)**

Noctilio albiventris

***Paradyschiria fusca* (227)**

Noctilio leporinus

***Paradyschiria parvula* (434)**

Noctilio albiventris

Paratrichobius longicrus **(159)**

Artibeus lituratus

Platyrrhinus lineatus *

Sturnira lilium *

Speiseria ambigua **(1)**

Glossophaga soricina

Strebla chrotopteri **(15)**

Chrotopterus auritus

Strebla diaemi **(38)**

Diaemus youngi

Eumops patagonicus *

Strebla guajiro **(31)**

Glossophaga soricina

Carollia perspicillata

Artibeus fimbriatus *

Strebla weidemanni **(76)**

Desmodus rotundus

Trichobius angulatus **(10)**

Platyrrhinus lineatus

Trichobius diaemi **(5)**

Diaemus youngi

Trichobius dugesii **(8)**

Glossophaga soricina

Trichobius galei **(6)**

Natalus stramineus

Trichobius joblingi **(67)**

Tonatia bidens

Carollia perspicillata

***Trichobius jubatus* (80)**

Eumops glaucinus *

Eumops patagonicus *

Molossops temminckii *

Molossus ater

Molossus molossus

***Trichobius parasiticus* (219)**

Desmodus rotundus

***Trichobius uniformis* (8)**

Glossophaga soricina

***Xenotrichobius noctilionis* (6)**

Noctilio albiventris

Ischnopsyllidae (32)

***Hormopsylla fosteri* (1)**

Nyctinomops laticaudatus

***Myodopsylla wolffsohni* (26)**

Myotis albescens

Myotis nigricans *

***Rothschildopsylla noctilionis* (5)**

Nyctinomops laticaudatus

APPENDIX D

SPECIES ABUNDANCE DISTRIBUTIONS OF THE ECTOPARASITES ASSEMBLAGES FROM EACH OF 39 HOST SPECIES

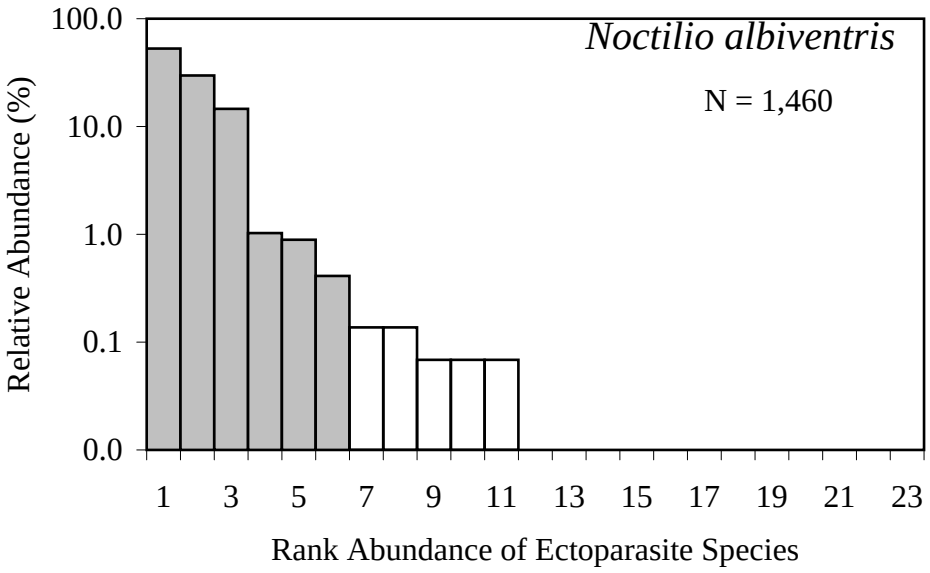

Figure D.1.-- Species abundance distribution of the ectoparasite species collected from *Noctilio albiventris.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

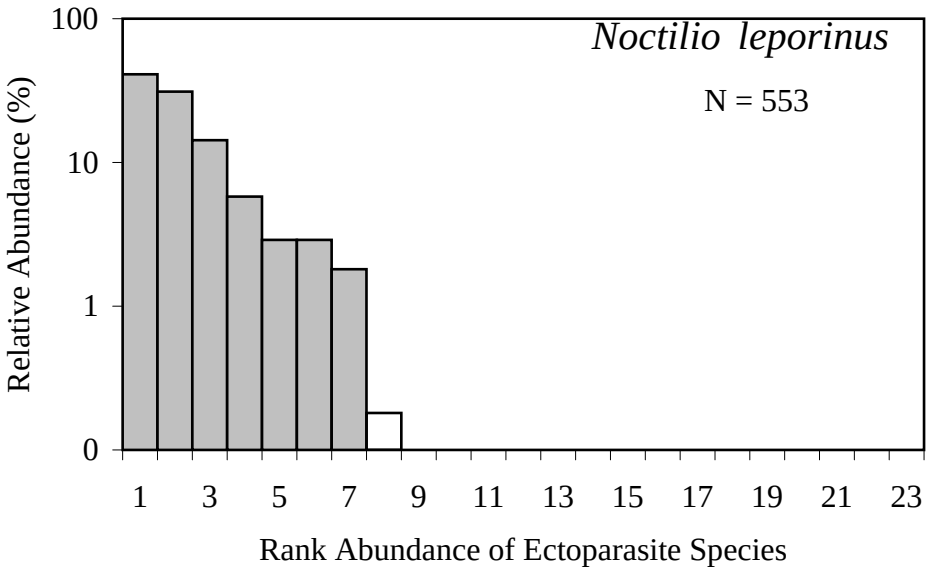

Figure D.2.-- Species abundance distribution of the ectoparasite species collected from *Noctilio leporinus* . N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

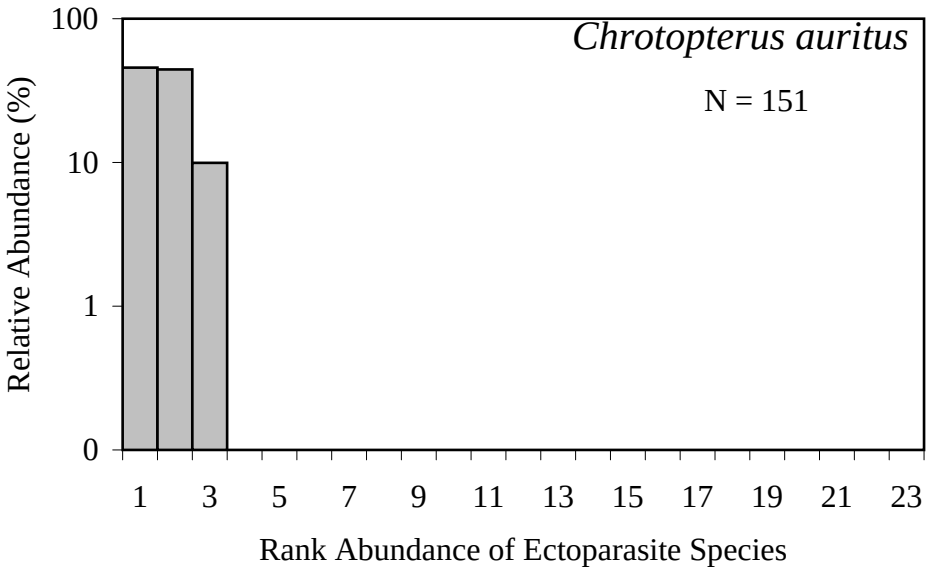

Figure D.3.-- Species abundance distribution of the ectoparasite species collected from *Chrotopterus auritus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

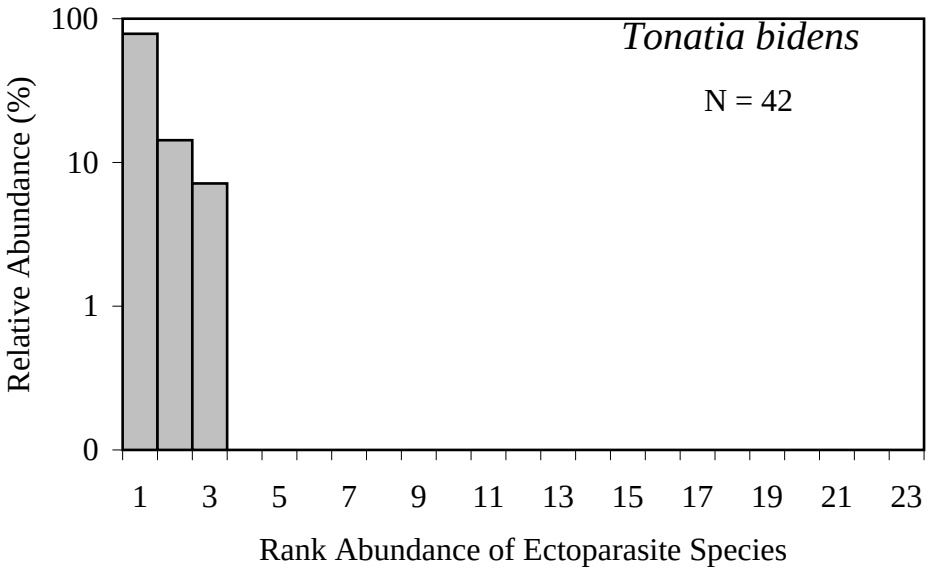

Figure D.4.-- Species abundance distribution of the ectoparasite species collected from *Tonatia bidens.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

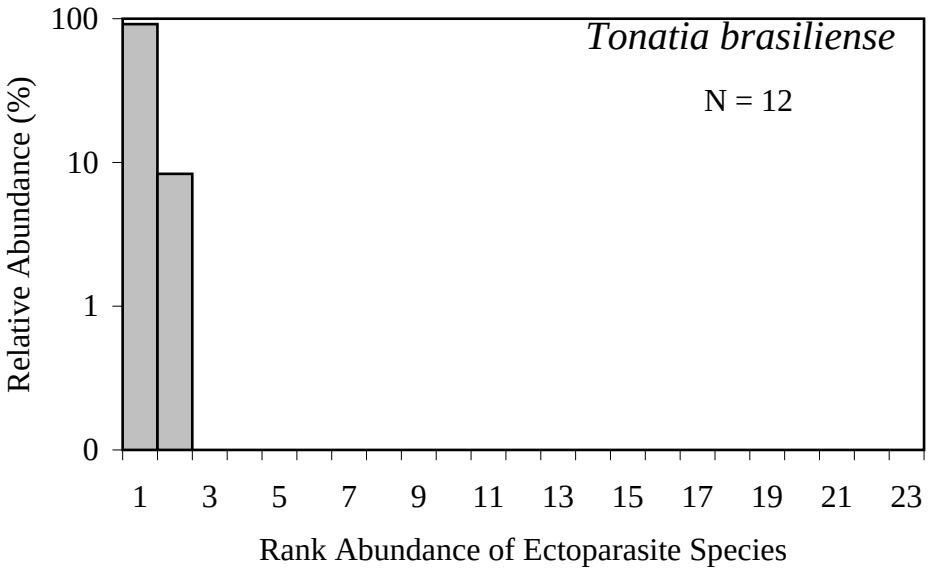

Figure D.5.-- Species abundance distribution of the ectoparasite species collected from *Tonatia brasiliense.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

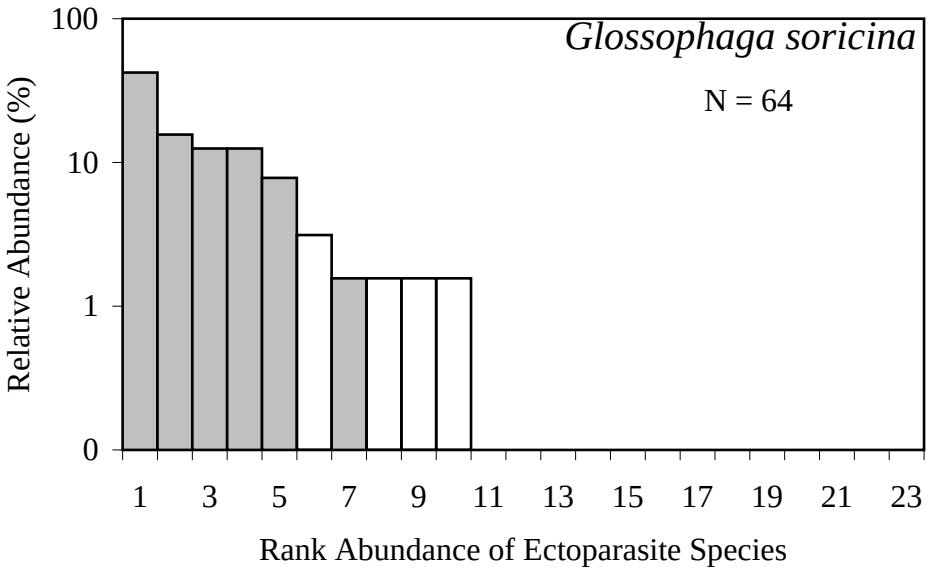

Figure D.6.-- Species abundance distribution of the ectoparasite species collected from *Glossophaga soricina.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

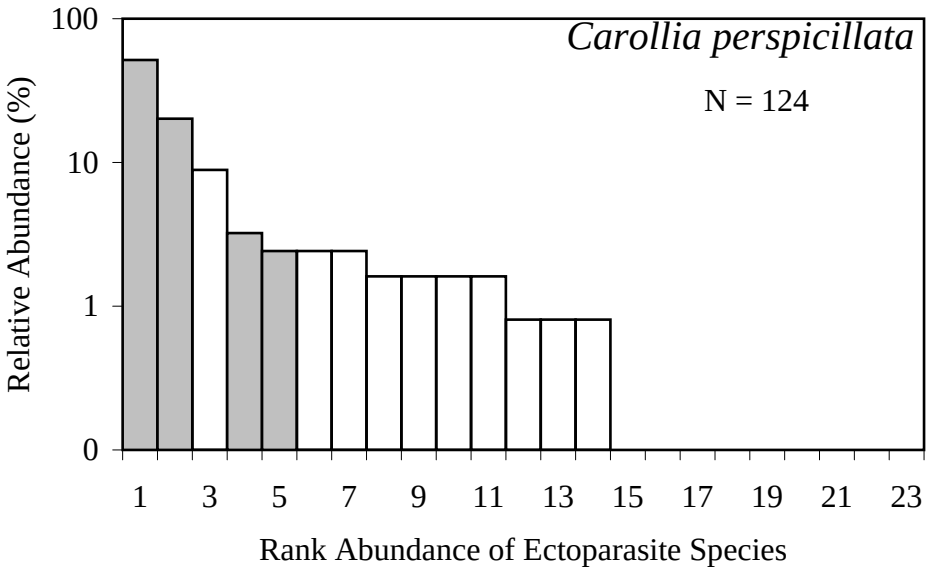

Figure D.7.-- Species abundance distribution of the ectoparasite species collected from *Carollia perspicillata.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

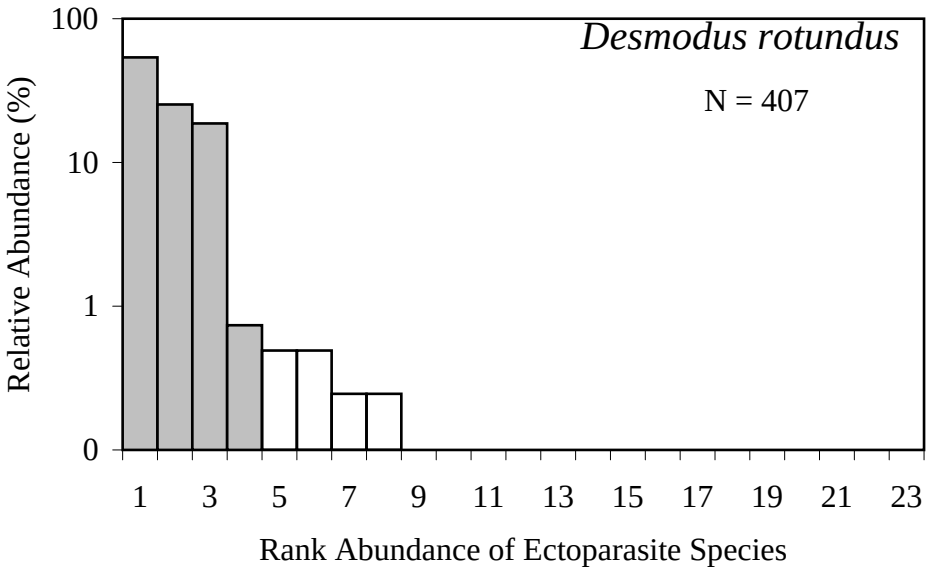

Figure D.8.-- Species abundance distribution of the ectoparasite species collected from *Desmodus rotundus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

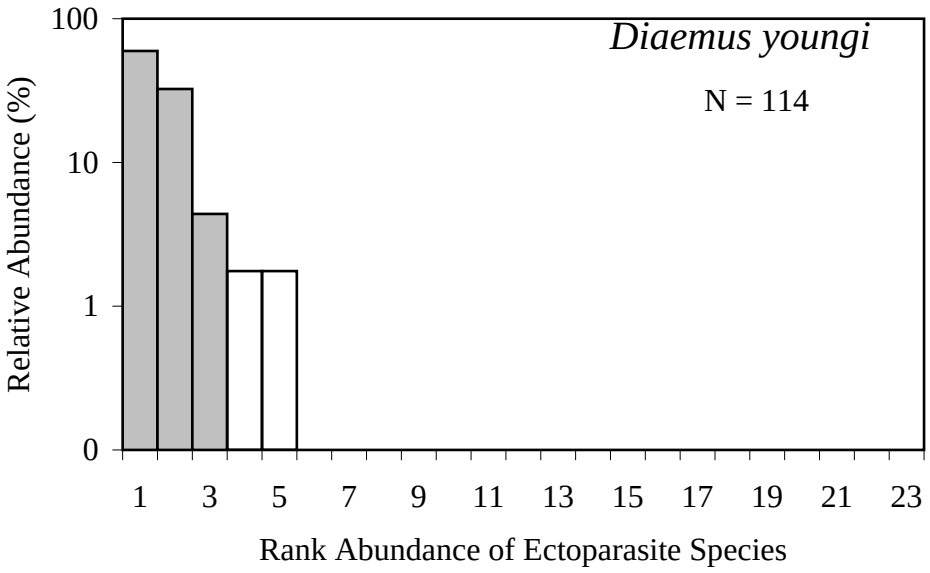

Figure D.9.-- Species abundance distribution of the ectoparasite species collected from *Diaemus youngi.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

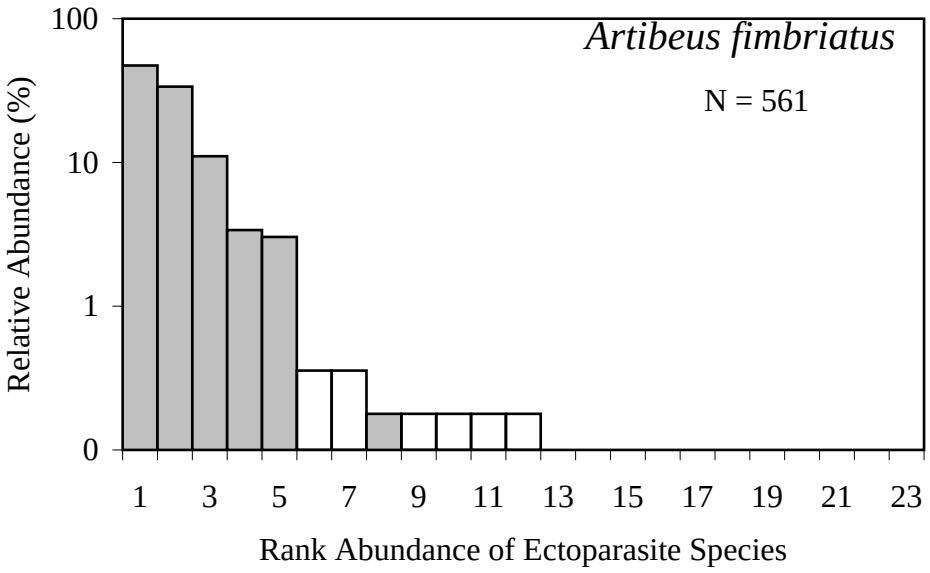

Figure D.10.-- Species abundance distribution of the ectoparasite species collected from *Artibeus fimbriatus*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

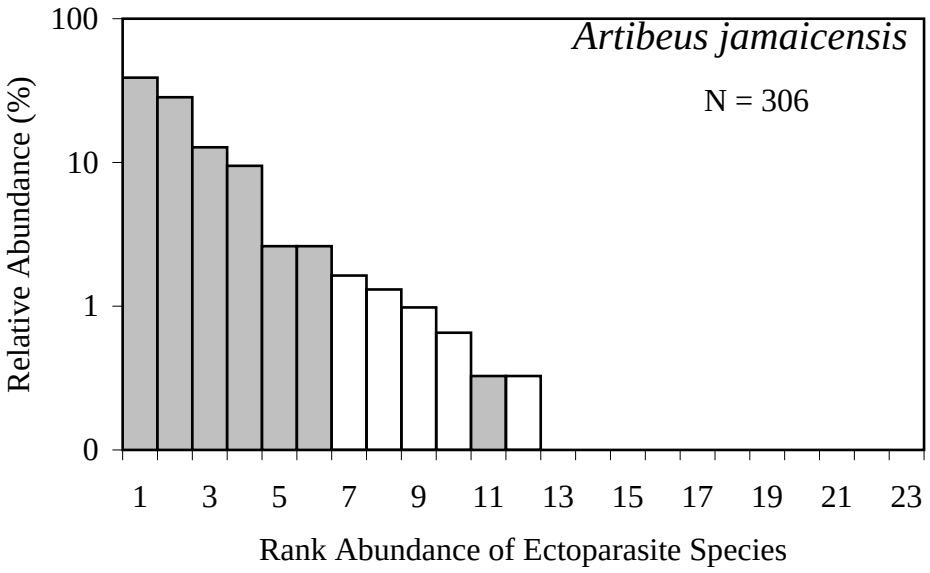

Figure D.11.-- Species abundance distribution of the ectoparasite species collected from *Artibeus jamaicensis.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

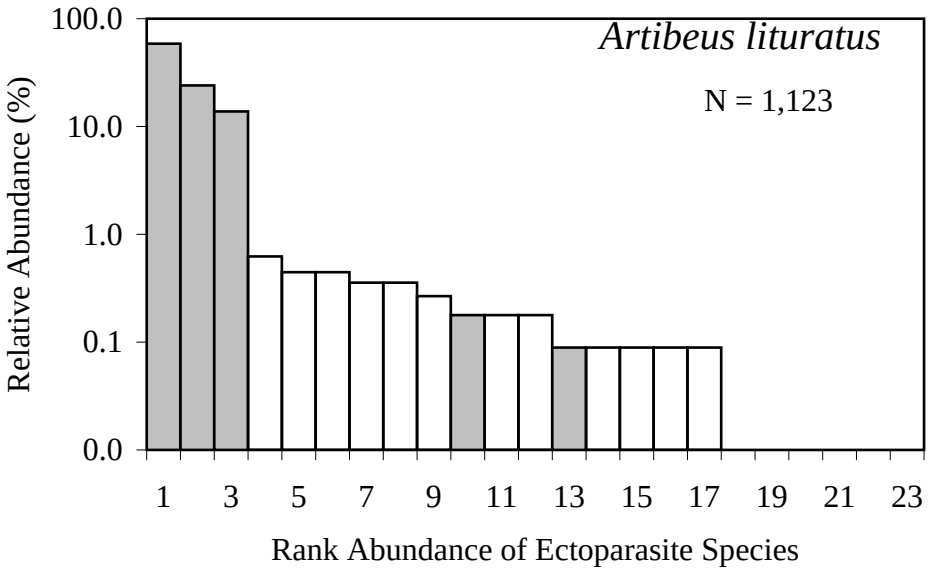

Figure D.12.-- Species abundance distribution of the ectoparasite species collected from *Artibeus lituratus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

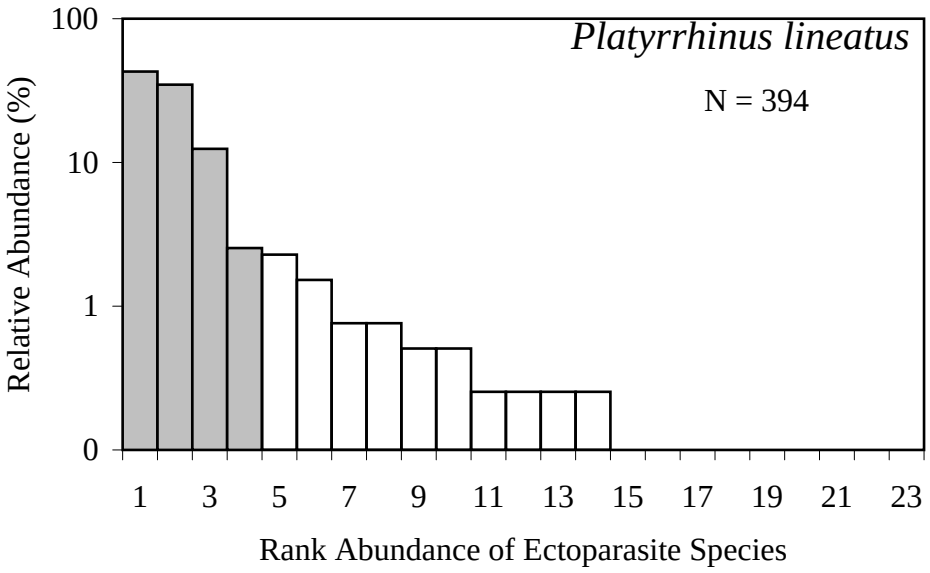

Figure D.13.-- Species abundance distribution of the ectoparasite species collected from *Platyrrhinus lineatus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

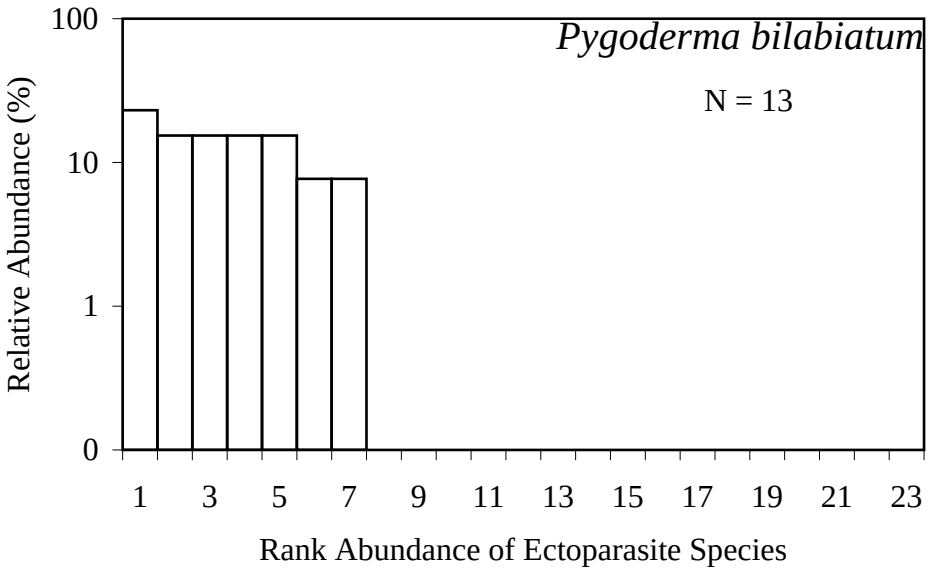

Figure D.14.-- Species abundance distribution of the ectoparasite species collected from *Pygoderma bilabiatum.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

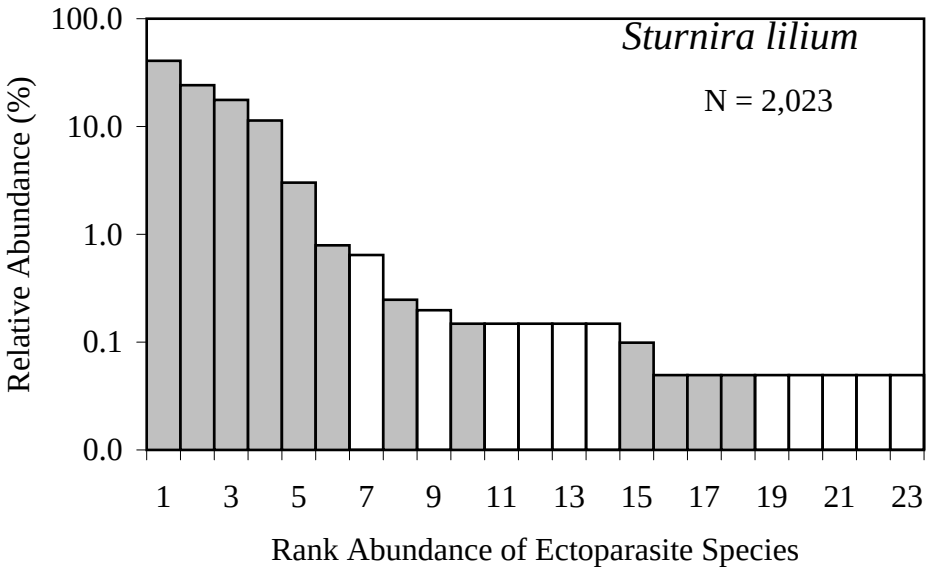

Figure D.15.-- Species abundance distribution of the ectoparasite species collected from *Sturnira lilium.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

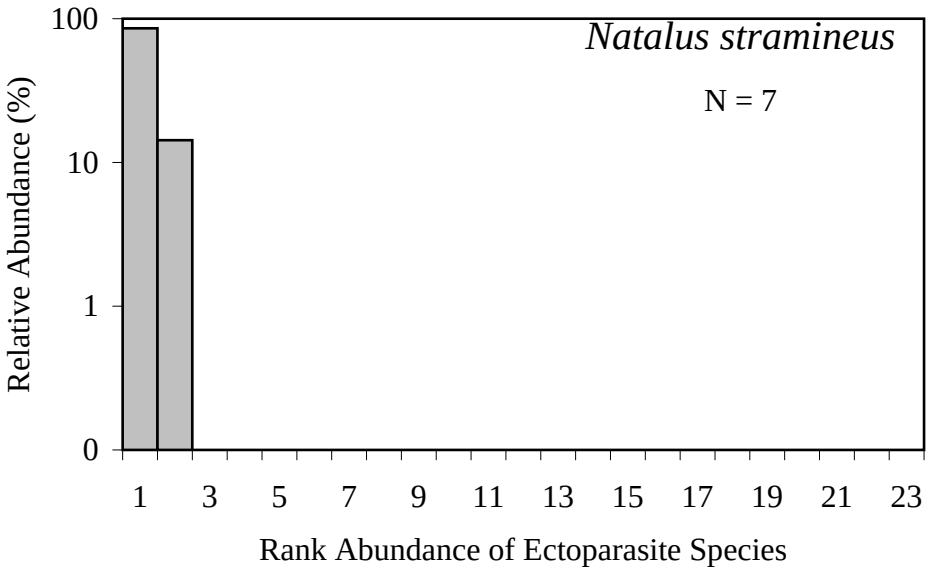

Figure D.16.-- Species abundance distribution of the ectoparasite species collected from *Natalus stramineus*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

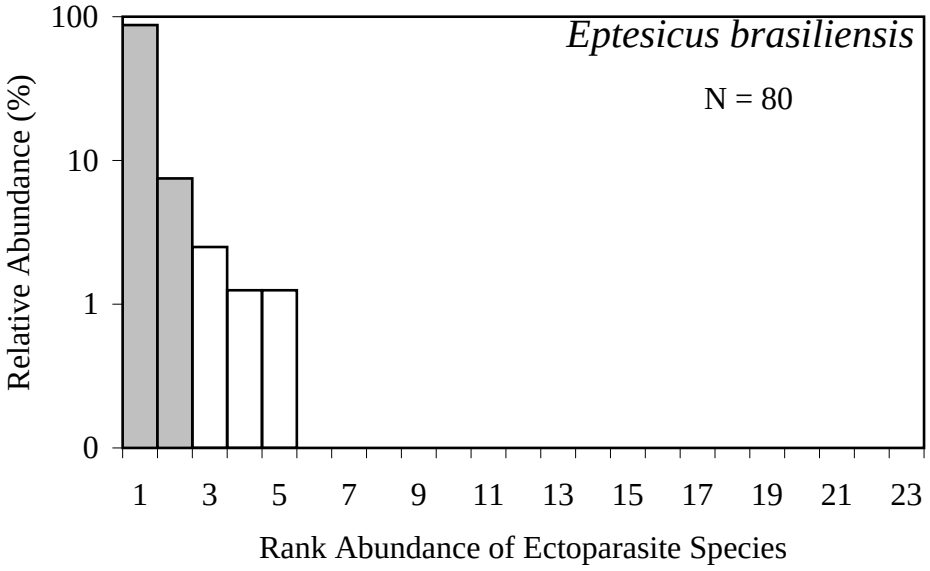

Figure D.17.-- Species abundance distribution of the ectoparasite species collected from *Eptesicus brasiliensis.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

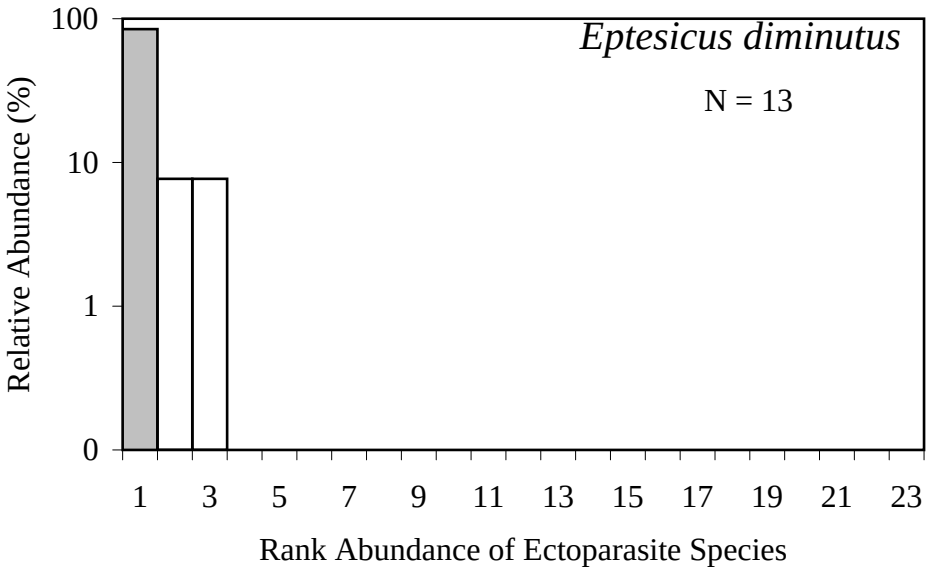

Figure D.18.-- Species abundance distribution of the ectoparasite species collected from *Eptesicus diminutus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

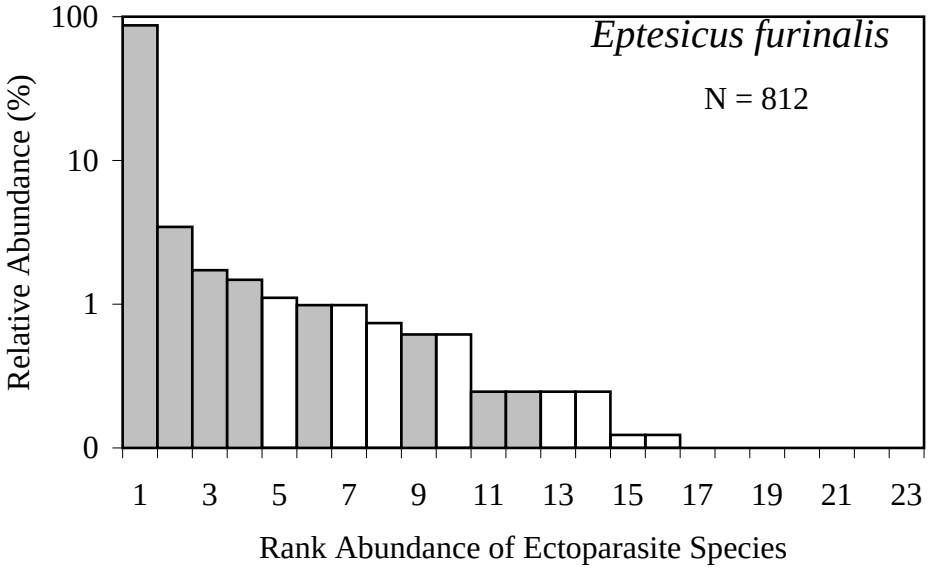

Figure D.19.-- Species abundance distribution of the ectoparasite species collected from *Eptesicus furinalis.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

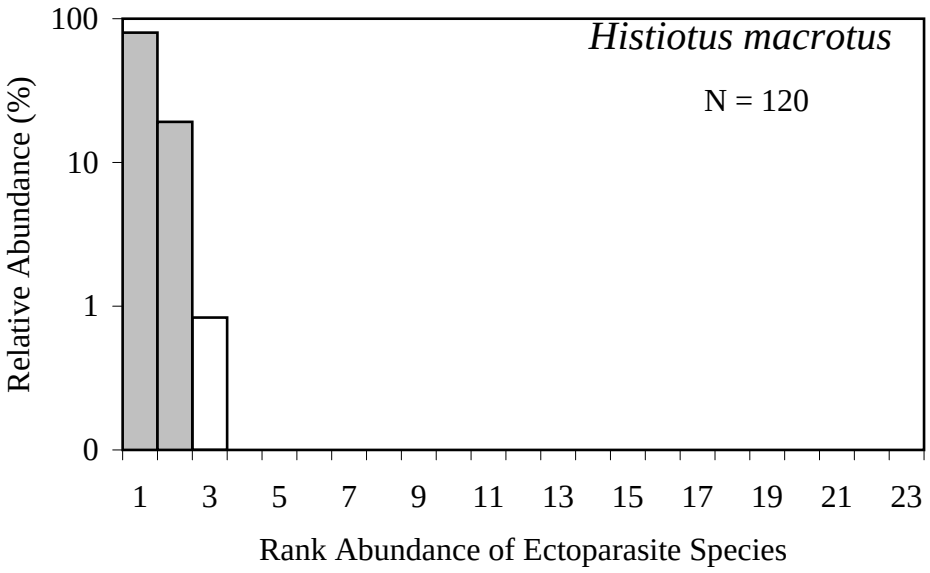

Figure D.20.-- Species abundance distribution of the ectoparasite species collected from *Histiotus macrotus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

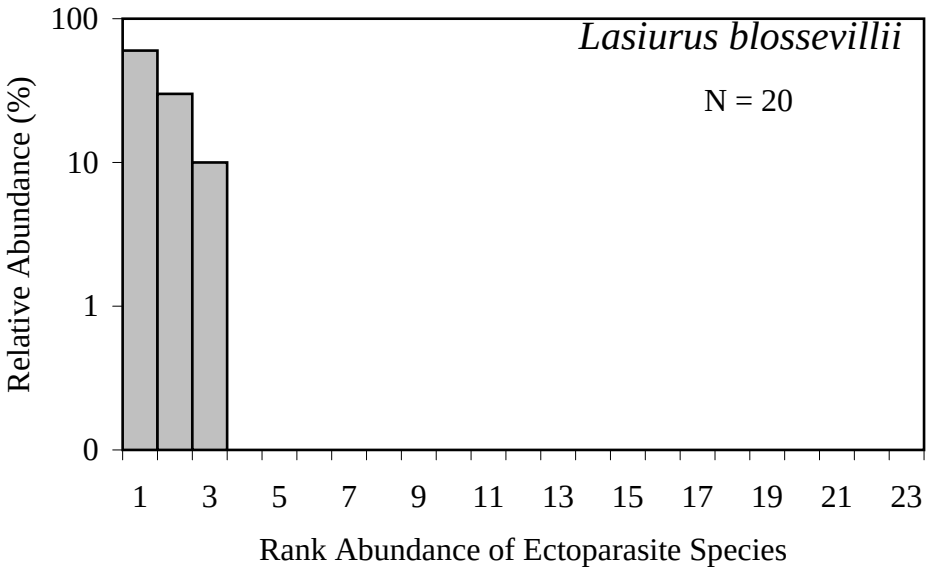

Figure D.21.-- Species abundance distribution of the ectoparasite species collected from *Lasiurus blossevillii*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

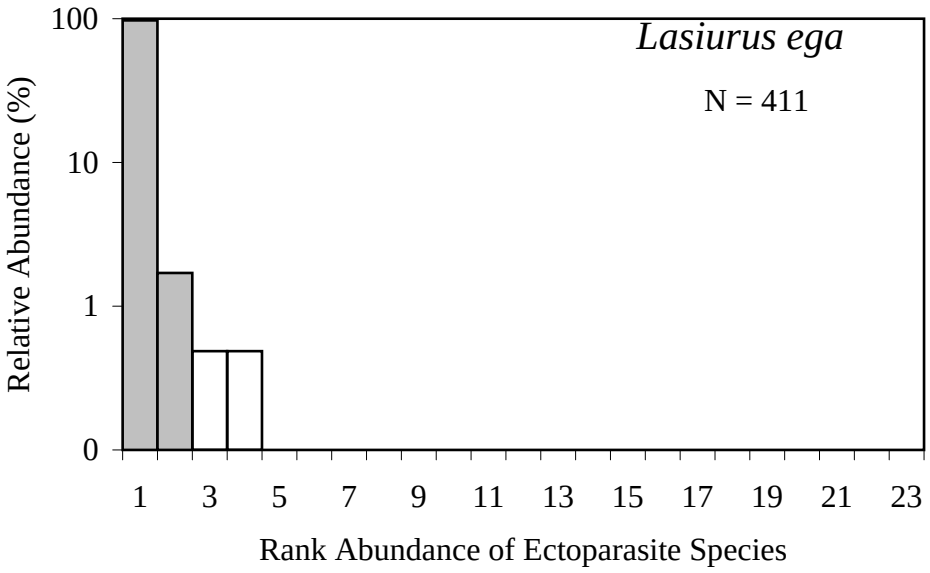

Figure D.22.-- Species abundance distribution of the ectoparasite species collected from *Lasiurus ega.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

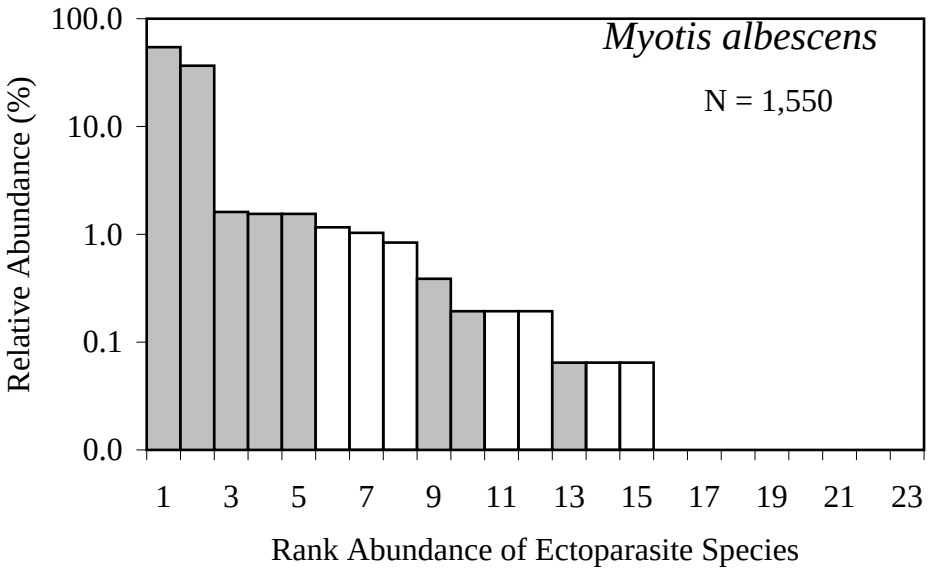

Figure D.23.-- Species abundance distribution of the ectoparasite species collected from *Myotis albescens.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

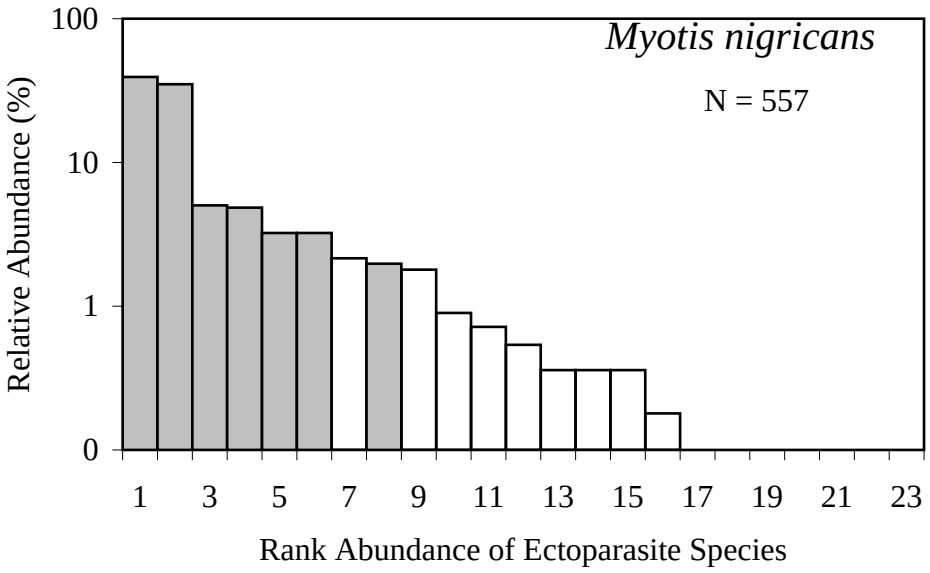

Figure D.24.-- Species abundance distribution of the ectoparasite species collected from *Myotis nigricans*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

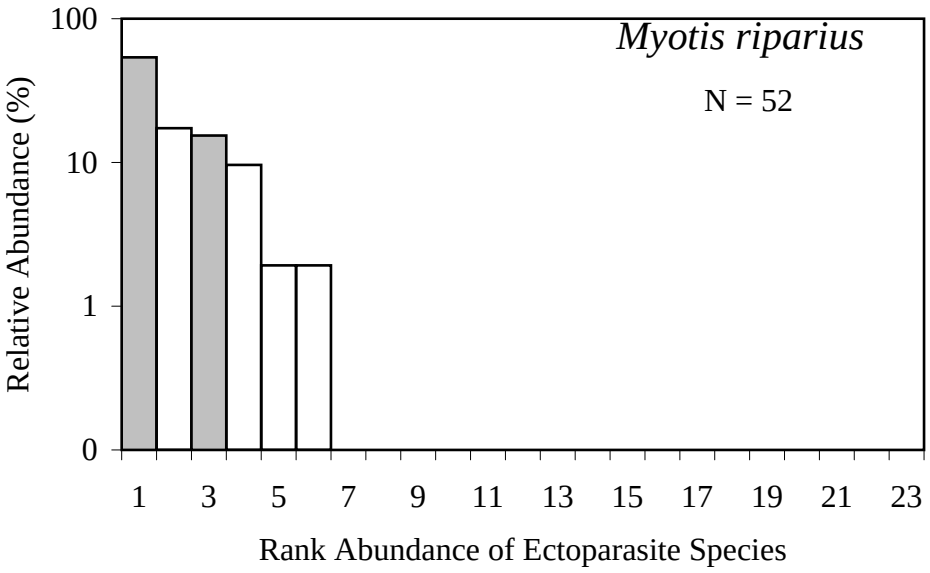

Figure D.25.-- Species abundance distribution of the ectoparasite species collected from *Myotis riparius.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

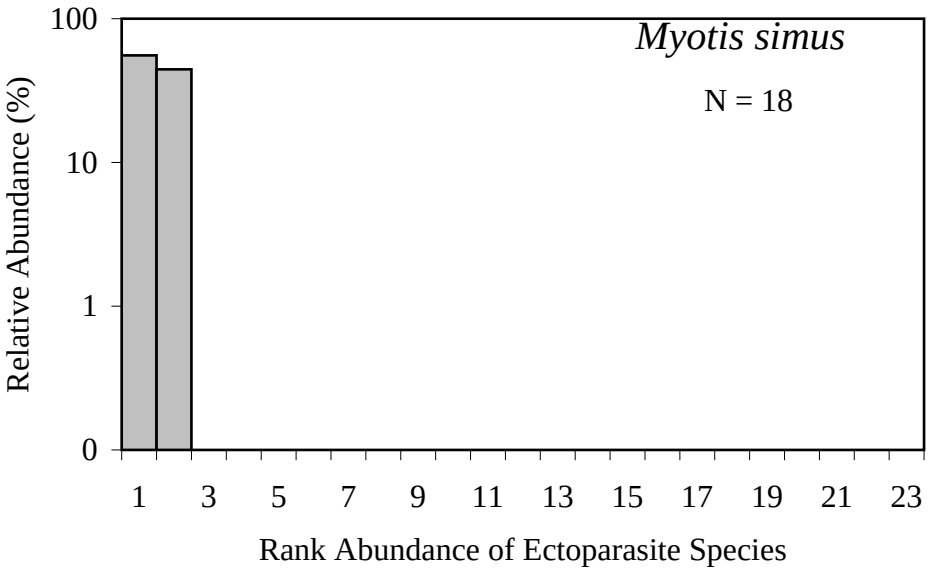

Figure D.26.-- Species abundance distribution of the ectoparasite species collected from *Myotis simus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

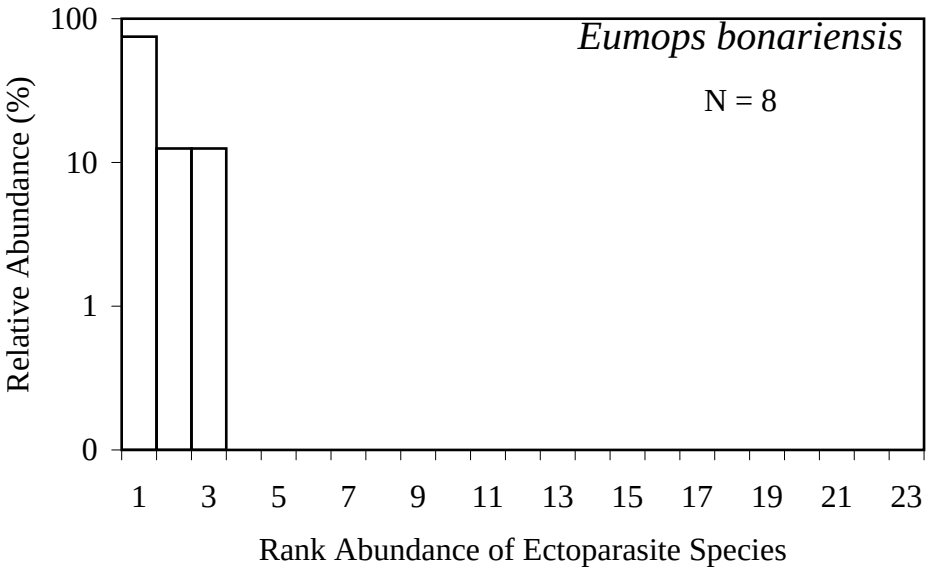

Figure D.27.-- Species abundance distribution of the ectoparasite species collected from *Eumops bonariensis.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

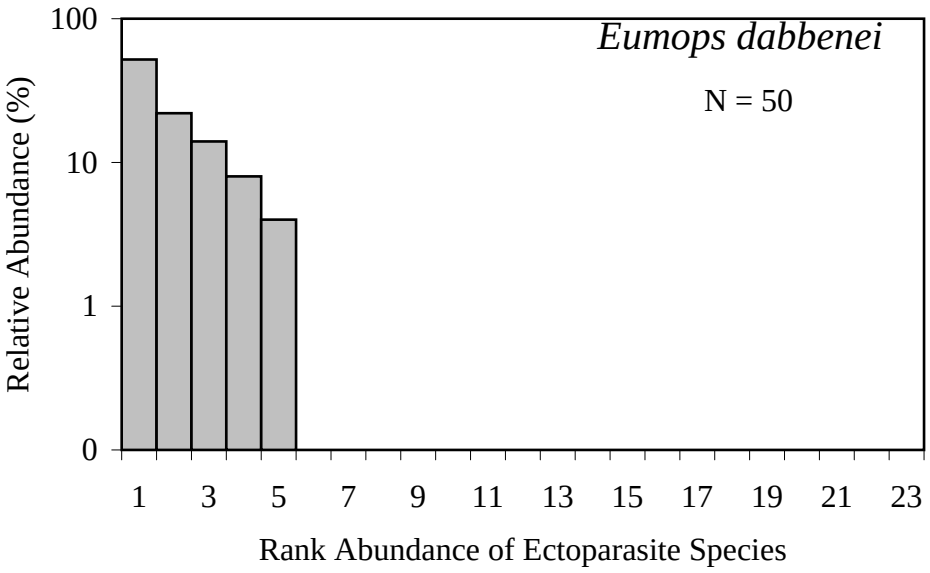

Figure D.28.-- Species abundance distribution of the ectoparasite species collected from *Eumops dabbenei*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

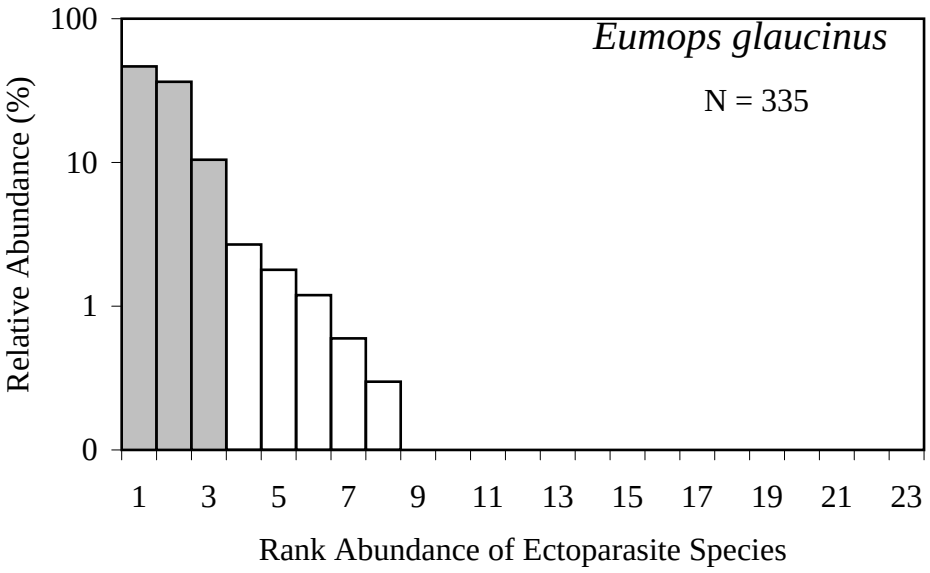

Figure D.29.-- Species abundance distribution of the ectoparasite species collected from *Eumops glaucinus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

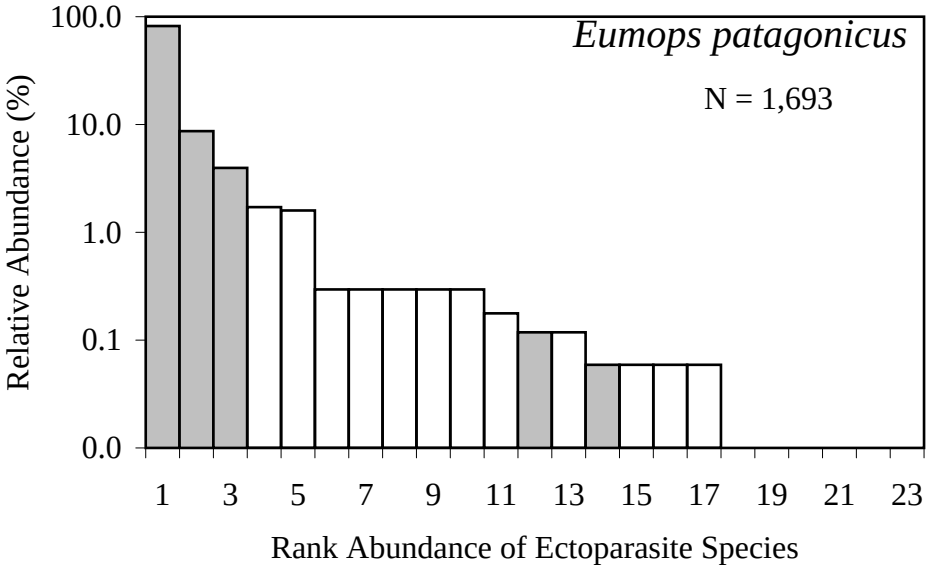

Figure D.30.-- Species abundance distribution of the ectoparasite species collected from *Eumops patagonicus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

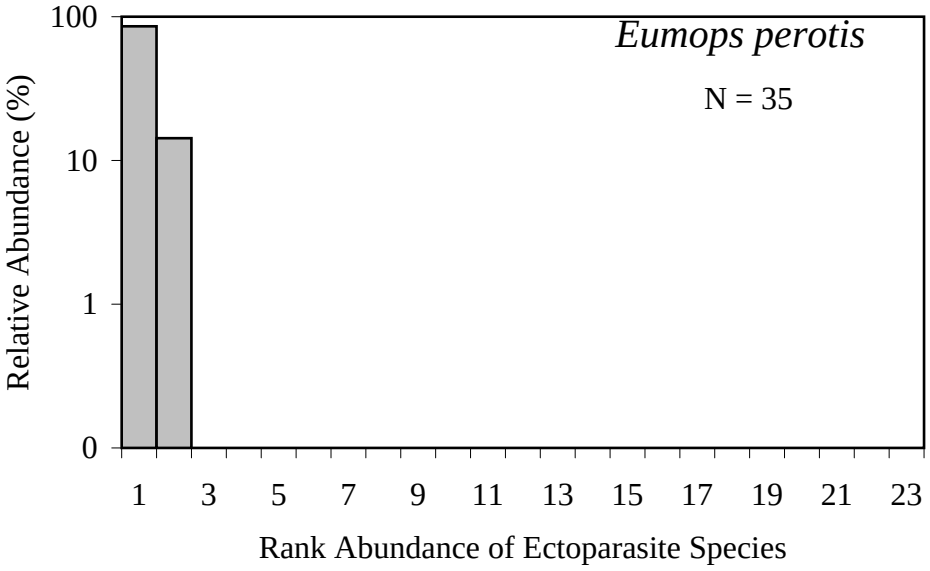

Figure D.31.-- Species abundance distribution of the ectoparasite species collected from *Eumops perotis*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

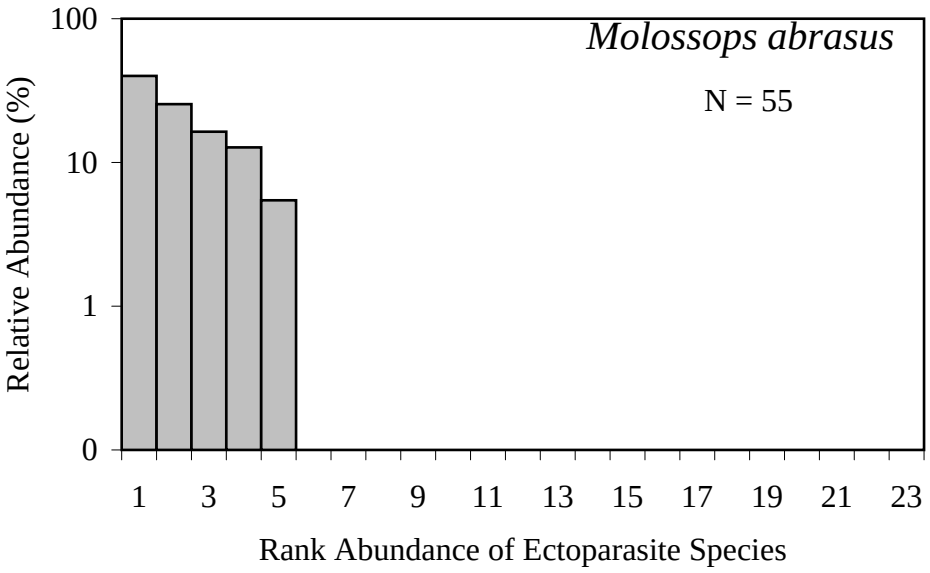

Figure D.32.-- Species abundance distribution of the ectoparasite species collected from *Molossops abrasus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

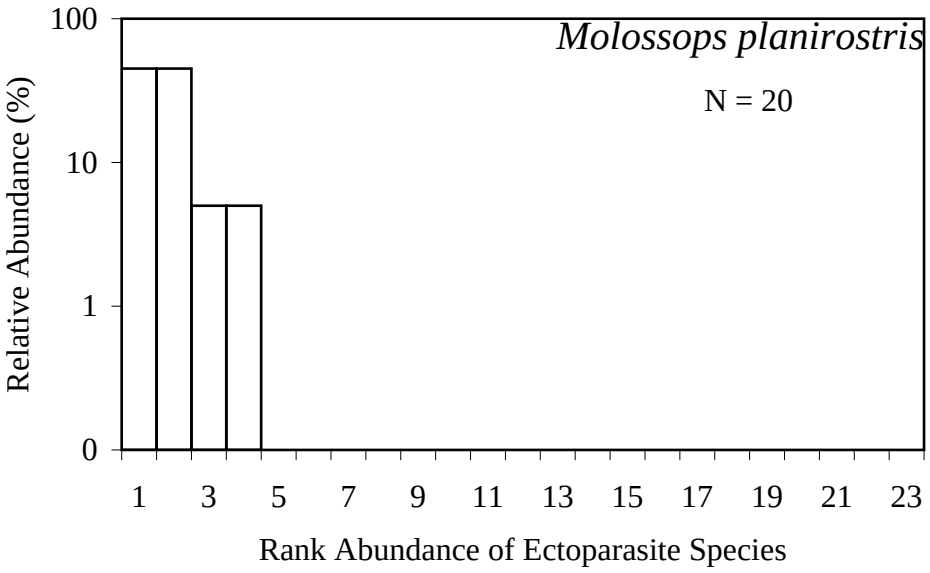

Figure D.33.-- Species abundance distribution of the ectoparasite species collected from *Molossops planirostris.* N = total number of ectoparasites.Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

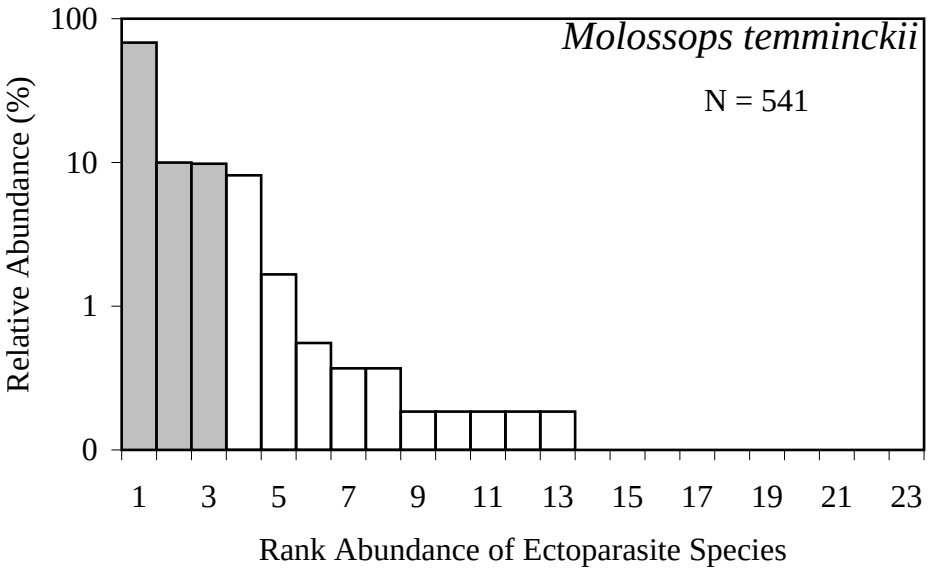

Figure D.34.-- Species abundance distribution of the ectoparasite species collected from *Molossops temminckii*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

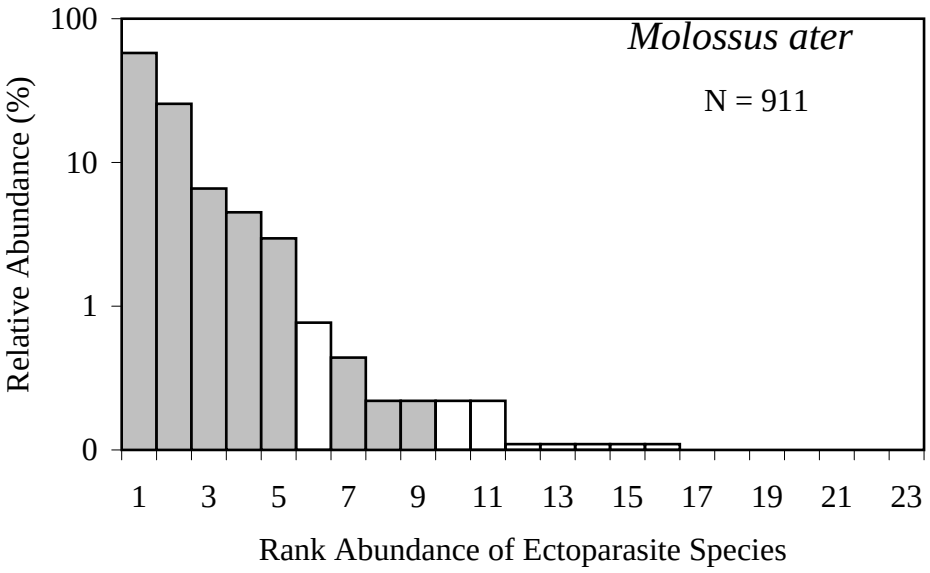

Figure D.35.-- Species abundance distribution of the ectoparasite species collected from *Molossus ater*. N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

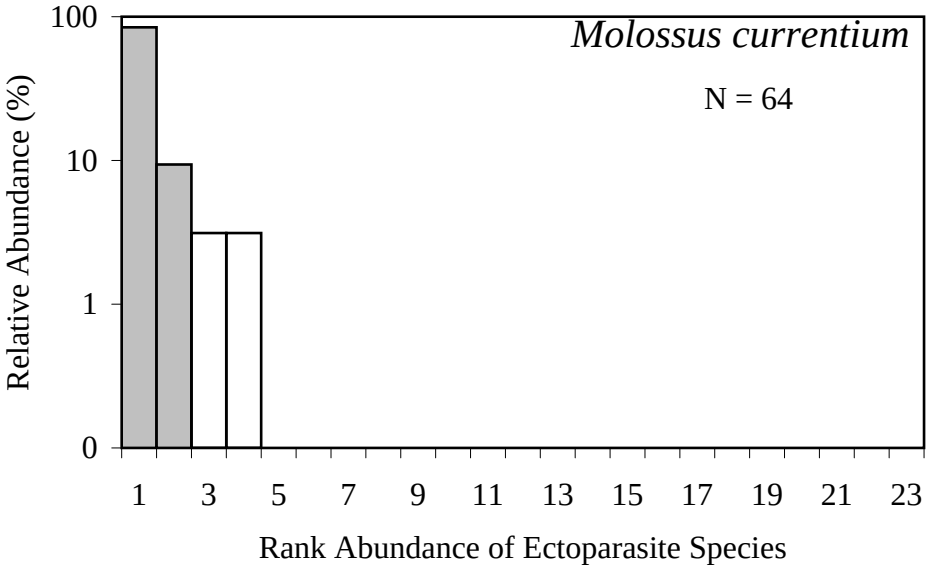

Figure D.36.-- Species abundance distribution of the ectoparasite species collected from *Molossus currentium.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

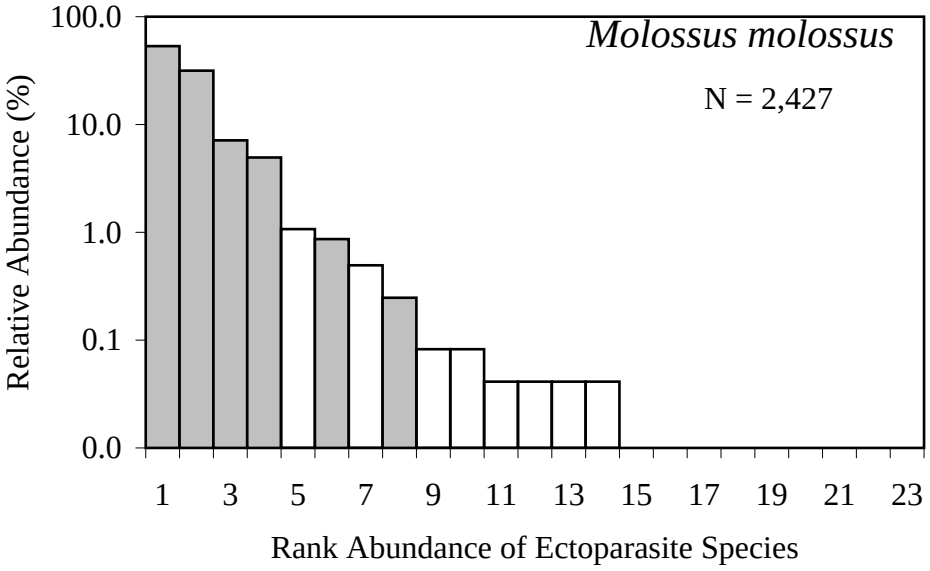

Figure D.37.-- Species abundance distribution of the ectoparasite species collected from *Molossus molossus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

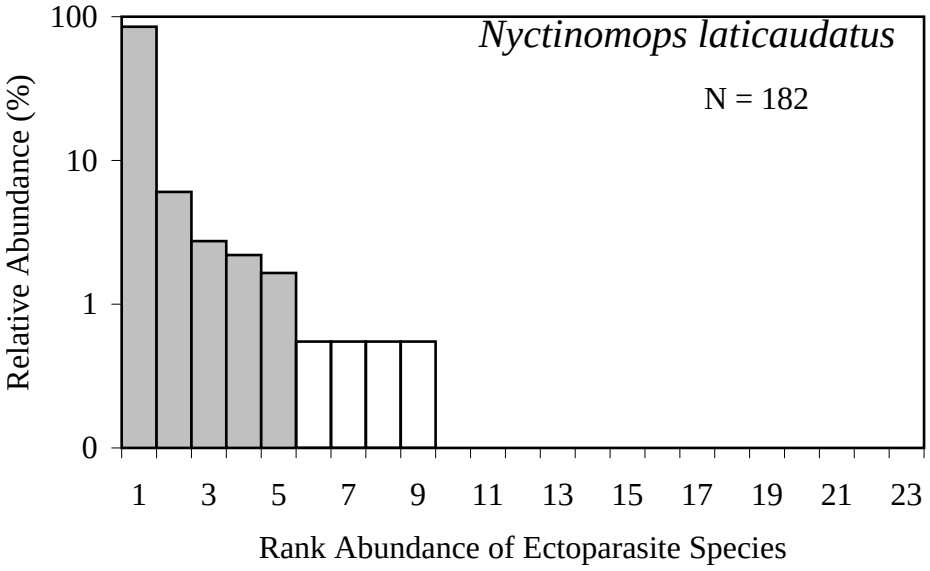

Figure D.38.-- Species abundance distribution of the ectoparasite species collected from *Nyctinomops laticaudatus.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

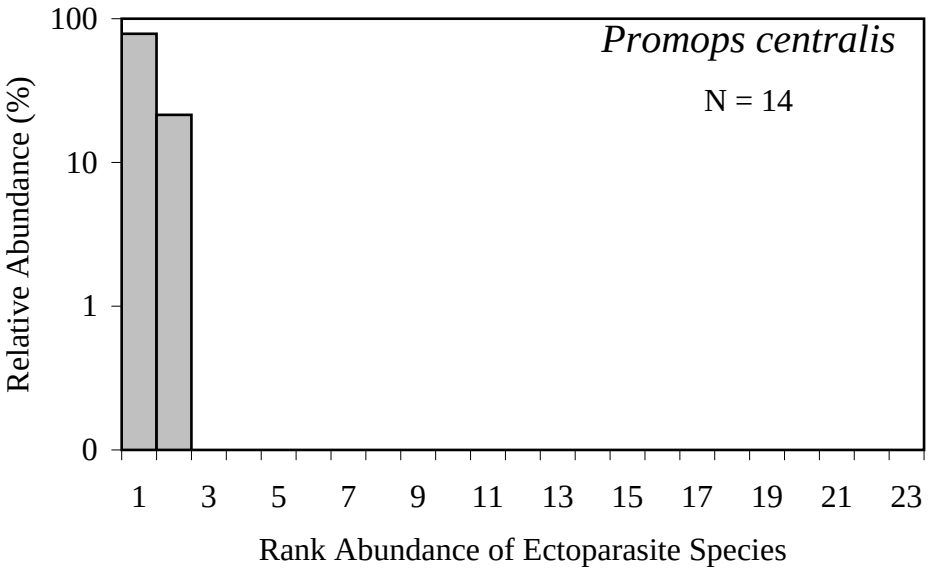

Figure D.39.-- Species abundance distribution of the ectoparasite species collected from *Promops centralis.* N = total number of ectoparasites. Shaded bars represent primary associations; unshaded bars represent transients or contamination. For comparative purposes, all species abundance distributions were graphed to the maximum number of ectoparasite species observed on a single host species (23).

APPENDIX E

MATLAB FUNCTIONS FOR CALCULATING

SPECIES RICHNESS ESTIMATE LOGS

```
%SPEACCUM:      returns [n x 1] vectors of species richness values
%               and plots the number of individuals by number of species given a
%               vector species abundances, the number of iterations and a
%               plot flag value.
%
%       Usage: [richness] = speaccum(x,{iter},{plot_flag})
%
%               richness =      a [n x 1] vector of average species richness
%                                       values (i.e., number of species) for all iter
%                                       iterations.
%
%               ------------------------------------------------------
%               x =                     a vector of species abundances.
%
%               iter =          number of iterations, optional argument, default
%                                       value = 1000.
%
%               plot =          value of 1 produces a plot of average richness
%                                       by number of individuals, default value = 1.
%
function [richness] = speaccum(x,iter,plot_flag)
        tic;
        if nargin<2                     %optional arguments
                iter = 1000;
        end;
        if nargin<3
                plot_flag = 1;
        end;

        [r,c] = size(x); %error checking

        if min(r,c)>1
                error('SPEACCUM:input must in a vector, not a matrix');
        end;

        if c~=1
                x=x';
        end;
```

```
riches = zeros(sum(x),iter);

ctr=0;
iterations=0;

for i=1:iter
        species_pool=[];
        for k=1:length(x)               %creates a vector of individuals from x
                individuals = k*(ones(x(k),1));
                species_pool = [species_pool;individuals];
        end;

        randnum = 1:length(species_pool);    %rearranges individuals in
                                    species_pool based on a random permutation
        randnum = randnum(randperm(1*length(species_pool)));
        species_pool = species_pool(randnum,:);      %rearranges observations

        population = [];

        for j=1:length(species_pool)
        %add individual to population
                population = [population;species_pool(j)];

        %calculate number of species present
                [groups,freqs] = unique(population);
                riches(j,i) = length(groups);

        end;

        ctr=ctr+1;
        if ctr==100                     %iteration counter
                iterations=iterations+100
                ctr=0;

                richness = mean(riches')';
                Std_richness = std(riches')';

                out=[richness Std_richness];
                tofile(out,'Hard:Desktop Folder:test');
                tofile(iterations,'Hard:Desktop Folder:iterations');

                time=toc;
                hours=floor(time/3600);
```

```
                minutes=floor((time-(hours*3600))/60);
                seconds=floor((time-(hours*3600)-(minutes*60)));
                Time = [hours minutes seconds]
                disp('    hours  mins  secs');
            end;

        end;

        if plot_flag==1;
            figure;
            pop_size = 1:length(richness);
            pop_size = pop_size';
            plot(pop_size(:,1),richness(:,1),'b');
            upper=richness+2*(Std_richness/sqrt(iter));
            lower=richness-2*(Std_richness/sqrt(iter));
            hold on;
            plot(pop_size(:,1),upper(:,1),'r');
            plot(pop_size(:,1),lower(:,1),'r');
        end;

return;
```

```
% UNIQUE:   Given a matrix, returns a vector containing of unique values,
%                       and a vector of their respective frequencies.
%
%    Usage: [values,frequencies] = unique(input)
%
%       input = matrix of values.
%
%       ------------------------------------------------------------
%       values =                column vector of unique labels.
%       frequencies = frequencies of respective unique values.
%
function [uniqs,freqs]=unique(in)

        if (any(in==NaN))|(any(in==-inf))|(any(in==inf))
                error('unique:  input matrix may not have non-finite values');
        end;

        if (in==[])
                uniqs=[];
                freqs=[];
                return;
        end;
%---------------------------------------------------------------

        in=in(:);                               %concatonates all columns of
                                                %matrix into one column vector
        uniqs=[in(1)];                          %creates ouput vector beginning
                                                %with first value of input vector
        freqs=[1];                              %creates frequency vector

        x=length(in);
        for (i=2:x)                             %begins for loop to survey input vector

                if in(i)~=(uniqs)               %defines conditions for adding
                                                %values to uniqs vector
                        uniqs=[uniqs;in(i)];    %adds unique values to ouput vector
                        freqs=[freqs;1];        %adds freqency value for new unique value
                else
                        [r,c] = size(freqs);    %redefines size of frequency vector

                        for (j=1:r)             %begins for loop to search
                                                %for matching unique value
                        if(in(i)) == (uniqs(j))         %finds location of previously
```

```
                                        %added unique values
            freqs(j) = freqs(j)+1;      %adds 1 to appropriate frequency
                                        %value in freqs vector
            end;                        %ends if loop
            end;                        %ends for loop

        end;                            %ends if statement

    end;                                %ends for loop
```

```
function [logistRa2,p2]=fitlog(area,sp)
% function [logistRa2,p1,p2,p3]=fitlog(area,sp)
% Fits the power, exponential, and logistic curves to the
% species/area relationship passed to the function. It  uses the
% Levenberg-Marquardt nonlinear regression technigue (function
% leasqr written by R.I. Shrager and modified by Jutan and Muzic).
% The output are adjusted R2 values (Ra2) for each fit using the adjusted
% coefficient of determination of Boecklen and Gotelli (1984), Loehle (1990),
% and He & Legendre (1996).


global verbose logistRa2

verbose=1;              % 1 = display animation of fits and extra output
                        % 0 = do not display

n=length(area);                 % n = sample size (number of quadrats)


% fit logistic function
[f2,p2,kvg2,iter2,corp2,covp2,covr2,stdresid2,Z2,r22]=...
  leasqr(area,sp,[1;.5;1],'logist',.0001,20,1,[.001;.001;.001],...
  'logistdfdp');
logistR2=r22;           % coefficient of determination for logistic function
logistRa2=1-((n-1)/(n-3))+((n-1)/(n-3))*logistR2;
```

LITERATURE CITED

Boecklen, W.J., and N. Gotelli. 1984. Island biogeographic theory and conservation practice: species-area or specious-area relationships? Biological Conservation 29:63-80.

He, F., and P. Legendre. 1996. On species-area relations. The American Naturalist 148:719-737.

Loehle, C. 1990. Home range: a fractal approach. Landscape Ecology 5:39-52.