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RARITY IN NEOTROPICAL BATS: CORRELATIONS WITH PHYLOGENY, DIET, AND BODY MASS¹

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Abstract. Bats are an important component of tropical faunas, both in terms of number of species and total biomass. Very little information, however, is available on the status and conservation of this diverse group. To contribute to the solution of this problem, rarity among Neotropical bats was analyzed using a set of 150 species. Rarity was quantified by local abundance and area of distributional range and by a combined index of rarity created by compounding these two variables. Nested analyses of variance showed local abundance to be more variable among genera than at any other taxonomic level, and area of distribution to be more variable among species. No significant correlation with body mass was found for local abundance or for area of distribution. Similarly, no correlation was found between distribution and abundance. Local abundance, but not area of distribution, varied significantly among taxonomic and trophic categories. At the local level, bats of the family Molossidae tend to be less abundant than other species. Bats that feed on plant parts or products (fruit, nectar, and pollen) are more abundant than insectivores and carnivores. The distribution of species among Rabinowitz' categories of rarity varied among taxonomic and trophic groups. The classification of rarity and the combined index of rarity introduced here can be used as guidelines for the identification of vulnerable species.

Key words: abundance; bats; body mass; classification of rarity; distribution; endangered species; feeding habits; rarity.

INTRODUCTION

Rare species play such a central role in conservation biology that the discipline has been defined as the science of scarcity and diversity (Soulé 1986). The study of the ecological traits that are shared by rare species has been the topic of some studies (Karr 1977, Thomas and Mallorie 1985, Hubbell and Foster 1986), and has been identified as one of the priorities for conservation (Soulé and Kohm 1989, Brussard 1991).

Rabinowitz (1981) proposed a binary classification of rare species based on their local abundance, distributional range, and habitat selectivity. Her model has been applied, with some modifications, for groups of plants (Rabinowitz et al. 1986), non-volant mammals (Arita et al. 1990), and birds (Kattan 1992). These studies have suggested that species that are naturally rare—those that are habitat specialists, that occur at low local density, or that have restricted distribution—deserve special consideration from conservationists.

This paper analyzes the relationship between distribution and local abundance for a set of Neotropical bats. After examining the phylogenetic constraints and the ecological correlates of these two variables of rarity, I explore the usefulness of the binary classification of rarity proposed by Rabinowitz (1981). Finally, results

are discussed in the context of current conservation theory and practice.

ANALYSIS OF RARITY

Sources of data

The database consisted of information on the distribution, local abundance, and body mass for a set of 150 bat species (Appendix 1), representing the nine Neotropical families and the whole gamut of feeding habits described by Wilson (1973) and Gardner (1977). I gathered information on local abundance from the literature (Hill 1964, Brosset and Dubost 1967, Fleming et al. 1972, Handley 1976, LaVal and Fitch 1977, Bonaccorso 1979, Genoways and Williams 1979, 1984, Williams and Genoways 1980, Anderson and Webster 1983, Willig 1983, dos Reis 1984, Medellín 1986, Fleming 1988, Bowles et al. 1990, Handley et al. 1991). Most of these papers provided complete lists of species and number of individuals captured, allowing the estimation of relative abundances. Some of the reports with incomplete lists complemented the database by providing information on the relative abundance of very rare species not included in the more comprehensive studies. To standardize the method, I considered only those specimens captured with mist nets and excluded individuals collected from roosting sites.

Because there is no reliable method to measure the absolute population density of bats, I used relative abundances. First, for each locality, I ranked the species by the number of netted individuals. Then, I divided the rank for each species by the total number of species

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in each locality, creating an index of relative abundance that measures the proportion of species that are less abundant than the species under consideration and that allows comparisons among several communities despite non-standardized capture efforts. Finally, for each species in the database, I calculated the average of this index for all localities in which the species is reported, creating a measure of overall local abundance. This average was used as an estimate of relative local abundance to rank the 150 species in the database.

Using a grid of 5-degree quadrats that extended between 25° North and South latitude, I estimated the area of distribution of the species based on Hall (1981), Koopman (1983), Jones et al. (1988), Eisenberg (1989), Emmons (1990), and Redford and Eisenberg (1992). The number of quadrats occupied by each species (an estimator of the area of distribution) was used to rank the 150 species according to the size of their distributional range.

A new variable, created by adding the rank value of distribution and of local abundance for each species, was used to rearrange the 150 species according to their combined rarity. A reversed ranking, with species with higher values of the variable having lower ranking, was used so species with higher rank of rarity had a more restricted distribution, a lower local abundance, or a combination of both.

From the literature, I obtained measurements of the forearm for each species (Davids and Carter 1978, Swanepoel and Genoways 1979, Hall 1981, Willig 1983, Genoways and Williams 1984, Handley 1984, Eisenberg 1989). Data from Eisenberg (1989) were used to construct regression lines for body mass vs. forearm length for each major family of Neotropical bats. These regressions were used to estimate the body mass of each species from their forearm length, allowing me to rank all species by size, even those with no information on body mass.

For analytical purposes, families with <6 species were included in the major family that is phylogenetically closest according to Koopman (1984). This procedure eliminated grouping categories with inadequate sample sizes. Noctilionids and mormoopids were classed with the Phyllostomidae, whereas thyropterids, natalids, and furpterids were grouped with the Vespertilionidae. Thus, comparisons among taxonomic groups contrasted four sets: the Emballonuridae, the Phyllostomidae and associate taxa, the Vespertilionidae and associate taxa, and the Molossidae.

Because most of the variation in feeding habits is found within the Phyllostomidae, I restricted the analysis of the association between rarity and diet to the taxa in this family. Using information from the literature (Wilson 1973, Gardner 1977, Nowak 1991 and citations therein), phyllostomid species were classified in four broad feeding categories: frugivores, nectarivores, animalivores (insectivores and carnivores), and vampires. Subsequently vampires, because of their in-

adequate sample size ($n = 3$ genera), were excluded from comparisons of feeding categories. A classification using more categories, such as the ones used in studies of Neotropical bat communities (Fleming et al. 1972, LaVal and Fitch 1977, Bonaccorso 1979, Willig and Moulton 1989) could not be used because relatively large sample sizes were required in some of the statistical analyses. A finer classification could have been more realistic, but it would have made impossible the statistical analysis of the data.

Phylogenetic constraints

Recently some authors have pointed out the inadequacy of comparative studies that ignore the phylogenetic history of the groups under study (Felsenstein 1985, Brooks and McLennan 1991, Harvey and Pagel 1991). By indiscriminately using species as independent data points, such studies are flawed because they neglect the fact that closely related species tend to be more similar to each other than species that are only remotely related (Harvey and Pagel 1991).

To overcome this problem, I used a nested analysis of variance (ANOVA) model to examine how the total variation among species was distributed among hierarchical taxonomic levels (Clutton-Brock and Harvey 1977, Harvey and Pagel 1991). Following Harvey and Pagel (1991) I described the total variation among species (ss_{tot}) with the model:

$$ss_{tot} = ss_{s(g)} + ss_{g(f)} + ss_{f(o)},$$

where $ss_{s(g)}$ is the variation of species within genera, $ss_{g(f)}$ is the variation of genera within families, and $ss_{f(o)}$ is the variation of families within the whole set. The percentage of the total variation accounted for by the individual variance components was calculated by multiplying each component by $100/ss_{tot}$.

I performed this analysis using the rank values for local abundance, area of distribution, and body mass. Although they are typically used with data that follow a normal distribution, ANOVA models can be applied to partition the variance of rank variables. For example, the H value in the non-parametric Kruskal-Wallis test can be calculated as the ratio of a sum of squares and a mean square (Zar 1984).

A high proportion of the total variation in local abundance and body mass corresponded to the variation of genera within families (Table 1). This observation coincides with the results of other studies (reviewed by Harvey and Pagel 1991) that have shown that most of the variation of ecological traits occurs at higher taxonomic levels. Read and Harvey (1989) found that variation among mammalian genera within families contributed only slightly to the total variation for several life-history variables. Their analyses, however, compared species from different mammalian orders, whereas I restricted my study to a single order—Chiroptera. My results indicate that, for local abundance and body mass, phylogenetic inertia strongly con-

TABLE 1. The distribution of the variance of three variables at different taxonomic levels. Variance was partitioned using a nested ANOVA model. $SS_{s(g)}$ is the variation among species within genera, $SS_{g(f)}$ is the variation of genera within families, and $SS_{f(o)}$ is the variation among families within the Order Chiroptera.

Variable	Percentage of variation*		
	$SS_{s(g)}$	$SS_{g(f)}$	$SS_{f(o)}$
Rank abundance	37.31	54.20	8.49
Rank area	68.39	30.51	1.10
Rank mass	14.93	42.73	42.34

* Percentages of the total variation among species (SS_{tot}).

strains the range of possible values for species within a given genus, but not for genera within a given family.

Area of distributional range was more variable among species within genera than at higher taxonomic levels (Table 1). The processes that determine the range of a species (speciation, extinction, colonization) operate at different time and spatial scales than those that affect local density (population dynamics, fluctuations in the levels of resources, interspecific interactions). My results suggest that the phylogenetic constraints that limit the variability in distribution among species with recent common ancestry are not effective at the scale in which speciation events occur.

Following Harvey and Pagel (1991) I conducted the statistical tests in the following sections using the average values for each genus. Analysis at the species level would have been adequate to describe the variation in area of distribution, but would have been flawed for abundance and body mass because of the use of data points (species) that are not statistically independent (Harvey and Pagel 1991).

Correlation between the variables

Correlations with body mass.—Among non-volant mammals, body mass correlates well with many ecological traits (Peters 1983, Calder 1984, Schmidt-Nielsen 1984), including distribution and abundance (Arita et al. 1990). In contrast, for genera of Neotropical bats I found no significant correlations of body mass with local abundance (Spearman rank correlation, $r_s = 0.01$, $n = 59$, $P > .05$) or with area of distribution (Spearman rank correlation, $r_s = 0.26$, $n = 59$, $P > .05$).

The lack of association between body mass and local abundance is surprising because such relationship has been demonstrated for other groups of mammals (Mohr 1940, Eisenberg 1980, Damuth 1981, Peters 1983, Peters and Raelson 1984, Robinson and Redford 1986, LaBarbera 1989). In Neotropical non-volant mammals, larger species have lower local densities (Eisenberg 1980, Robinson and Redford 1986). Among Neotropical bats, some species follow this trend; the large carnivores such as *Vampyrum spectrum* and *Chrototerus auritus* are locally rare, and small species like

Glossophaga soricina are very abundant. Some large species, however, such as *Artibeus* spp. and *Phyllostomus* spp. are among the most abundant, whereas some small species such as *Centronycteris maximiliani* are very scarce.

As with local density, the lack of correlation between area of distribution and body mass contrasts with the significant correlations that have been reported for other animal groups (Brown 1981, Cristoffer 1990, Pagel et al. 1991), including Neotropical non-volant mammals (Arita et al. 1990).

One possible cause for the null correlation between body mass and the variables of rarity is the comparatively small range of sizes within Neotropical Chiroptera. The ratio between the smallest (*Furipterus horrens*) and the largest (*V. spectrum*) species in the data set is 3 g:169 g = 1:56. In contrast, the same ratio in the data set of Robinson and Redford (1986) and Arita et al. (1990) for Neotropical non-volant mammals is 1:20 000. An alternative explanation is Brown and Maurer's (1987) finding that, for North American bird species, the relationships between the logarithms of the variables considered here are not linear, and that the scatterplots are limited by minimum and maximum values determined by ecological or physiological constraints.

Correlations between the variables of rarity.—The usefulness of Rabinowitz' (1981) binary classification of rarity depends on the correlation between local density and area of distribution (Arita et al. 1990). Ideally, if the correlation is close to zero, the two variables constitute independent estimators of rarity. Conversely, if the correlation is close to 1.0 or -1.0, the use of both variables is redundant because in that case it is possible to predict the value of one of the variables by knowing the other. In the real world the correlation between distribution and abundance has been found to be positive in some cases (MacNaughton and Wolf 1970, Hanski 1982, Bock and Ricklefs 1983, Bock 1984, 1987, Brown 1984, Brown and Maurer 1987, Gotelli and Simberloff 1987), and negative in others (Willson 1974, Adams and Anderson 1982, Arita et al. 1990, Cristoffer 1990).

For Neotropical bats the correlation was not significantly different from zero (Spearman rank correlation, $r_s = 0.103$, $n = 59$, $P > .05$). Arita et al. (1990) showed a significant negative correlation between these variables for Neotropical non-volant mammals. The correlation, however, was not significant when body mass was controlled for, or within smaller taxonomic or feeding groups. Cristoffer (1990) constructed a model that predicts stronger and more negative correlations between distribution and abundance for groups of species with wider variation in body mass than for groups with small ranges of size. Results for non-volant (Arita et al. 1990) and volant (this paper) Neotropical mammals are consistent with this prediction. Body mass, or a variable closely associated with size, seems

to be a key factor in determining the relationship between distribution and abundance.

The effect of taxonomic and dietary grouping

I used Kruskal–Wallis tests to compare distribution and abundance among the taxonomic groups. Subsequently, pairs of taxonomic groups were compared using a non-parametric test for multiple comparisons (Zar 1984). Comparisons were made using the averages of the genera as data points. I performed identical analyses for the phyllostomid species using diet as the classification criterion.

Local abundance.—Local abundance differed among the taxonomic and trophic categories (Table 2). The Kruskal–Wallis tests showed a significant effect of taxonomic group ($H = 10.45$, $df = 3$, $P = .01$) and of diet within the Phyllostomidae ($H = 8.2$, $df = 2$, $P = .02$). The multiple comparisons showed that molossids differ significantly ($P < .05$) from the other three categories, which did not differ among each other ($P > .05$). Within the Phyllostomidae, animalivores differed significantly ($P < .05$) from nectarivores and frugivores, which did not differ between each other.

These results are in accord with the observations of Robinson and Redford (1986) that frugivorous and omnivorous non-volant mammals occur at higher densities than insectivorous and carnivorous species. According to their predictions based on energy availability, species that feed on plants or plant products (such as fruit, nectar, and pollen) should be more abundant than species that depend on animal food (insects and vertebrates). My results suggest that frugivorous and nectarivorous bats tend to be more abundant than insectivores and carnivores.

These conclusions are to be taken with caution, however, because of possible biases inherent in field work with bats. Frugivores and nectarivores are probably easier to catch in mist nets than animalivores, because the echolocation capabilities of the latter are more developed. Furthermore, sampling can be biased if mist nets are set close to a blooming or fruiting tree, creating an apparent overabundance of plant-visiting species (Handley et al. 1991). Despite these problems of sampling, the generalization that fruit- and nectar-eating bats are more abundant in Neotropical forests is probably true. Frugivorous phyllostomids, for example, appear to be more abundant than insectivorous phyllostomids even in samples taken from roosting sites or in mist nets set over courses of water, far from fruiting trees (H. T. Arita, *personal observation*).

Another possible caveat is that diet categories coincide closely with the phylogeny of the Phyllostomidae. All frugivores and all nectarivores belong to the monophyletic tribes Stenodermatini and Glossophagini, respectively (Baker et al. 1989). Carnivorous species form the subfamily Vampyrinae, and the vampires constitute the subfamily Desmodontinae (Baker et al. 1989). The rest of the species, belonging to the tribe

TABLE 2. Mean rank values of two variables of rarity for taxonomic and trophic groups. Values in the same column with the same superscript letter did not differ significantly in Kruskal–Wallis ANOVAs or in subsequent multiple-comparison procedures.

	<i>n</i> (no. genera)	Mean rank	
		Distribution	Abundance
Taxonomic group			
Emballonuridae	6	40.17 ^a	22.33 ^a
Phyllostomidae*	38	28.88 ^a	34.62 ^a
Vespertilionidae†	9	24.72 ^a	27.33 ^a
Molossidae	6	34.83 ^a	12.42 ^b
Trophic group (Phyllostomidae only)			
Frugivores	16	17.56 ^a	20.97 ^a
Nectarivores	8	11.44 ^a	17.56 ^a
Animalivores	9	20.94 ^a	9.44 ^b

* Includes Phyllostomidae and associated families (Noctilionidae and Mormoopidae).

† Includes Vespertilionidae and associated families (Furipteridae, Natalidae, and Thyropteridae).

Phyllostomini and the subfamilies Macrotinae and Microcycterinae (Van Den Bussche 1992), are mostly foliage-gleaner insectivores (Humphrey et al. 1983). Because diet is not independent of phylogeny, differences among trophic categories could be a mere reflection of phylogenetic history.

Area of distribution.—Area of distribution did not differ significantly among taxonomic ($H = 3.59$, $df = 3$, $P = .31$) or trophic ($H = 4.20$, $df = 2$, $P = .12$) groups (Table 2). Among Neotropical non-volant mammals, herbivores, myrmecophages, and carnivores are more widespread than insectivores and frugivores (Arita et al. 1990). Most of this variation can be explained, however, by the positive correlation between distribution and body mass. Since variation in body mass among bats is not as pronounced as it is for non-volant mammals, a lower variation in area of distribution should not be surprising.

CATEGORIES OF RARITY

Following the modifications of Arita et al. (1990) to the classification of Rabinowitz (1981), I grouped the bats in the database using dichotomous categories of rarity based on distribution and abundance (Table 3, Fig. 1). I used the medians of these variables as the limits for the categories. In this way, half of the species were considered locally rare and half locally abundant. Similarly, half of the species were classified as restricted and half as widespread. As discussed by Arita et al. (1990), this categorization is arbitrary but recognizes the comparative nature of the variables of rarity.

I used species, not genera, as data points to construct the categories of rarity because species are the units used in most conservation programs. Analyses at the genus level are appropriate to test evolutionary hypotheses (such as those in the previous sections), but they would be of limited use for conservation purposes.

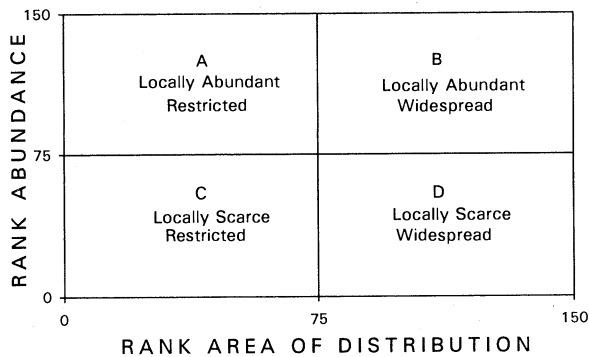


FIG. 1. Four categories of rarity, defined by local abundance and area of distributional range. Limits of the categories are defined by the medians of the two variables.

If it is true that tests using higher taxonomic levels can provide better information on the evolution of the variables of rarity, it is also true that it is the rarity of species, not of genera, that is of interest for conservation biologists.

In the combined arrangement of both variables (Fig. 1), categories B (widespread and locally abundant) and C (restricted and locally rare) had more species (44 each) than categories A and D (31 each, Table 3). I used a three-dimensional contingency table (Zar 1984) to analyze the association among distribution, abundance, and taxonomic group (with four states: Emballonuridae, Phyllostomidae and associated taxa, Vespertilionidae and associated taxa, and Molossidae). The null hypothesis of mutual independence among the three variables was rejected ($\chi^2 = 20.78$, $df = 10$, $P < .05$), allowing me to test the null hypothesis of partial independence of taxonomy from distribution and

TABLE 3. Frequency distribution among categories of rarity for Neotropical bats arranged by taxonomic and feeding groups. Rarity categories are as in Fig. 1. For analytical purposes, some of these groups were merged or eliminated (see *Analysis of rarity: Sources of data* for details).

	Categories			
	A	B	C	D
All species	31	44	44	31
Family				
Emballonuridae	1	3	3	6
Noctilionidae	0	2	0	0
Mormoopidae	1	2	1	1
Phyllostomidae	21	31	25	11
Natalidae	0	0	2	0
Furipteridae	0	0	0	1
Thyropteridae	0	1	0	0
Vespertilionidae	4	2	7	6
Molossidae	4	3	6	6
Feeding group (Phyllostomidae only)				
Vampires	0	2	0	1
Frugivores	16	15	8	3
Nectarivores	5	4	6	1
Animalivores	0	10	11	6

abundance (Zar 1984). This second hypothesis was also rejected ($\chi^2 = 17.03$, $df = 9$, $P < .05$), indicating that species in different taxonomic groups are distributed differently among the categories of rarity (Fig. 2). The most obvious pattern in Fig. 2 is that phyllostomids and associated taxa tend to be located in the upper half of the graph (higher local density), whereas the other groups tend to be located in the lower half (low local density).

The contingency-table tests were repeated for the phyllostomid species using diet (with three states: frugivores, nectarivores, and animalivores) as the grouping variable. The null hypothesis of mutual indepen-

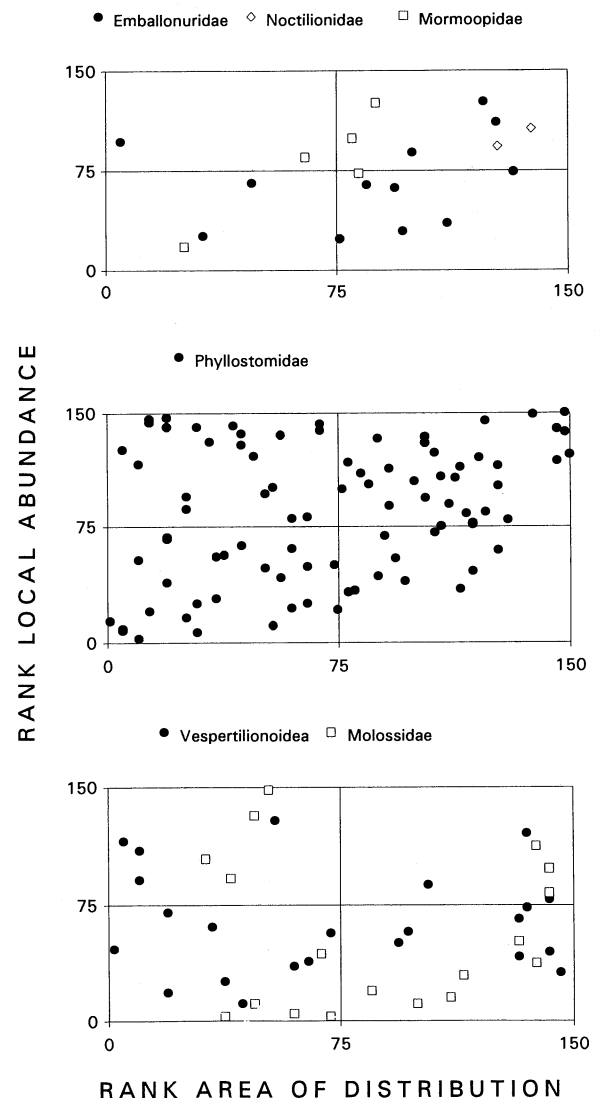


FIG. 2. Classification by taxa of Neotropical bats among categories defined by local abundance and area of distributional range. The lines bisecting the graphs are the medians of the two variables of the whole data set, and define the four categories of rarity described in Fig. 1. Vespertilionoidea includes Vespertilionidae, Natalidae, Thyropteridae, and Furipteridae.

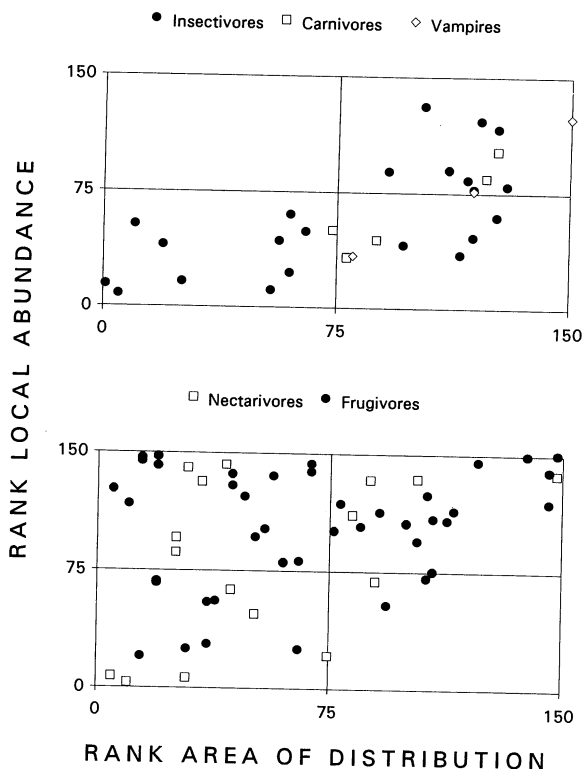


FIG. 3. Classification by feeding groups of Neotropical bats among categories defined by local abundance and area of distributional range. The lines bisecting the graphs are the medians of the two variables for the whole data set, and define the four categories of rarity described in Fig. 1.

dence among diet, distribution, and abundance was rejected ($\chi^2 = 163.55$, $df = 7$, $P < .001$). Subsequently, the null hypothesis of partial independence of diet from distribution and abundance was also rejected ($\chi^2 = 122.91$, $df = 6$, $P < .001$), showing that the species within feeding groups are not distributed randomly among categories of rarity (Fig. 3). Animalivores had no representatives in category A (locally abundant and restricted), whereas nectarivores and frugivores had fewer representatives in cell D (low density and widespread) than in the other categories. These results coincide partially with those for Neotropical non-volant mammals (Arita et al. 1990), among which frugivore-granivores and herbivores tend to occupy the upper cells (A and B), whereas myrmecophages and carnivores tend to occur more frequently in the lower right cell (D).

IMPLICATIONS FOR CONSERVATION

As discussed by Arita et al. (1990), species in the different categories of rarity would require different conservation strategies. In particular, species in category C (locally rare and restricted) would deserve special attention for further studies—more so than species in category B (locally abundant and widespread), which

could be considered less vulnerable. The combined index of rarity proposed here could be used as a simple tool to estimate vulnerability to extinction. Species with higher rank values for this variable (Table 4) could be considered as the most vulnerable, or at least the ones deserving more immediate attention from conservation studies. All these suggestions, however, are based on the intuitive but still controversial premise that rare species are more prone to extinction than more abundant and widespread species (Terborgh 1974, Terborgh and Winter 1980, Diamond 1984, but see McIntyre 1992).

In several demographic and genetic models, the probability of extinction decreases with increasing initial population size (MacArthur 1972, Richter-Dyn and Goel 1972, May 1973, Frankel and Soule 1981, Schonewald-Cox et al. 1983, Goodman 1987, Lande and Barrowclough 1987, Lande 1988, Pimm et al. 1988, Ralls et al. 1988). Although some field studies have validated these models (Diamond 1984, Pimm et al. 1988, Berger 1990, Bolger et al. 1991, Newmark 1991),

TABLE 4. The rarest and the most common Neotropical bat species. Rare species are those with a combined rarity rank > 113; common species are those with combined rarity rank < 36.

Rare species	Common species
<i>Balantiopteryx plicata</i>	<i>Peropteryx macrotis</i>
<i>Didelidurus ingens</i>	<i>Rhynchonycteris naso</i>
<i>Peropteryx kappleri</i>	<i>Saccopteryx bilineata</i>
<i>Mormoops megalophylla</i>	<i>Noctilio albiventris</i>
<i>Lonchorhina orinocensis</i>	<i>Noctilio leporinus</i>
<i>Micronycteris brachyotis</i>	<i>Pteronotus parnellii</i>
<i>Micronycteris daviesi</i>	<i>Micronycteris megalotis</i>
<i>Micronycteris schmidtorum</i>	<i>Phyllostomus discolor</i>
<i>Phyllostomus latifolius</i>	<i>Phyllostomus elongatus</i>
<i>Tonatia carrikeri</i>	<i>Phyllostomus hastatus</i>
<i>Tonatia evotis</i>	<i>Trachops cirrhosus</i>
<i>Tonatia schulzi</i>	<i>Tonatia silvicola</i>
<i>Anoura cultrata</i>	<i>Anoura geoffroyi</i>
<i>Choeroniscus minor</i>	<i>Glossophaga soricina</i>
<i>Lichonycteris obscura</i>	<i>Lionycteris spurrelli</i>
<i>Scleronycteris ega</i>	<i>Carollia brevicauda</i>
<i>Centurio senex</i>	<i>Carollia perspicillata</i>
<i>Sturnira bidens</i>	<i>Rhynophylla pumilio</i>
<i>Sturnira bogotensis</i>	<i>Artibeus jamaicensis</i>
<i>Sturnira erythromos</i>	<i>Artibeus lituratus</i>
<i>Vampyressa brocki</i>	<i>Dermanura cinerea</i>
<i>Vampyressa nymphaea</i>	<i>Dermanura phaeotis</i>
<i>Platyrrhinus brachycephalus</i>	<i>Sturnira lilium</i>
<i>Platyrrhinus infuscus</i>	<i>Sturnira tildae</i>
<i>Natalus tumidirostris</i>	<i>Uroderma bilobatum</i>
<i>Bauerus dubiaquercus</i>	<i>Vampyroides caraccioli</i>
<i>Eptesicus diminutus</i>	<i>Platyrrhinus helleri</i>
<i>Eptesicus fuscus</i>	<i>Platyrrhinus lineatus</i>
<i>Lasiurus intermedius</i>	<i>Desmodus rotundus</i>
<i>Myotis nesopolus</i>	<i>Eptesicus furinalis</i>
<i>Myotis oxyotus</i>	<i>Myotis albescens</i>
<i>Eumops dabbenei</i>	<i>Myotis nigricans</i>
<i>Eumops hansae</i>	<i>Eumops auripendulus</i>
<i>Molossops greenhalli</i>	<i>Molossus molossus</i>
<i>Promops centralis</i>	<i>Molossus rufus</i>
<i>Promops nasutus</i>	

others have found no correlation between initial rarity and extinction (Karr 1982, 1990, Laurance 1991).

In general, species with restricted distribution are considered more vulnerable (Terborgh 1974). If a species occurs in several sites, the extinction of localized populations can be overcome by the rescue effect, the recolonization by individuals from adjacent locations (Brown and Kodric-Brown 1977, Burkey 1989). Conversely, if a species has a very restricted distribution, the entire species can be exterminated by a single catastrophic event such as a hurricane, a volcanic eruption, or a urbanization project. Thomas (1991) has shown that Costa Rican butterflies with narrow distributional ranges are less capable of surviving in human-perturbed habitats than are widespread species. Among marine invertebrates, widespread species show lower extinction rates in the geological time scale (Jablonski 1986, 1991). The association between area of distribution and extinction, however, is yet to be completely validated.

Because of these uncertainties, rarity should be used only as a preliminary criterion in the evaluation of endangered species. The statistical trends discussed here represent general patterns, not absolute laws obeyed by all species. The objective of this and other studies of rarity should be to provide guidelines to identify the species that might be threatened and that could be targeted for further research. Rarity should not be used as the sole criterion for establishing the conservation status of particular species.

A particularly dangerous misinterpretation of rarity is to assume that the most common species are not threatened, when in reality these species are not necessarily less vulnerable (McIntyre 1992). For example, it is possible that bat species that form huge colonies in caves require such big concentrations because of social or physiological constraints, and even a small reduction in abundance could compromise the viability of the population because of the Allee effect (Andrewartha and Birch 1954, Lande 1988). Even at high population densities these species would be particularly vulnerable to perturbation in their habitat. Similarly, migratory species with apparent large distributional ranges might actually be more vulnerable than sedentary species with more restricted distributions.

Another caveat is that the applicability of studies on rarity is restricted to the area of study. Some of the rarest bats in the Neotropics are certainly not uncommon in subtropical Mexico or in Nearctic areas (e.g., *Balantiopteryx plicata*, *Mormoops megalophylla*, *Centurio senex*, *Eptesicus fuscus*). Clearly, North American countries would need studies on rarity specifically tailored to their conservation needs. Studies of rarity for individual countries would be not only scientifically interesting but also useful for the design of particular conservation strategies.

As suggested by Brussard (1991), one of the priorities of conservation biology should be the study of the nat-

ural history and autecology of rare species. To set protection priorities, conservation biologists need objective criteria to attach relative conservation values to species. The assessment of the relative value of rare vs. common species, coupled with appraisals based on evolutionary history (Erwin 1991, Vane-Wright et al. 1991) might be the first step in this endeavor, which has been called the calculus of biodiversity by May (1990).

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APPENDIX

Ranks for three variables of rarity and for body mass for 150 species of Neotropical bats. Rarity indicates the reversed ranking of the combined index of rarity (see *Analysis of rarity: Sources of data*).

	Rank				Category*
	Area	Abundance	Rarity	Body mass	
Emballonuridae					
<i>Balantiopteryx plicata</i>	19.5	13.5	146.0	14.0	A
<i>Centronycteris maximiliani</i>	97.0	30.0	94.5	23.0	D
<i>Cormura brevirostris</i>	94.0	62.0	74.0	33.0	D
<i>Diclidurus albus</i>	100.0	88.0	47.5	113.0	B
<i>Diclidurus ingens</i>	31.5	25.5	136.0	123.0	C
<i>Diclidurus isabellus</i>	5.0	96.5	112.0	74.0	A
<i>Diclidurus scutatus</i>	47.5	65.0	105.0	66.0	C
<i>Peropteryx kappleri</i>	76.5	23.0	114.0	40.0	D
<i>Peropteryx macrotis</i>	132.5	74.0	33.0	25.0	D
<i>Rhynchonycteris naso</i>	123.0	127.0	10.0	5.0	B
<i>Saccopteryx bilineata</i>	127.0	111.0	15.0	18.0	B
<i>Saccopteryx canescens</i>	111.0	36.0	83.0	8.0	D
<i>Saccopteryx leptura</i>	85.0	64.0	79.5	13.0	D
Noctilionidae					
<i>Noctilio albiventris</i>	127.0	93.0	24.5	131.0	B
<i>Noctilio leporinus</i>	138.5	106.0	11.0	147.0	B
Mormoopidae					
<i>Mormoops megalophylla</i>	25.5	17.5	140.0	81.0	C
<i>Pteronotus davyi</i>	80.5	99.0	57.0	37.0	B
<i>Pteronotus gymnonotus</i>	65.0	85.0	78.0	88.0	A
<i>Pteronotus parnellii</i>	88.0	125.0	27.0	103.0	B
<i>Pteronotus personatus</i>	82.5	72.0	77.0	32.0	D
Phyllostomidae					
Desmodontinae					
<i>Desmodus rotundus</i>	150.0	123.0	5.0	141.0	B
<i>Diaemus youngi</i>	119.0	76.0	43.0	137.0	B
<i>Diphylla ecaudata</i>	80.5	33.0	103.0	126.0	D
Micronycterinae					
<i>Micronycteris brachyotis</i>	56.5	42.0	116.0	57.0	C
<i>Micronycteris daviesi</i>	60.0	22.0	126.0	127.0	C
<i>Micronycteris hirsuta</i>	65.0	49.0	102.0	62.0	C
<i>Micronycteris megalotis</i>	130.0	79.0	29.0	24.0	B
<i>Micronycteris minuta</i>	119.0	46.0	68.0	28.0	D
<i>Micronycteris nicefori</i>	60.0	60.0	99.5	44.0	C
<i>Micronycteris schmidtorum</i>	25.5	16.0	141.0	30.0	C
<i>Micronycteris sylvestris</i>	97.0	40.0	88.0	60.0	D
Vampyrinae					
<i>Chrotopterus auritus</i>	88.0	43.0	91.5	148.0	D
<i>Trachops cirrhosus</i>	123.0	84.0	31.5	135.0	B
<i>Vampyrum spectrum</i>	78.5	32.0	107.5	150.0	D
Phyllostominae					
Phyllostomini					
<i>Lonchorhina aurita</i>	119.0	77.0	42.0	106.0	B
<i>Lonchorhina orinocensis</i>	10.0	53.0	133.0	63.0	C
<i>Macrophyllum macrophyllum</i>	127.0	59.0	50.0	35.0	D
<i>Mimon bennetti</i>	74.0	50.0	97.0	129.0	C
<i>Mimon crenulatum</i>	111.0	90.0	36.0	100.0	B
<i>Phyllostomus discolor</i>	121.0	121.0	13.0	139.0	B
<i>Phyllostomus elongatus</i>	103.5	130.0	17.0	143.0	B
<i>Phyllostomus hastatus</i>	127.0	102.0	19.5	149.0	B
<i>Phyllostomus latifolius</i>	19.5	39.0	134.0	134.0	C
<i>Phyllostomus stenops</i>	115.0	34.0	79.5	145.0	D
<i>Tonatia bidens</i>	117.0	83.0	37.5	128.0	B
<i>Tonatia brasiliense</i>	91.5	89.0	55.0	26.0	B
<i>Tonatia carrikeri</i>	54.0	10.5	130.0	87.0	C
<i>Tonatia evotis</i>	5.0	8.0	148.0	108.0	C
<i>Tonatia schulzi</i>	1.0	13.5	147.0	65.0	C
<i>Tonatia silvicola</i>	127.0	116.0	12.0	116.0	B
Glossophagini					
<i>Anoura caudifer</i>	82.5	110.0	44.0	59.0	B

APPENDIX. Continued.

	Rank				Category*
	Area	Abundance	Rarity	Body mass	
<i>Anoura cultrata</i>	5.0	7.0	150.0	91.0	C
<i>Anoura geoffroyi</i>	103.5	134.0	16.0	86.0	B
<i>Anoura latidens</i>	33.5	131.0	69.0	96.0	A
<i>Choeroniscus godmani</i>	43.5	63.0	109.0	41.0	C
<i>Choeroniscus minor</i>	75.0	21.0	117.0	52.0	C
<i>Glossophaga commissarisi</i>	29.0	140.0	66.0	39.0	A
<i>Glossophaga soricina</i>	148.5	137.0	3.0	55.0	B
<i>Hylonycteris underwoodi</i>	25.5	86.0	106.0	38.0	A
<i>Lichonycteris obscura</i>	51.0	48.0	115.0	31.0	C
<i>Lionycteris spurrelli</i>	88.0	133.0	22.0	50.0	B
<i>Lonchophylla mordax</i>	41.0	142.0	53.0	43.0	A
<i>Lonchophylla robusta</i>	25.5	95.0	53.0	95.0	A
<i>Lonchophylla thomasi</i>	90.0	69.0	72.0	34.0	D
<i>Scleronycteris ega</i>	10.0	2.5	149.0	49.0	C
Stenodermatini					
<i>Ametrida centurio</i>	56.5	135.0	45.0	29.0	A
<i>Artibeus jamaicensis</i>	148.5	150.0	67.0	140.0	B
<i>Artibeus lituratus</i>	146.0	139.0	35.0	146.0	B
<i>Carollia brevicauda</i>	123.0	145.0	45.0	94.0	B
<i>Carollia castanea</i>	47.5	122.0	57.0	61.0	A
<i>Carollia perspicillata</i>	138.5	149.0	61.0	114.0	B
<i>Carollia subrufa</i>	19.5	147.0	1.0	80.0	A
<i>Centurio senex</i>	35.5	28.0	4.0	104.0	C
<i>Chiroderma salvini</i>	51.0	96.5	131.5	121.0	A
<i>Chiroderma trinitatum</i>	106.5	71.0	82.0	84.0	D
<i>Chiroderma villosum</i>	108.5	75.0	59.0	115.0	D
<i>Dermanura anderseni</i>	43.5	136.0	57.0	138.0	A
<i>Dermanura concolor</i>	76.5	100.0	61.0	119.0	B
<i>Dermanura cinerea</i>	115.0	114.0	52.0	79.0	B
<i>Dermanura phaeotis</i>	69.0	138.0	19.5	64.0	A
<i>Dermanura tolteca</i>	19.5	141.0	31.5	82.0	A
<i>Ectophylla alba</i>	14.0	146.0	70.0	27.0	A
<i>Ectophylla macconnelli</i>	103.5	94.0	71.0	46.0	B
<i>Enchisthenes harti</i>	60.0	80.0	40.0	75.0	A
<i>Platyrrhinus aurarius</i>	5.0	126.0	91.5	132.0	A
<i>Platyrrhinus brachycephalus</i>	65.0	25.5	121.5	71.0	C
<i>Platyrrhinus helleri</i>	108.5	108.0	26.0	72.0	B
<i>Platyrrhinus infuscus</i>	35.5	55.0	121.5	136.0	C
<i>Platyrrhinus lineatus</i>	69.0	143.0	28.0	117.0	A
<i>Platyrrhinus umbratus</i>	14.0	144.0	73.0	111.0	A
<i>Platyrrhinus vittatus</i>	54.0	101.0	75.5	142.0	A
<i>Rhinophylla pumilio</i>	91.5	113.0	87.0	51.0	B
<i>Sphaeronycteris toxophyllum</i>	65.0	81.0	84.0	77.0	A
<i>Sturnira bidens</i>	19.5	68.0	124.0	90.0	C
<i>Sturnira bogotensis</i>	29.0	25.5	137.0	105.0	C
<i>Sturnira erythromos</i>	38.0	56.0	120.0	93.0	C
<i>Sturnira lilium</i>	146.0	119.0	7.0	101.0	B
<i>Sturnira ludovici</i>	43.5	129.0	64.0	109.0	A
<i>Sturnira mordax</i>	10.0	117.0	94.5	118.0	A
<i>Sturnira tildae</i>	106.5	124.0	18.0	112.0	B
<i>Uroderma bilobatum</i>	113.0	107.0	24.5	99.0	B
<i>Uroderma magnirostrum</i>	94.0	54.0	80.5	102.0	D
<i>Vampyressa bidens</i>	85.0	103.0	47.5	67.0	B
<i>Vampyressa brocki</i>	19.5	67.0	124.5	48.0	C
<i>Vampyressa nymphaea</i>	14.0	20.0	145.0	69.0	C
<i>Vampyressa pusilla</i>	78.5	118.0	41.0	42.0	B
<i>Vampyrodes caraccioli</i>	100.0	105.0	34.0	130.0	B
Natalidae					
<i>Natalus stramineus</i>	72.0	57.0	93.0	4.0	C
<i>Natalus tumidirostris</i>	33.5	61.0	119.0	21.0	C
Furipteridae					
<i>Furipterus horrens</i>	94.0	51.0	85.0	2.0	D
Thyropteridae					
<i>Thyroptera tricolor</i>	103.5	87.0	46.0	9.0	B

APPENDIX. Continued.

	Rank				Category*
	Area	Abundance	Rarity	Body mass	
Vespertilionidae					
<i>Bauerus dubiaquercus</i>	19.5	70.0	123.0	85.0	C
<i>Eptesicus brasiliensis</i>	132.5	41.0	63.0	53.0	D
<i>Eptesicus diminutus</i>	43.5	10.5	138.0	17.0	C
<i>Eptesicus furinalis</i>	142.5	78.0	23.0	20.0	B
<i>Eptesicus fuscus</i>	38.0	25.5	131.5	58.0	C
<i>Lasiurus blossevilli</i>	146.0	31.0	60.0	22.0	D
<i>Lasiurus cinereus</i>	65.0	38.0	111.0	83.0	C
<i>Lasiurus ega</i>	142.5	45.0	49.0	47.0	D
<i>Lasiurus intermedius</i>	19.5	17.5	143.0	76.0	C
<i>Myotis albescens</i>	135.5	73.0	30.0	16.0	D
<i>Myotis elegans</i>	10.0	109.0	101.0	10.0	A
<i>Myotis keaysi</i>	54.0	128.0	54.0	12.0	A
<i>Myotis nesopolus</i>	2.0	47.0	139.0	7.0	C
<i>Myotis nigricans</i>	135.5	120.0	8.0	11.0	B
<i>Myotis oxyotus</i>	60.0	35.0	118.0	19.0	C
<i>Myotis riparius</i>	132.5	66.0	39.0	15.0	D
<i>Pipistrellus subflavus</i>	5.0	115.0	99.5	6.0	A
<i>Rhogeessa minutilla</i>	10.0	91.0	113.0	1.0	A
<i>Rhogeessa tumida</i>	97.0	58.0	75.5	3.0	D
Molossidae					
<i>Eumops auripendulus</i>	138.5	112.0	9.0	125.0	B
<i>Eumops bonariensis</i>	138.5	37.0	62.0	78.0	D
<i>Eumops dabbenei</i>	38.0	2.5	142.0	144.0	C
<i>Eumops glaucinus</i>	132.5	52.0	51.0	133.0	D
<i>Eumops hansae</i>	47.5	10.5	135.0	70.0	C
<i>Molossops abrasus</i>	100.0	10.5	107.5	92.0	D
<i>Molossops greenhalli</i>	60.0	5.0	129.0	68.0	C
<i>Molossops planirostris</i>	111.0	15.0	96.0	56.0	D
<i>Molossops temminckii</i>	69.0	44.0	104.0	54.0	C
<i>Molossus bondae</i>	31.5	104.0	89.0	107.0	A
<i>Molossus molossus</i>	142.5	98.0	14.0	73.0	B
<i>Molossus pretiosus</i>	52.0	148.0	37.5	98.0	A
<i>Molossus rufus</i>	142.5	82.0	21.0	120.0	B
<i>Molossus sinaloae</i>	40.0	92.0	90.0	110.0	A
<i>Neoplatymops mattogrossensis</i>	47.5	132.0	57.0	45.0	A
<i>Nyctinomops laticaudatus</i>	115.0	29.0	86.0	97.0	D
<i>Promops centralis</i>	72.0	2.5	127.5	124.0	C
<i>Promops nasutus</i>	72.0	2.5	127.5	122.0	C
<i>Tadarida brasiliensis</i>	85.0	19.0	110.0	89.0	D

* Categories of rarity are: A (locally abundant, restricted), B (locally abundant, widespread), C (locally rare, restricted), and D (locally rare, widespread).