CHAPTER 13

Patterns of Range Size, Richness, and Body Size in the Chiroptera

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Introduction

Macroecology seeks to quantify broad-scale patterns of species richness, species range size, body size, and abundance and to understand them from ecological and historical perspectives (Brown 1995). It primarily examines patterns that occur at regional to global spatial scales—patterns that have been produced as a consequence of mechanisms operating over decades to millennia. Consequently, macroecology is concerned with: the statistical distribution of variables and is nonexperimental by nature; nevertheless, it is subject to rigorous assessment by comparative studies.

Studies of bats provide important insights into macroecological patterns and the mechanisms that give rise to them. This derives from the high taxonomic and ecological diversity of the order Chiroptera (Simmons 2003), its broad distribution on all continents except Antarctica (Koopman 1984), and the tremendous spatial variation that exists in the abundances of species and their assembly into local communities (Findley 1993; Stevens and Willig 1999, 2000, 2002). Moreover, as the only volant mammals, bats are excellent candidates for comparative macroecological studies with nonvolant mammals, such as rodents, or with other volant homeotherms (i.e., birds).

Bats constitute approximately one-fifth of the living species of mammals recognized by Wilson and Reeder (2003). Only the Rodentia is more species-rich, with more than 40% of all mammalian species. Although the Chiroptera now includes 18 families and 202 genera, almost 80% of the species are exclusively tropical, with the family Vespertilionidae making the largest contribution to temperate-zone faunas. Paralleling the taxonomic richness of the order, ecological diversity is equally impressive, with bats occupying frugivorous, nectarivorous, animalivorous, insectivorous, piscivorous, and sanguinivorous ensembles (guilds).

Studies of Chiroptera are only beginning to contribute to macroecological understanding. In part, this may be a consequence of the difficulty of quantifying the abundances of local populations of small, vague, nocturnal species, especially those in highly diverse and vertically stratified tropical ecosystems.

Moreover, the spatial distribution of species at the continental scale is only available for the New World (see references in Willig and Lyons [1998] or Willig and Gannon [1997]) and Australia (Strahan 1995) in an easily accessible format with reasonably accurate detail. Nonetheless, the foundational work of Corbet and Hill (1992) and Corbet (1978) for Eurasia, Kingdon (1997) for Africa, and Strahan (1983, 1995) for Australia represent productive points of departure for macroecological analyses of Old World mammals. Thus, by necessity, most of the discussion that follows emphasizes patterns in North and South America. Analyses from Africa, Australia, and the Philippines are included for illustrative purposes.

Macroecological conclusions based on bats in the New World may be widely applicable to bats in general. Nonetheless, the considerable differences in the geography of landmasses or the systematics and evolutionary history of bats in Old and New Worlds offer significant challenges. For example, the shapes, sizes, and connectivity of Old World continents are quite distinct from those in the New World. The New World comprises two large interconnected continents, a conterminous tropic region, and few large associated islands. The Old World comprises three disconnected continents (Africa, Eurasia, and Australia), three distinct tropical areas, and a multitude of associated large islands. Similarly, all New World bats are members of the Microchiroptera, whereas Old World bats include members in both the Micro- and Macrochiroptera. The world is not a simple place. Profitable research agendas of the future would assemble data for all continents, quantify patterns, and compare that information with data for other taxa, resulting in a more synthetic and comprehensive understanding that distinguishes broad-scale biogeographic and macroecological patterns from patterns that are regional or idiosyncratic in nature.

**Patterns of Species Range Size**

The emergence of macroecology (Brown 1995) as a dynamic research focus in contemporary ecology has provided incentive to document patterns in the distribution of species range sizes, determine the mechanisms that effect such patterns, and understand their consequences to local species assemblages. Within a particular taxonomic group, species range sizes can be quite variable. However, complications associated with the absence of a universal metric of range size (e.g., latitudinal extent vs. geographic range area), biases associated with underestimating the range sizes of species with low local densities, the dynamic nature of species ranges over time, and uneven sampling intensities for species in a taxon reduce the number of comparative studies that are possible. Nonetheless, a growing body of evidence suggests that species range-size distributions are right-skewed or “hollow curves,” which appear to be normally distributed when frequency is evaluated for log-transformed range
sizes (Gaston 1994; Pagel et al. 1991; Rapoport 1994). Lognormal distributions could be the consequence of the interaction of a multitude of mechanisms acting independently and in concert or could be a consequence of a few processes related to the evolutionary development and age of a higher taxon (Gaston 1994; Lawton 1993), the manner in which the likelihood of speciation or extinction is associated with range size (Chown 1997; Tokeshi 1993), or any of a broad suite of ecological processes (Gaston and Kunin 1997; Kunin and Gaston 1993). For example, some of the variation in range sizes for a higher taxon may be related to latitude and its correlates. The propensity for range sizes of species to be smaller in the tropics than toward the poles has been designated as "Rapoport's rule" and has been used to account for the latitudinal gradient in species density (Brown 1995; Stevens 1989). However, a growing body of empirical and theoretical research suggests that the empirical relationship is equivocal (Gaston 1999; Gaston et al. 1998; Rohde et al. 1993; Roy et al. 1994) and may be spurious (Colwell and Hutt 1994; Colwell and Lees 2000; Lyons and Willig 1997).

Variation in Range Size

Lyons and Willig (1997) determined the latitudinal extent (in degrees) of the distributional ranges of 255 species of bats (fig. 13.1) in the continental New World. Unfortunately, similar distributional ranges have not been compiled for bats on other continents. Consequently, comparisons of Old World versus New World faunas, or Megachiroptera versus Microchiroptera, await resolution of taxonomic and distributional status.

In the New World, species differ in latitudinal range size by over two orders of magnitude (fig. 13.1), from 1° of latitude for Myotis cobanensis (known from a single collection locality) and Rhogeessa gracilis, to over 100° of latitude for Lasiusus cinereus (mean = 28.9; SD = 19.1; SEM = 1.2). Similarly, central tendencies and dispersions of latitudinal range sizes differ among New World bat families (table 13.1), with the species of Noctilionidae and Natalidae having the largest and smallest mean latitudinal range sizes, respectively, and the species of Molossidae and Noctilionidae having the most and least variable latitudinal range sizes, respectively (fig. 13.2A–E).

Like the situation for most terrestrial taxa, the distribution of latitudinal range sizes for all New World bats differs from a lognormal distribution and is left-skewed, with a greater-than-expected number of small-sized ranges (skewness, \( g_1 = -0.9221 \), \( P < 0.001 \); kurtosis, \( g_2 = -0.480 \), \( 0.2 > P > 0.1 \)). Moreover, the latitudinal ranges of three of the four chiropteran families with more than 15 species in the New World exhibited significant deviations from a lognormal distribution and were left skewed (Phyllostomidae, \( g_1 = -0.855 \), \( 0.001 < P < 0.002 \) and \( g_2 = -0.786 \), \( P > 0.2 \); Vespertilionidae, \( g_1 = -0.868 \), \( 0.005 < P < 0.01 \) and \( g_2 = 0.218 \), \( P > 0.2 \); Molossidae, \( g_1 = -0.953 \), \( 0.05 < P \)
Figure 13.1. Frequency distribution of latitudinal extents (in degrees) for the distributional ranges of 235 species of New World bats.

Table 13.1. Descriptive statistics for latitudinal extent (in degrees) of range sizes for continental New World bat species by family

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of species</th>
<th>Mean</th>
<th>SD</th>
<th>SE</th>
</tr>
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<tbody>
<tr>
<td>Emballonuridae</td>
<td>18</td>
<td>26.5</td>
<td>15.4</td>
<td>3.6</td>
</tr>
<tr>
<td>Pteropodidae</td>
<td>2</td>
<td>31.0</td>
<td>14.1</td>
<td>10.0</td>
</tr>
<tr>
<td>Molossidae</td>
<td>29</td>
<td>37.7</td>
<td>23.5</td>
<td>4.4</td>
</tr>
<tr>
<td>Mormoopidae</td>
<td>5</td>
<td>40.6</td>
<td>5.9</td>
<td>2.7</td>
</tr>
<tr>
<td>Natalidae</td>
<td>2</td>
<td>17.5</td>
<td>9.2</td>
<td>6.5</td>
</tr>
<tr>
<td>Noctilionidae</td>
<td>2</td>
<td>52.0</td>
<td>8.5</td>
<td>6.0</td>
</tr>
<tr>
<td>Phyllostomidae</td>
<td>128</td>
<td>27.0</td>
<td>16.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Thyropterygidae</td>
<td>2</td>
<td>37.0</td>
<td>11.3</td>
<td>8.0</td>
</tr>
<tr>
<td>Vespertilionidae</td>
<td>67</td>
<td>28.0</td>
<td>23.0</td>
<td>2.8</td>
</tr>
</tbody>
</table>
Figure 13.2. Comparison of frequency distributions of the natural logarithm (log) of range size in degrees of latitude (left col.) and natural log of body size in kilograms (right col.) for all bats (A, F), ammalarisids (B, C), phyllostomids (C, H), vespertilionids (D, I), and molossids (E, J) from the New World.
< 0.02 and \( g_1 = -0.301, P > 0.20 \). In contrast, the distribution of latitudinal range sizes for the Emballonuridae did not differ from a log normal (\( g_1 = -0.732, 0.2 > P > 0.1; g_2 = -0.786, 0.2 > P > 0.1 \)), but the fewer species in the family results in lower statistical power to detect deviations if they are real (note that \( g_2 \) is negative in this situation also). Thus, New World bats in general, as well as constituent larger families, tend to be more constrained with respect to their maximum range size than with respect to their minimum range size. Genetic differentiation by distance or geographic barriers to gene flow may enhance the likelihood of speciation by broad-ranging taxa, resulting in less variation than expected based on a lognormal distribution.

Much of the variation in the latitudinal extent of species ranges may be a consequence of differences among species in body mass. Indeed, several researchers have postulated or observed that larger-bodied species have larger geographic ranges than do small-bodied species (Arita et al. 1990; Brown and Maurer 1987, 1989; Lawton et al. 1994; Rapoport 1975, 1982; Taylor and Gotelli 1994). Two general mechanisms have been hypothesized to account for such patterns. The first, espoused by Brown and Maurer (1987), is that the upper limits to range size are determined by the available continental land area, whereas the lower limit is defined by the minimum viable population size of the taxon. Because home-range size scales positively and population density scales negatively with body mass, the minimum range size of species would tend to increase with increasing body size. Because of small total population sizes, large-bodied species with small geographic ranges would have high probabilities of extinction, thus predisposing a positive correlation between body mass and range size.

A second mechanism, suggested by Gaston (1990), regards small-bodied species as more sensitive to density-independent perturbations, diminishing the likelihood of their persistence over broad geographic areas and, thereby, affecting a positive association between body mass and range size. Conversely, Gaston (1988) and Gaston and Lawton (1988a, 1988b) suggested a mechanism whereby small body size would lead to larger geographic distributions. This mechanism is based on the observation that the intrinsic rate of population increase decreases with increasing body size. Thus, small-bodied species that colonize a site should be able to increase more rapidly to population densities that are sufficiently large to avoid stochastic extinction. At the same time, the smaller equilibrium densities of large species would make them more susceptible to stochastic extinction, regardless of their rates of increase. In general, the salient differences between the two sets of ideas are predicated on whether species persist because of the size of their total populations throughout their distribution (positive correlations between body mass and range size) or persist as a consequence of local abundance and demographic attributes (negative correlations between body mass and range size).
Despite theory calling for positive or negative relationships on a log-log scale (fig. 13.3), the latitudinal extent of a species range is not related significantly to body mass for all New World bats ($r = 0.101, P > 0.05$). Moreover, the lack of a significant relationship is not consequence of the different families evincing strong but opposing patterns. Indeed, the relationship between log of latitudinal extent and body mass for the Emballonuridae (fig. 13.3B), Phyllostomidae (fig. 13.3C), and Molossidae (fig. 13.3E) are all non-significant. Only the Vespertilionidae (fig. 13.3D) shows a significant and positive correlation ($r = 0.331, 0.01 > P > 0.001$). The same statistical inferences follow if all analyses are conducted in arithmetic space. A number of conclusions are possible based on these results. For bats in general, and for the Emballonuridae, Phyllostomidae, and Molossidae in particular, neither mechanism may be in operation, or the mechanisms may counteract each other, resulting in the absence of a clear statistical pattern. Because critical life-history traits of bats (e.g., litter size or number of litters per year) do not vary with body size in the same manner as in other taxa (e.g., Barclay and Herder, this volume) or are unknown (e.g., association between body size and either home-range size or population density), the demographic linkages required to produce an association between body size and range size may be inoperative or weakened in the Chiroptera in general. Alternatively, latitudinal extent may not be an appropriate metric for assessing range size, and analyses with actual range areas may yield different insights.

In a broad analysis of 150 species of New World bats, Arita (1993) documented that the distribution of species was not mutually independent among categories (three-dimensional contingency test, $X^2 = 20.78, P < 0.05$) defined by species range size (above and below the median range area), abundance (above or below the median abundance), and taxonomy (Emballonuridae, Phyllostomidae and associated taxa, Vespertilionidae and associated taxa, and Molossidae). Decomposition of the three-way interaction into a component assessing the partial independence of taxonomy from distribution and abundance was rejected as well ($X^2 = 17.03, P < 0.05$), suggesting that there are taxonomic differences in the allocation of species to conditions of "rarity" as defined by a classification based on abundance and distribution (i.e., locally abundant but restricted distribution, locally abundant and widespread distribution, locally scarce and restricted distribution, locally scarce but widespread distribution). Species in the Phyllostomidae generally are equally common in all categories of rarity, except that they are infrequent in the locally scarce and restricted category. In contrast, each of the other three groups disproportionately occurred in two categories of rarity: locally rare but widespread distributions or locally rare and restricted distributions. Using an index of rarity based on both local abundance and distributional area, Arita (1993) identified a list of rare species that would be of special conservation
Figure 13.3. Correlation between log-transformed latitudinal extent (degrees) and body size (kilograms) for all bats (A; $r = 0.101, n = 235, P > 0.05$), Emballonuridae (B; $r = 0.169, n = 16, P > 0.05$), Phyllostomidae (C; $r = -0.004, n = 115, P > 0.05$), Vespertilionidae (D; $r = 0.311, n = 56, P < 0.01$), and Molossidae (E; $r = -0.022, n = 25, P > 0.05$) in the New World.
Table 13.2. List of Neotropical bats species of special conservation concern based on considerations of patterns of local abundance and geographic range area (after Aréa, 1995)

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
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<tbody>
<tr>
<td>Emballonuridae</td>
<td>Balantiopteryx plicata</td>
</tr>
<tr>
<td></td>
<td>Diclidurus ingens</td>
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<tr>
<td></td>
<td>Peropteryx huppieri</td>
</tr>
<tr>
<td>Mormoopidae</td>
<td>Mormoops megalophylla</td>
</tr>
<tr>
<td>Phyllostomidae</td>
<td>Glyphonycteris davisi</td>
</tr>
<tr>
<td></td>
<td>Lampronycteris brachyotis</td>
</tr>
<tr>
<td></td>
<td>Lonchorhina arnocaensis</td>
</tr>
<tr>
<td></td>
<td>Micronycteris schmidtorum</td>
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<td></td>
<td>Phyllostomus latifolius</td>
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<tr>
<td></td>
<td>Tsonatra carrikeri</td>
</tr>
<tr>
<td></td>
<td>T. rota</td>
</tr>
<tr>
<td></td>
<td>T. schulzi</td>
</tr>
<tr>
<td></td>
<td>Aorura cultrata</td>
</tr>
<tr>
<td></td>
<td>Choeremisicus minor</td>
</tr>
<tr>
<td></td>
<td>Lichonycteris obscura</td>
</tr>
<tr>
<td></td>
<td>Scleronycteris ega</td>
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<tr>
<td></td>
<td>Centurio senex</td>
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<tr>
<td></td>
<td>Sturnira bidens</td>
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<tr>
<td></td>
<td>S. bogotensis</td>
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<tr>
<td></td>
<td>S. erythromos</td>
</tr>
<tr>
<td></td>
<td>Vampyressa brocki</td>
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<tr>
<td></td>
<td>V. nymphae</td>
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<tr>
<td></td>
<td>Platyrhinus brachycephalus</td>
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<td></td>
<td>P. infuscus</td>
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<tr>
<td>Natalidae</td>
<td>Natalus tumidirostris</td>
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<tr>
<td>Vespertilionidae</td>
<td>Bauerus dubiaquercus</td>
</tr>
<tr>
<td></td>
<td>Eptesicus diminutus</td>
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<td>E. fuacus</td>
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<td>Lasius intermedius</td>
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<td>Myotis nesopolis</td>
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<tr>
<td></td>
<td>M. oxytus</td>
</tr>
<tr>
<td>Molossidae</td>
<td>Eumops dabbenei</td>
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<tr>
<td></td>
<td>E. huerae</td>
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<tr>
<td></td>
<td>Molossops grimmalli</td>
</tr>
<tr>
<td></td>
<td>Promops centrulis</td>
</tr>
<tr>
<td></td>
<td>P. nasutus</td>
</tr>
</tbody>
</table>

Note. Taxonomic designations are updated based on Simmons (1996) and Wetterer et al. (2000).

concern, targeting them as conservation priorities and as foci for studies of autecology and natural history (table 13.2).

In a study restricted to species whose distributions were wholly North American, Pagel et al. (1991) documented a hollow curve for bats based on an arithmetic plot of the geographic areas of their distributions. Almost 70% of the 91 North American species occupied less than 7% of the continental area,
and less than 5% of the species had ranges that included more than half of the continental area (median, 1.9%; average, 6.5%). In a more regional analysis, Arita et al. (1997) documented a right-skewed distribution of range areas for bats as well as for nonvolant mammals based on arithmetic plots. Indeed, Anderson (1977) noted a hollow curve for all mammalian orders, including bats, and subsequently developed a quantitative model to account for variation in range size distributions that proved equally applicable to birds, reptiles, amphibians, and fish (Anderson 1985). Nonetheless, caution must be exercised in considering and interpreting analyses that only consider a portion of a particular landmass or a portion of the geographic ranges of species. Moreover, exclusion of bats with ranges that extend into South America likely biased detection of pattern in an appreciable manner, especially given the increase in species richness toward tropical areas.

Smith et al. (1994) explored macroecological patterns of mammalian taxa prior to the arrival of Europeans in mainland Australia based on distributional data in Strahan (1983). For 37 species of bats whose distributions are limited to Australia or Tasmania (thereby excluding 20 species with broader distributions in Asia and the Pacific), they examined range size characteristics within mainland Australia. Compared to most other mammalian orders (Dasyuromorpha, Diproptodontia, and Rodentia but not Peramelemorpha), bats generally have quite large ranges, almost twice the size of those in other orders (table 13.3; see also Rapoport 1982, table 2.1). In addition, they have the least right-skewed and most platykurtic distribution of range sizes of all Australian orders. Only 13 of 214 mammal species (62%) have range distributions that are large enough to make up at least half of the mainland; eight of them (62%) are bats. In contrast, the great majority of Australian mammals (87%) occupy less than a third of the continent, and only 14% of these are bats. The

<table>
<thead>
<tr>
<th>Order</th>
<th>Number of Species</th>
<th>Mean</th>
<th>Median</th>
<th>Large</th>
<th>Small</th>
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<tr>
<td>Chiroptera</td>
<td>37</td>
<td>24.9</td>
<td>10.6</td>
<td>8</td>
<td>26</td>
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<td>Dasyuromorpha</td>
<td>39</td>
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<td>6.7</td>
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<td>35</td>
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<tr>
<td>Peramelemorpha</td>
<td>10</td>
<td>20.0</td>
<td>14.8</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Diproptodontia</td>
<td>74</td>
<td>10.5</td>
<td>4.7</td>
<td>3</td>
<td>67</td>
</tr>
<tr>
<td>Rodentia</td>
<td>52</td>
<td>8.4</td>
<td>3.4</td>
<td>0</td>
<td>48</td>
</tr>
<tr>
<td>All species*</td>
<td>214</td>
<td>13.4</td>
<td>6.2</td>
<td>13</td>
<td>186</td>
</tr>
</tbody>
</table>

Note: Descriptive statistics are for percent of area of mainland Australia. Large and small ranges are arbitrarily defined as those occupying at least half or no more than 30% of the continental area, respectively.

*Statistics for all species include data on platypus and marsupial mole, which are not included in table otherwise.
observation that Australian mammals on average occupy a larger proportion of their continental landmass than is the case for North American and Palearctic mammals may be a consequence of the reduced topographic heterogeneity there (Smith et al. 1994) but may reflect the disproportionate contribution of bats to the right-hand tail of the range-size distribution in Australia, compared to the situations in Nearctic or Palearctic regions.

The extent to which variation in the area of species ranges is associated with taxonomic affiliation or ecological function has been assessed for Mexican bats by Arita et al. (1997). They classified bats into two broad categories: widespread and restricted. Widespread bats are those species with range areas that are greater than the median range of all bats in Mexico, whereas restricted species are those ranging over areas smaller than the median (Arita 1993). No differences in the proportion of widespread versus restricted species existed among four taxa (fig. 13.4A): Emballonuridae, Phyllostomidae (plus Mormoopidae and Noctilionidae), Vespertilionidae (plus Natalidae and Thyropteridae), and Molossidae ($X^2 = 4.56$, df = 3, $P > 0.05$). In contrast, highly significant differences ($X^2 = 14.39$, df = 3, $P < 0.01$) occurred among feeding

Figure 13.4. Comparison of the proportion of restricted and widespread species of Mexican bats within taxonomic (A) or ecological (B) groups (from Arita et al. 1997). See text for details concerning criteria for restricted and widespread classifications. Group richness on which the proportion of species is based is nine for Emballonuridae, 62 for Phyllostomidae (including species in the Noctilionidae and Mormoopidae; hence the Noctilionoidea), 47 for Vespertilionidae (including Natalidae and Thyropteridae), 18 for Molossidae, 76 for aerial insectivores, 21 for gleaning animalivores, 22 for frugivores, and 12 for nectarivores (the two noctilionids and three desmodontines were not included in analyses because of low species richness).
categories (i.e., aerial insectivores, gleaning animalivores, frugivores, and nectarivores; fig. 13.4B). Thus, the ecological characteristics of bats are associated more intimately with the size of their geographic distributions than are the phylogenetic affinities of the species, per se.

In a comparative study of South American mammals, Ruggiero (1994) documented considerable variability in the area of the geographic ranges of bats. Along with hystricognath rodents and carnivores, the frequency distribution of range size for bats differed significantly from a lognormal distribution. More specifically, widespread taxa were more common in bats than predicted by a lognormal distribution. Indeed, a quarter of the species had ranges less than or equal to 900,000 km², half of the species had ranges between 900,000 and 9,200,00 km², and a quarter of the species had ranges greater than 9,200,000 km². By convention (Rapoport 1975, 1982), these groups of species, as classified by their quartile representation in the Chiroptera with regard to range size, are microareal (i.e., lower quartile), mesoareal (middle two quartiles), and macroareal (upper quartile) species. Microareal species are not randomly distributed throughout South America (Ruggiero 1994). Rather, they are clustered at the coasts of the continent and commonly are associated with the tropical Andes. This has important ramifications for conservation because areas of highest richness (e.g., Amazonian lowlands) often harbor species with the highest vulnerability to extinction (i.e., microareal species).

Latitudinal Gradients

Early work concerning the propensity for the geographic ranges of species to become progressively smaller toward the equator resulted in the formulation of Rapoport's rule (Stevens 1989). Subsequent work identified significant complications for assessing the veracity of the rule. For example, detection of the pattern may be predicated on the measure of central tendency used for its quantification (Roy et al. 1994). Moreover, violations of spatial independence and phylogenetic independence among latitudinal measures compromise statistical assessments (Lecher and Harvey 1994; Rohde et al. 1993; Taylor and Gotelli 1994). Finally, geometric constraints may predispose the distribution of species ranges to evoke a pattern coincident with the predictions of Rapoport's rule (Colwell and Hurtt 1994; Colwell and Lees 2000; Lyons and Willig 1997).

For bats, Ruggiero (1994) was the first to document the empirical pattern of decreasing mean latitudinal range size toward the tropics using Stevens's method of plotting the mean latitudinal range of all species that occur within a band versus the latitude of the band (Stevens 1989). In Ruggiero's analysis, species whose ranges extended into Central America were truncated and estimated by only their South American areas, which would underestimate the distribution of tropical species. Ruggiero also documented the increase in variability in latitudinal extent away from the tropics. A similar empirical pattern was documented by Lyons and Willig (1997) using Stevens's method for
Figure 13.5. Latitudinal gradients of mean range size of New World bats based on (A) Stevens's method and (B) the midpoint method (see text for descriptions of methods) from Lyons and Willig (1997). Negative values for latitude represent the southern hemisphere, whereas positive values represent the northern hemisphere. Vertical bars represent 1 SEM; bars without standard errors represent latitudinal bands occupied by single species.

of the entire New World (fig. 13.5A). Nonetheless, the spatial nonindependence of species distributions tends to smooth the pattern and may affect statistical significance, even if it cannot create a pattern per se (Pagel et al. 1991). The midpoint method of Rohde et al. (1993) circumvents this problem by calculating the midlatitudinal point in the distribution of each species in a fauna, and evaluating the degree to which the extent of latitudinal ranges are a function
of their midlatitudes. An evaluation of Rapoport's rule based on the midpoint method for New World bats (Lyons and Willig 1997) confirmed that range size decreases with decreasing latitude in North America to about 20° N latitude; however, the pattern in South America did not conform to the predictions of Rapoport's rule (fig. 13.5B). Thus, both Stevens's method and the midpoint method failed to consider constraints imposed by the geometry of the continental landmasses on which a fauna occurs (Colwell and Hurtt 1994).

Based on a series of simulation analyses, it appears that the variation in range sizes of New World bats differs from that produced by stochastic processes, and the rate at which range size decreases with increasing latitude was not as precipitous as predicted by a null model (Lyons and Willig 1997). Because of geometric constraints, tropical species are predisposed to have large ranges and extratropical species are predisposed to have small ranges (fig. 13.6), and they do (i.e., the correlation between latitudinal range size and midlatitude is −0.233). However, the spirit of Rapoport's rule is met because the correlation is much less negative than produced by chance (fig. 13.7). Tropical species have smaller ranges and extratropical species have larger ranges than those produced by stochastic processes alone.

![Graphical representation of the relationship between latitudinal range size and midlatitude for New World bats (Lyons and Willig 1997). The vertical line represents the Isthmus of Panama. Negative values for latitude represent the southern hemisphere, whereas positive values represent the northern hemisphere. The triangular shaded area represents the values of range size that are possible given geometric constraints, whereas the dots represent the actual latitudinal ranges of bat species.](image)

Figure 13.6. Graphical representation of the relationship between latitudinal range size and midlatitude for New World bats (Lyons and Willig 1997). The vertical line represents the Isthmus of Panama. Negative values for latitude represent the southern hemisphere, whereas positive values represent the northern hemisphere. The triangular shaded area represents the values of range size that are possible given geometric constraints, whereas the dots represent the actual latitudinal ranges of bat species.
Correlation Coefficients

Figure 13.7. The significance of the correlation between latitudinal range size and midlatitude for New World bats (n = 244) was evaluated using a simulation approach because of biases related to geometric constraints on range size (Lyons and Willig 1997). In the simulation model, the northern and southern termini of 244 ranges were produced at random, and the correlation between latitudinal range size and latitudinal midpoint were calculated. These random correlation coefficients were generated 1,000 times, producing a probability density function (histogram). The actual correlation coefficient (arrow) was among the rarest of outcomes produced by chance (r = -0.233, P < 0.001), suggesting that although the empirical pattern is for range size to increase with decreasing latitude, the ranges of tropical species are smaller and the ranges of extratropical species are larger than geography of the New World would impose because of geometric constraints.

Elevational Gradients

Prior to the 1990s, elevational gradients in species range size received little attention in the literature; the focus was on the description of pattern rather than on an assessment of causal mechanisms. The extension of Rapoport's rule to elevational gradients by Stevens (1992) provided renewed interest in such patterns by suggesting alternative mechanisms to those historically thought to produce the elevational gradient in richness (see MacArthur 1972) and by linking latitudinal and elevational mechanisms thought to effect patterns of richness and range size. A number of climatic characteristics are known to affect range limits of species; these include humidity, precipitation, evapotranspiration, and temperature (Stevens and Fox 1991). Because the breadth of climatic conditions experienced by mountain residents in an individual's lifetime increases with increasing elevation (Adams et al. 1920; Merriam 1894), high-elevation species must be adapted to a broader range of climatic conditions than are their lowland counterparts, and this, in turn, facilitates broad range size in high-elevation species. Indeed, Stevens's (1992) claim of parallel gradients of species richness (decreasing with increasing elevation) and species
range size (increasing with increasing elevation) for a wide range of montane organisms (i.e., trees, mammals, birds, reptiles, insects, and amphibians) catalyzed research on elevational gradients in range size from a conceptual perspective. Nonetheless, considerable controversy surrounds these issues (Rahbek 1997).

Elevational gradients in range size for bats are well documented at two sites: Manu National Park and Biosphere Reserve in the Andes of southeastern Peru (Patterson et al. 1996, 1998) and the Sierra de Manantlan Biosphere Reserve in the Sierra Madre del Sur of west-central Mexico (Iniguez Davalos 1993). Both sites span broad elevational profiles of more than 2,000 m and include a number of botanical life zones; nonetheless, the way in which range size varies with elevation differs between sites.

The elevational gradient in Manu traversed approximately 3,000 m and included five major life zones: lowland rainforest, montane rainforest, cloud forest, elfin forest, and pura. Species richness declined monotonically with increasing elevation (fig. 13.8A). Moreover, the elevational ranges of the 129 bat species showed a striking pattern (fig. 13.8B) of increasing elevational amplitude with increasing elevation, with no indication of a mid-elevational peak in range amplitude. Indeed, after classifying species into pentiles based on elevational midpoints (fig. 13.8C), pentile rank accounted for significant variation in mean elevational amplitude ($P < 0.003$, adjusted $R^2 = 0.95$). Most species (111 of 129) extend into the lowlands ($<500$ m) and only a few species have elevational maxima above 1,000 m. In fact, only five species (<4% of the fauna)—Sturnira bidens (1,990–2,865 m), S. nana (1,600–1,700 m), Anoura sp. nov. (3350–3450 m), Carollia sp. nov. (1,700–2,250 m), and Mormopterus phrudos (1,850 m)—have their entire distributions above 1,500 m. The elevational amplitude of species occupying the highest elevations (top pentile) is approximately two-thirds of the length of the entire gradient (mean amplitude, 2,196 m). Taken together, these data provide strong support for “Stevens’s rule” of range size and elevational gradients. Indeed, because bats have no center of endemism on the altiplano, and because highland species do not replace lowland species along the gradient, agreement with Stevens’s rule is almost guaranteed. Birds and murid rodents, which exhibit distinctly endemic faunas in the altiplano, fail to show such correlations between elevation and range amplitude.

The elevational gradient in the Sierra de Manantlan of Mexico traversed over 2,500 m (400–2,980 m) and included savanna, tropical deciduous forest, tropical semideciduous forest, gallery forest, oak forest, pine-oak forest, pine forest, and montane mesophytic forest. Although 55 species of bats occurred in the general region, Iniguez Davalos (1993) analyzed the distributional amplitudes of only the 27 species actually collected during his study. Species richness in the Sierra de Manantlan varies with elevation in an idiosyncratic manner (fig. 13.9A): low elevations harbor intermediate numbers of species;
Figure 13.8. Elevational gradients of bats in the Manu National Park and Biosphere Reserve of southeastern Peru (from Patterson et al. 1998).

A. Species richness ($S$) decreases with elevation ($E$) along a 3,000-m transect ($S = 138.7005 - 0.07835E + 0.000011E^2$; $P < 0.001$ for all regression coefficients; adjusted $R^2 = 0.99$).

B. Elevational range profiles (vertical lines) of each species arranged according to mid-elevation (squares).

C. Range amplitude (mean, filled circle; standard error, vertical bar) as a function of elevation for each of five classes corresponding to percentiles of species ranks by elevational midpoint.
Figure 13.9. Elevational amplitudes of beta from the Sierra de Manantlan Biosphere Reserve in the Sierra Madre del Sur of west central Mexico (derived from Iñiguez Davalos 1993). A, Species richness is unrelated to elevation. B, Elevational range profiles (vertical lines) of each species arranged according to mid-elevation (filled circles). C, Range amplitude (mean, filled circle; standard error, vertical bar) as a function of elevation for each of five classes corresponding to percentiles of species ranks by elevational midpoint.
high elevations harbor few species; and mid-elevations support the highest number of species. In contrast to the pattern showed by Andean bats, the elevational amplitudes of species shows a modal distribution (fig. 13.9B), with largest elevational amplitudes exhibited by species occupying the second and third pentiles (fig. 13.9C). Species with the smallest elevational amplitudes had midpoints in their elevational distribution located either below 1,250 m (five species) or above 1,750 m (eight species). In contrast, species with the broadest elevational amplitudes had elevational midpoints at intermediate elevations. Indeed, pentile rank accounted for appreciable variation in mean elevational amplitude as expressed by a second-degree polynomial (adjusted $R^2 = 0.61$). Less than half of the species extended into the lowlands (<500 m), although over half of the species have elevational minima below 1,000 m. Over a third of the fauna have elevational minima above 1,750 m. Clearly bat distributions in the Sierra Manantlan do not conform to Stevens’s rule. These data are consistent with the idea that discrete highland and lowland faunas meet on the slopes of the Sierra Manantlan. Mid-elevation species, by virtue of being eurytopic, exhibit the greatest elevational amplitude, regardless of their faunal (or historical) affinities.

Summary and Prospectus

A number of generalities are possible regarding the geographic range sizes of bats. First, range sizes are relatively large compared to those of other mammalian taxa. Second, range size varies considerably but independently of body size. Third, range size is associated positively with species abundances. Fourth, range size is related to elevation and latitude, but patterns are variable (monotonic vs. modal) and are context dependent. Fifth, the propensity to be wide ranging is constrained more by ecological than by phylogenetic considerations, although history clearly defines some elevational patterns. Sixth, the geographic range size is more constrained by considerations of being large than of being small.

These descriptive patterns provide a springboard for future research investigations. Methodological issues regarding the consequences of employing different metrics of range size need to be evaluated, with mechanistic explanations for patterns linked more explicitly with particular metrics. Dissecting latitudinal patterns of range size into components related to consequences of empirical variability in range size and actual geographic placement of ranges should help illuminate underlying mechanistic processes. At least as important, increased attention needs to be devoted to assessing the effects of phylogeny on patterns of range size and, then, to decoupling those effects prior to assessments of biogeographic or ecological mechanisms. Independent contrasts and other explicit statistical tools that account for phylogenetic pattern clearly can contribute to this. Scale dependence affects most macroecological patterns, and those of range size likely are not immune. Although most stud-
ies of range size focus on the level of regional faunas, studies that focus on the local level will likely offer new perspectives concerning mechanisms guiding the local assembly of species into communities. More specifically, the utility of linking considerations of range size with abundance as a way to provide insight into conservation status and likelihood of extirpation is an exciting area for future research. Furthermore, little is known about the internal configuration of a species range, and additional focus on the way in which local abundance differs throughout the ranges of widespread versus more narrow-ranging species has both conservation relevance and utility in building foundational theory in macroecology.

**Patterns of Species Richness**

Broad-scale patterns of species richness have received considerable attention during the past quarter century. This attention is a consequence of revitalized interest in biodiversity and the mechanisms giving rise to it, as well as of increasing concern about the unprecedented rate of species loss at the global scale (e.g., Myers and Giller 1988; Rosenzweig 1995). Areographic patterns of species richness for bats are well documented, at least with respect to latitude in North and South America, with equally promising research forthcoming for Africa. Elevational patterns have been described as well but at only a small number of sites, so the generality of patterns is less clear than those for latitude.

**Latitudinal Gradients**

The study of mammals has contributed substantively to quantification of the gradient of increasing species richness from high to low latitudes. Early research focused on the latitudinal gradient in North America (e.g., Hagemeier 1966; Hagemeier and Stults 1964; McCoy and Connor 1980; Pagel et al. 1991; Simpson 1964; Wilson 1974). Although patterns were striking, it was unclear whether the gradient in richness was a product of latitude and its environmental correlates (i.e., temperature, insolation, and seasonality) or a consequence of the unique shape or history of North America. Fortunately, recent efforts have considered South America (e.g., Mares and Ojeda 1982; Ruggiero 1994) or have quantified patterns throughout the New World (Kaufman 1995; Kaufman and Willig 1998; Willig and Gannon 1997; Willig and Sandlin 1991; Willig and Selcer 1989), conclusively documenting that species richness significantly increases toward the tropics in both North and South America.

Findley (1993, fig. 6.3), created a global map of bat species richness based on the number of species in 500 × 500-km² quadrats. Even at this broad scale, it is clear that latitudinal gradients are not similar on all continents. The Neotropics near northwestern Brazil and the Guianas (120 species) and the Paleotropics near the Indomalayan region (100 species) harbor the greatest
richnesses of bats, with reasonably symmetrical reductions in diversity toward the poles. More recent works (Patterson et al. 1996, 1998) have described faunas that are even more species rich from smaller areas in Peru. In contrast to the general pattern in the New World, a latitudinal transect through Africa and Europe shows no regular pattern. Richness is low in arid regions of the Arabian Peninsula and Saharan Africa; increases in the savannas and grasslands to the south (ca. 60 species); and actually declines in the equatorial rainforests of Central and West Africa!

The Chiroptera make a strong contribution to the overall mammalian pattern in the New World (Kaufman 1995; McCoy and Connor 1980; Wilson 1974). The number of species in a 1° band ranges from 80 to 150 species between 0° and 20° latitude, from 10 to 80 species between 20° and 40° latitude, and from zero to 20 species between 40° and 60° latitude (fig. 13.10). Although the details of the form of the increase in richness toward the tropics depend on the size and shape of the sampling units (e.g., cf. Kaufman and Willig 1998; Lyons and Willig 1999; Willig and Lyons 1998; Willig and Sandlin 1991; Willig and Selcer 1989), a rapid increase in species at midlatitudes is characteristic of the order as a whole.

Analyzing patterns of species density for African mammals, Castro-Arellano (1997) documented considerable variability in the latitudinal gradient among orders. Of the 198 species of bats in mainland Africa excluding Madagascar, 156 were endemic to the continent. His quantitative analyses, based on 165 species (124 endemics) distributed over 167 square quadrats (445 km on a side), revealed that over half of the variation in species density was related to latitude, with an additional 5.5% related to longitude. Given that latitude had such a dominant effect on species density, he more precisely evaluated the form of the relationship. He showed that the rate of increase in species toward the tropics was not constant. Rather, it is characterized by a second-degree polynomial in the northern hemisphere (accounting for almost three-quarters of the variation in species density) and a third-degree polynomial in the southern hemisphere (accounting for about 65% of the variation in species density). Thus, like North and South American bats, those in Africa show a strong latitudinal gradient. But unlike the symmetrical pattern north and south of the equator in the New World (Kaufman and Willig 1998), strong asymmetry characterizes the gradient north and south of the equator in Africa.

Species richness of a large area, such as a latitudinal band (gamma diversity), can be a consequence of two factors: alpha diversity and beta diversity (Whittaker 1972). Alpha diversity is the species richness of a standardized sampling unit (e.g., quadrat), whereas beta diversity reflects turnover in species composition between adjacent sampling units (e.g., quadrats within bands). Some have suggested that tropical regions contain more species because of high beta diversity in tropical areas compared to temperate counterparts.
Figure 13.10. Comparisons of actual species richness gradients of bats (filled circles represent counts of species whose ranges overlap a 1-degree latitudinal band) and those predicted by a stochastic model (inner curves represent actual predictions, outer lines define the 95% confidence bands) for three different latitudinal domains: A, the continental New World, B, the distributional limits for all bats, and C, the smallest latitudinal distribution within which 95% of all species occurs (from Willig and Lyons 1998).
Rohde 1992; Rosenzweig 1995). For New World bats (Willig and Sandlin 1991), this hypothesis is unsupported, at least at large spatial scales; species turnover does not increase toward tropical latitudes for any of the larger families in the New World (i.e., Phyllostomidae, Emballonuridae, Mormoopidae, Vespertilionidae, or Molossidae). In fact, tropical regions have higher richness despite an empirical latitudinal gradient in which beta diversity decreases toward the tropics, primarily as a consequence of patterns in families other than the Phyllostomidae, particularly in the Vespertilionidae.

The form, strength, and peak of the latitudinal gradient in bat species richness is taxon dependent for analyses based on quadrats of equal size (250,000 km²) in the New World (Willig and Scler 1989). However, at the spatial scale of that analysis, variation in bat species richness was little affected by variation in longitude, biome richness, or land area. The Phyllostomidae and Molossidae each exhibited a linear increase in richness with decreasing latitude, whereas the Vespertilionidae exhibited a unimodal pattern. Phyllostomids increased most rapidly toward the tropics, with about 73% of the variation in richness related to latitude. Molossids increased most slowly toward the tropics, with about 72% of the variation in richness related to latitude. Moreover, the unimodal pattern for vespertilionids was quite platykurtic (i.e., flat); maximum richness arises at the interface of tropical and temperate regions, with only 49% of the variation related to latitude.

Latitudinal patterns of species richness may depend on the size of the sampling unit. Recently, Lyons and Willig (1999) found no evidence for scale dependence in the latitudinal gradient of species density at spatial scales between 1,000 and 25,000 km². Nonetheless, their approach is predicated on a priori knowledge of the form and parameterization of gradients of species richness (S) with respect to both area (A) and latitude. In a reanalysis, modeled after the approach of Pastor et al. (1996), Lyons and Willig (2002) showed that the parameters (slope, z; intercept, C) of the log form of the power function \( S = CA^z \) differ with latitude. Latitudinal variation in z represents scale dependence, whereas latitudinal variation in C is a scale-free measure of the latitudinal gradient of diversity. In general, any macroecological pattern that is affected by species richness may also exhibit scale dependence because the exponential increase in richness with area will introduce nonadditive components to the broader macroecological pattern.

Most hypotheses proposed to account for the latitudinal gradient in diversity are circular or unsubstantiated by empirical evidence (Rohde 1992), and none lead to direct quantitative predictions about the form of the relationship (Willig 2000). Nonetheless, a general null model, first advanced by Colwell and Hurtt (1994), has been applied successfully in its analytical form to empirical data for New World bats (Willig and Lyons 1998). In essence, if the distribution of the boundaries of species ranges is stochastic with respect to latitude, then species richness should increase symmetrically, from the edges of
continental landmasses to their center (i.e., as a hyperbolic function). In the New World, the model predicts a tropical peak in species richness, which accounts for two-thirds or more of the latitudinal variation in bat species richness (fig. 13.10), depending on geographic domain (i.e., 67% if the New World; 71% if the latitudinal limits of the Chiroptera; 77% if the smallest latitudinal bounds that wholly contain 95% of New World bat species). Moreover, for any randomized latitudinal domain, the gradient of richness for species endemic to that domain should peak at the middle of that domain. For 20 different random latitudinal domains from within the New World, the null model accounted for significant variation in endemic bat species richness. Geometric constraints associated with the bounded nature of terrestrial landmasses predispose latitudinal gradients in the New World toward a tropical peak. Nonetheless, systematic deviations from the predictions of the null model characterize the empirical gradient. Species richness is higher in the tropics and lower in the temperate zones than predicted by the stochastic model, and the residuals are not related to the breadth of the continent at each latitude (i.e., area). Future research should explore the degree to which deviations from the predictions of such null models are related to environmental, evolutionary, or historical factors.

Elevational Gradients

The way in which species richness changes with elevation long has been of interest to biogeographers and ecologists (Brown 1955). Regional richness often is enhanced by the beta diversity that arises with changes in elevation (Brown and Lomolino 1998). Moreover, the elevational gradient may recapitulate the latitudinal gradient in richness, in part because similar mechanisms (Brown 1988) may be in operation (i.e., temperature and productivity decrease with increasing elevation and increasing latitude). Indeed, these mechanisms may be more clearly evident in cases of elevational gradients because points along an elevational gradient are closer and less likely to have undergone distinctive geological or evolutionary histories.

Nonetheless, the existence of a uniform, "general pattern" has been questioned recently, primarily based on issues related to inadequate experimental design (Rahbek 1995). Most studies of the elevational gradient fail to control for the effect of decreasing area on species richness as elevation increases. Thus, at least some of the decrease in richness with increasing elevation may be confounded by areal effects. Similarly, sites often are not stratified or evenly sampled along the elevational gradient, with lowland sites frequently excluded from analyses. Without equivalent sampling along the entire elevational landscape, it may be difficult to detect nonlinearities or modal relationships. Finally, if fewer individuals are sampled at higher elevations, "passive sampling" (Coleman et al. 1982) may obscure the actual variation of species richness by biasing richness to be higher toward the lowlands.
Mountains in Peru

The most comprehensive understanding of elevational gradients of richness for bats derives from the work of Graham (1983, 1990) and Patterson et al. (1996, 1998) in the Andes of Peru. The former author defined elevational patterns based on regional sampling of localities spanning almost 10° of latitude, whereas the latter authors assembled data from a more restricted landscape representing a 3,200-m elevational transect in the Manu Biosphere Reserve (spanning only a single degree of latitude). Despite differences in the spatial focus of their research, the general patterns were congruent in that no modality was evident in the gradient, and species richness decreased with increasing elevation (fig. 13.8A).

Building on the early work of Koopman (1978) and Tuttle (1970), Graham (1983) quantified an elevational decrease in bat species richness ($r = -0.978, P < 0.001$) and diversity ($r = -0.848, 0.001 < P < 0.01$) and an elevational increase in evenness ($r = 0.669, 0.01 < P < 0.05$) in the Andes of central Peru. Richness ranged from over 80 species at low elevations (ca. 200 m) to approximately 10 species at high elevations (ca. 3,400 m). Moreover, the rate at which bat species richness decreased with increasing elevation was dependent on the feeding ensemble associations of the bats. Frugivores (ca. eightfold) and insectivores (ca. sevenfold) showed indistinguishably fast rates of elevational decline, whereas other ensembles (i.e., piscivores, carnivores, sanguinivores, and nectarivores) declined more gradually. Some of these differences in rates among ensembles may be a consequence of the disparity in their overall species richness, especially for sanguinivores (three species maximum) and piscivores (two species maximum). Moreover, the piscivore guild is an artificial construct: evidence for a fish-eating diet in *Noctilio albiventris*, for instance, is lacking; the species pervasively consumes insects. In general, elevational decreases in temperature, foliage height diversity, and food abundance were postulated as ecological filters that exact an energetic cost on the ability of lowland species to exploit higher elevational habitats, resulting in their progressively lower richness (Graham 1983, 1990).

Despite differences in age and richness of their lineages, birds and bats have had approximately equivalent times to diversify and evolve along the eastern slopes of the Andes, making them appropriate taxa to contrast, given that they are homeotherms and the only extant vertebrate taxa that are volant. Graham (1990) documented that changes in elevation account for significant variation in the proportional richness (i.e., percent of the regional fauna) of bats (89 species, $b_1 = -0.249, r^2 = 0.94$), diurnal birds (555 species, $b_1 = -0.131\%$ per 1,000 m, $r^2 = 0.90$), and nocturnal birds (18 species, $b_1 = -0.131\%$ per 1,000 m, $r^2 = 0.62$) along the eastern slopes of the Andes. The decline in proportional richness of bats was greater than that for diurnal birds (Bonferroni adjusted $P = 0.01$) as well as for nocturnal birds (Bonferroni adjusted $P = 0.064$), but the two avian groups declined at indistinguishable rates (Bonferroni adjusted...
Two factors may contribute to these differences. First, the proportional richness of lowland bat faunas (>80%) is appreciably higher than that of either diurnal (<60%) or nocturnal (<70%) bird faunas. Second, the rate of turnover between elevational faunas is greater for birds than for bats. In fact, only a single bat species treated by Graham, *Histiophorus macrotis*, is a true highland specialist (1% of the fauna), whereas approximately 10% and 31% of faunal pools are highland specialists for diurnal and nocturnal birds, respectively. Hence, bat assemblages at high elevations contain a smaller proportion of the fauna, include fewer species restricted to highlands, and consist of species with broader elevational breadths than do faunas comprising nocturnal or diurnal birds. This suggests that lowland bats have been less successful at colonizing or radiating at high elevations compared to birds.

Differences between bats and birds in their success of occupying high-elevation habitats may be related to three factors (Graham 1990; Schmitt-Nielsen 1971). First, bat and bird respiratory systems are quite different. The crosscurrent blood flow to the parabronchial lungs of birds guarantees that gases in air capillaries repeatedly meet freshly deoxygenated blood. In contrast, alveolar ducts in the lungs of bats represent a tidal ventilation system, which at best can equilibrate partial pressures of oxygen in the lungs with that in the pulmonary capillaries. Where partial pressures of oxygen are low, as at high elevations, this may represent a design constraint that limits the ability of bats to exploit high-elevation habitats. Second, rates of energy expenditure at higher elevations associated with thermoregulation are greater for bats than for birds. The generally smaller size of bats compared to birds (hence greater loss of heat because of larger surface to volume ratios) and the increased exposure of vascular tissue in the membranous wings of bats compared to the insulated, feathered wings of birds, result in a greater energetic cost to bats while exploiting cooler regions. Perhaps even more important, the obligate nocturnal habits of bats expose them to considerably lower temperatures during their peak periods of activity compared to the situation enjoyed by diurnal organisms, such as birds. Third, the elevational decline of food resources of bats may be much greater than that for birds. For example, species of trees that produce fruits and that are consumed by bats (e.g., figs and palms) become much rarer at mid- and high elevations, compared to trees that bear fruits on which birds feed (Gentry 1982). Hummingbird-pollinated plants may even increase (e.g., ericaceous plants) in richness at higher elevations, whereas few species of bat-pollinated plants are known to occur at high elevations (Fleming 1988; Gentry 1988; Heithaus 1982). Moreover, the elevational decrease in abundance and diversity of nocturnal insects is greater than that of diurnal insects (Terborgh 1977), although the available data are far from comprehensive. In summary, bat richness may decrease more rapidly than does bird richness because of a greater diminution in the diversity and quantity of resources they consume as well as because of a greater energetic cost of metabolism at higher elevations.
Patterson et al. (1996) documented that most species present in the Manu Biosphere Reserve of southeastern Peru are broadly distributed in lowland Amazonia and that highland assemblages are reduced and are proper subsets of lowland faunas. Although changes in species composition (Jaccard index) were erratic along the elevational gradient, most values were high (>0.8), with an indication of appreciable faunal turnover at the elfin forest-altiplano transition (>2,600 m). Species richness dramatically decreased with increasing elevation. Richness differed greatly among point samples and was related significantly to elevation ($b_1 = -0.060$ species per m, $R^2 = 0.851, 0.01 < P < 0.05$), with only a single species captured at 3,200–3,300 m and 59 species captured at 300–400 m. Nonetheless, part of the elevational variation in species richness was related to differences in sampling effort (nights of netting, $r = 0.76$) and capture rates (number of individuals captured, $r = 0.72$) among elevational sites. To control for this, species presence at each elevation was inferred from elevational range data for each species based on the capture results from all sites along the transect. Again, elevation accounted for almost all of the variation among sites in species richness ($b_1 = -0.053$ species per m, $R^2 = 0.971, P < 0.001$). When species richness per site was further increased based on presumed or possible presence of taxa as suggested by literature records, the form of the relationship became more complex (quadratic or cubic) but in all cases the linear component remained strong and significant. In these cases, the richness of lowland sites is augmented more than is richness of highland sites, a reflection of the fact that few Amazonian species are highland specialists and lowland sites exhibit greater beta diversity. Moreover, the richness of elevational assemblages was correlated inversely to the number of endemic species. This negative correlation has important ramifications for conservation and suggests that protection of species-rich areas does not necessarily protect endemic taxa.

The manner in which richness diminishes with elevation depends on the ecological classification of the species. Nine ensembles were recognized in lowland assemblages (i.e., omnivorous predators, insectivorous piscivores, low-flying frugivores, high-flying frugivores, low-flying insectivores, high-flying insectivores, omnivorous nectarivores, sanguinivores, and insectivorous carnivores), but only six occurred above 3,000 m with the loss of high-flying insectivores, insectivorous piscivores, and omnivorous predators. High-flying insectivores composed an appreciable proportion (ca. 15%) of the fauna at low elevations, decreased rapidly around 1,000–1,500 m, and were absent above 2,000 m. Members of the insectivorous carnivore ensembles similarly represented about 15% of the fauna at low elevations and decreased rapidly at 1,000–1,500 m but persisted at low levels of richness, well into the highlands. In contrast, low-flying insectivores and high-flying frugivores were represented in the lowlands by about 20 and 25 species, respectively, and consistently decreased with elevation until 3,000–3,500 m, where they were represented by three and seven species, respectively.
Elevational patterns of bats contrasted with those of mice as well as birds (Patterson et al. 1998). By demonstrating a gradual decline in richness with increasing elevation (fig. 13.8A), it could be seen that bats were more similar to birds than to mice, whose variation in richness was unrelated to elevation. Although zonations in faunal assemblages were observed between lowland and montane faunas for all three groups, the elevational boundaries of the assemblages differed among groups (i.e., birds, 500 m; bats, 750 m; mice, 1000 m). Moreover, these faunal zones were less discrete for birds and least discrete for bats and did not correspond to vegetational ecotones. A similar lack of congruence between phytogeographic zones and bat assemblages in Venezuela was documented by Willig and Mares (1989). Differences in the elevational zonation of these three groups may reflect phylogenetic histories as well as other biological attributes and suggest limited utility of using one taxon (e.g., birds) as an indicator of general patterns in other groups or as an umbrella group on which to base conservation decisions.

Mountains in the Philippines

The numerous islands of the Philippines harbor 73 species of bats, of which about 40% are endemic to the country (Heaney 1986; Heaney et al. 1998). In the most detailed study of elevational gradients of species richness of flying foxes (Pteropodidae but excluding Acerodon and Pteropus because of their wide-ranging habits), Heaney et al. (1989) compared patterns on an oceanic (Negros) and landbridge (Leyte) island. Each island supported eight species of smaller flying fox, with seven common to both islands.

Species richness was greatest in the lowlands on both islands (seven to eight species), with substantial declines in ridgetop mossy forest (three species). Indeed, changes in species richness were associated more with changes in forest type than with changes in elevation per se. For example, the bat species richness of two mossy forest sites that differed in elevation by 150 m (i.e., the 950-m site on Leyte and the 1,500-m site on Negros) was the same (three species). The most abundant species in agricultural lands were taxa that are widespread in Southeast Asia, whereas the most abundant species in forested areas were Philippine endemics. However, elevational gradients may be difficult to quantify in an unequivocal manner from these data because of three factors. First, elevational relief is not great on either island: 950 m on Leyte and 1,500 m on Negros. Second, only four or five survey stations were established along the elevational gradient, compromising an ability to distinguish linear from nonlinear forms of the elevational relationship with richness. Finally, anthropogenic activities dominated the lowest site on Leyte (agriculture and secondary forest at 50 m) and the lower two sites on Negros (urban and agriculture at 10 m and upland farmland at 600 m). Thus, richness may be responding to a gradient of increasing anthropogenic disturbance toward the lowlands as well as to gradients of biotic and abiotic factors that are correlated with elevation.
Mountains in Mexico

The state of Oaxaca in Mexico harbors one of the most species-rich mammalian faunas in Central America and Mexico and contains many endemic species (Peterson et al. 1993; Sanchez-Cordero 1993). In a comparative study of two elevational transects in Oaxaca (640–2,600 m in Sierra Mazateca, 700–3,000 m in Sierra Mixteca), Sanchez-Cordero (2001) documented elevational changes in richness, trophic diversity, and endemism. Both elevational transects harbored similar species richness (16 species in Sierra Mazateca and 17 species in Sierra Mixteca), with 11 species shared in common.

Variation in elevation was not associated significantly with variation in bat species richness in the Sierra Mazateca ($r_s = -0.63, n = 5, P > 0.10$) but was significantly and negatively associated with elevation in the Sierra Mixteca ($r_s = -0.96, n = 7, P < 0.05$). The small number of elevational sites reduces the power of statistical analyses, especially in the Sierra Mazateca. Nonetheless, combining these results in a meta-analysis (Sokal and Rohlf 1995) suggests that a significant negative association exists between elevation and species richness (Fisher's test for combining probabilities, $X^2 = 11.98, df = 4, P < 0.05$).

The similarities between transects become stronger when assessing habitat-specific patterns of richness. In the Sierra Mazateca, richness was highest in pine-oak forest and high in thorn scrub and tropical semideciduous forest and decreased abruptly in high-elevation oak and cloud forest. In the Sierra Mixteca, richness was highest in lowland tropical semideciduous forest and low in high-elevation cloud, oak, and pine-oak forests.

Paralleling changes in species richness, trophic richness was greater at lower than at higher elevations. All four bat ensembles recognized in the study (i.e., frugivores, nectarivores, insectivores, and sanguinivores) occurred at lowland elevations in thorn scrub, tropical semideciduous forest, and tropical deciduous forest. Sanguinivores and nectarivores did not extend above 1,050 m, frugivores did not occur above 2,450 m, and insectivores peaked at intermediate elevations (between 1,850 m and 2,100 m).

Summary and Prospectus

Regardless of continent or scale, latitudinal gradients of richness are qualitatively similar: species number increases within decreasing latitude. However, important quantitative differences in the form or parameterization of the latitudinal gradient exist among taxa, continents, or scales. Bat richness generally decreases with increasing elevation, however, the form and parameterization of the elevational gradient is geographically variable and sometimes modal.

The extensive documentation of gradients of richness for bats suggests more sophisticated macroecological analyses in the future. The roles of geographic constraints or stochastic processes in affecting latitudinal and elevational gradients need to be assessed more broadly, and the environmental correlates responsible for deviations from null model predictions need to be
identified explicitly. Geographically explicit and scale-dependent analyses based on latitude, longitude, and elevation need to be executed on all continents using Geographic Information Systems (GIS) to identify regional hot spots of bat diversity or areas with unusually high numbers or proportions of species with threatened or endangered status. Quantitative analyses, combining information about all components of diversity at the local level (e.g., richness, evenness, dominance, diversity) and regional patterns related to the composition of faunal pools need to be conducted across a wide array of latitudes in both the New and Old Worlds to understand the interplay between biogeographic and evolutionary processes, on the one hand, and ecological processes, on the other hand. Regional, hemispheric, and global analyses of the way in which variation in productivity might contribute to latitudinal and elevational patterns of richness is ripe for future research. Similarly, the extent to which beta diversity contributes to high regional diversity ought to be explored in a latitudinally and elevationally explicit fashion. Finally, the extent to which functional diversity and species diversity are interrelated should be examined in a number of different geographic settings.

**Patterns of Body Size**

Body size is an incisive phenotypic character that integrates the results of evolution at the levels of morphology, physiology, behavior, and ecology (Barclay and Harder, this volume; Calder 1984; LaBarbera 1989; Peters 1983; Schmidt-Nielsen 1984; Simmons and Conway, this volume; Speakman and Thomas, this volume; Swartz et al., this volume). It can be estimated conveniently by body mass, regardless of the shape or taxonomic affiliation of species (Brown 1995). Thus, it is an ideal comparative character to examine in a macroecological context. Moreover, early work (Hutchinson and MacArthur 1959) suggested that, within a given biota, distributions of body size were right-skewed on a lognormal scale—that is, relatively small size is common, whereas extremely small or large size is rare. Subsequent empirical work generally corroborated that observation for a diversity of organisms from bacteria to mammals (e.g., Brown and Nicoletto 1991; Maurer et al. 1992).

Considerations of the Central Limit Theorem suggest that, because body-size distributions are not usually normal on a logarithmic scale, empirical patterns are not the consequence of random multiplicative factors acting in concert. The ways in which deviations from log normal differ with taxon or scale might implicate underlying mechanisms. More specifically, Brown (1995) noted three general phenomena: (1) body-size distributions are "highly modal," (2) a gradual decline in the frequency of larger body masses produces an extended tail to the right of the mode, and (3) a sharp decline in frequency occurs from the mode toward the left (i.e., small size). Moreover, as geographic scale defining the biota shrinks, the shape of the distribution changes to be-
come more platykurtic while retaining the same range of body sizes but with
gaps (i.e., some body-size classes become absent) in distributions at small spa-

Taxonomic Variation in the Distribution of Body Size

Based primarily on body-size information (body mass) from Silva and Downt-
ing (1995), New World bats, like other taxa, do not have a lognormal frequency
distribution of body masses at the hemispheric scale. Rather, they exhibit
significant right-skewness ($g_1 = 0.328, 0.05 > P > 0.02$) and platykurtosis
($g_2 = -0.858, 0.05 > P > 0.02$). Nonetheless, the pattern for bats (fig. 13.2F)
shows a number of remarkable contrasts with patterns described for other taxa
(Brown et al. 1993). First, the modal value is not as dominant as in other
groups. Second, the decline in frequency to the left of the mode is gradual and
approximately linear. Third, the right-hand tail is less extended and not as
sharply concave.

In part, this distinctive pattern for bats may be a consequence of hetero-
genreity in the distribution of body sizes among the larger families (fig. 13.2G–
J, representing the Emballonuridae, Phyllostomidae, Vespertilionidae, and
Molossidae). For example, the distribution for phyllostomids is more like the
general pattern, with a highly distinctive mode, an extensive right-hand tail,
and a sharply declining left-hand tail. In contrast, the vespertilionids have a
more platykurtic distribution and the molossids essentially exhibit a bimodal
distribution of body masses.

Scale Dependence in Distributions of Body Size

As geographic scale changes from local, through regional, to continental or
hemispheric, so do the attributes of the distribution of body size in bats
(fig. 13.11). However, observed changes in the distribution of body sizes in
bats are not completely coincident with the observations of Brown (1995).
As predicted, the range of body masses (log of mass in grams from 0.8 to
2.0) is conserved proceeding from the distribution at the hemispheric scale
(fig. 13.11A) to that of a site representing a local community (fig. 13.11F).
Moreover, the body-size distribution is more highly platykurtotic ($g_2 =
-0.947, 0.05 > P > 0.02$) in South America than at the hemispheric scale, but it
is not significantly skewed to the right ($g_1 = 0.157, P > 0.2$). Unfortunately,
species richness at smaller spatial scales is sufficiently reduced, compromising the
power to detect significant kurtosis or skewness in body-size distributions
(Sokal and Rohlf 1995). However, examination of the modes and moment sta-
tistics (i.e., $g_1$ and $g_2$) indicates that at the local level (e.g., interior Atlantic rain-
forest at Reserva Natural de M'baracayu in eastern Paraguay), distributions
are least platykurtotic ($g_2 = -0.437$) and most right-skewed ($g_1 = 0.523$)
compared to any other spatial scale.

Similarly, Arita and Figueroa (1999) investigated the scale dependence of
Figure 13.11. Hierarchical evaluation of the logarithmic distribution of body sizes at the level of (A) the continental New World (skewness, $g_1 = 0.328$; kurtosis, $g_2 = -0.858$), (B) South America ($g_1 = 0.157; g_2 = -0.947$), (C) Paraguay ($g_1 = 0.037; g_2 = -0.912$), (D) mesic eastern Paraguay ($g_1 = 0.110; g_2 = -0.937$), (E) the Paraguay central biome ($g_1 = 0.090; g_2 = -0.834$) in the mesic east, and (F) a local site (Reserva Natural de M'baracayu) in the Paraguay central biome ($g_1 = 0.523; g_2 = -0.437$).
patterns of body size in Mexican bats. In general, body mass ranged from 3 g in some vespertilionids, to 150 g in the carnivorous phyllostomid, *Vampyrus spectrum*. At the scale of the entire country, the body-size distribution was unimodal and right-skewed on a semilogarithmic plot. Unlike the pattern of scale dependence exhibited by nonvolant Mexican mammals in which the distribution of body sizes progressively became more even with decreasing spatial scale, for bats this was not so.

The distribution of body sizes in bats retained its right-skewness, even at the smallest spatial scale (0.5 × 0.5 degree quadrats). Moreover, the distribution of body sizes at smaller scales was indistinguishable from those based on a random selection of the same number of species from the entire Mexican bat fauna. Finally, bats differed considerably from nonvolant mammals in Mexico in that they did not exhibit the expected latitudinal increases in body size.

Correlates of Body Size

Based on a subset of 150 New World bat species representing all families and feeding assemblages, Arita (1993) documented that a high proportion of the variation among bats in body size is a consequence of phylogenetic constraints. Indeed, variation among genera within families (42.7%) and among families within the order (42.3%) accounted for most of the variation in body size (85%). Indeed, variation among species within genera accounted for no more than 15% of the total variation. This corroborates a general pattern (see Harvey and Pagel 1991) in which most of the variation in ecologically relevant traits is associated with higher levels in the taxonomic hierarchy.

After controlling for phylogenetic constraints by using means of genera in analyses (following Harvey and Pagel [1991]), Arita (1993) found no association between mean generic body mass and measures of local abundance ($r_s = 0.01, n = 59, P > 0.05$) or with area of geographic distribution ($r_s = 0.26, n = 59, P > 0.05$). This contradicts conventional wisdom (Brown 1995; Maurer 1999) and is surprising because other groups of mammals show a significant association of body mass with density (e.g., Damuth 1981; Eisenberg 1980; LaBarbera 1989; Mohr 1940; Robinson and Redford 1986) and with geographic range size (e.g., Arita et al. 1990; Brown 1981; Cristoffer 1990; Pagel et al. 1991). As expected, some large species of bat such as *Vampyrus spectrum* and *Chiropterus auritus* are locally rare, and some small species such as *Glossophaga soricina* are relatively abundant. However, large species of *Phyllostomus* or *Artibeus* are among the most abundant, and small species such as *Centronycteris centralis* (see Simmons and Handley 1998) are extremely rare members of local assemblages. In part, the absence of an association may be a consequence of the smaller ratio of body masses in the New World Chiroptera (1 : 56; 3 g for *Furipterus horrens* and 169 g for *V. spectrum*) compared to other groups, such as nonvolant mammals (1 : 20,000) or a consequence of nonlinearities in the associations between variables (Brown and Maurer 1987). The latter explana-
tion can be discounted in cases when nonparametric correlations fail to detect patterns.

Summary and Prospectus

Although distributions of body size have only begun to be studied in bats, with the most extensive analyses restricted to New World faunas, a number of emerging generalizations are possible. First, the distributions of body size are generally unimodal, right-skewed, and platykurtic for most families of the Chiroptera. Second, empirical patterns for bats are not congruent with those documented for terrestrial mammals, perhaps because of additional constraints imposed on bat evolution related to tradeoffs involving flight and echolocation. Third, the significant relationship between body size and abundance, at least in Mexican bats, is mostly a consequence of phylogenetic trends.

Research questions related to body mass have only begun to be explored, with many avenues of investigation worthy of pursuit. Once accurate estimates of body mass are available for most species of bat, general questions concerning taxon-specific and geographically explicit characteristics of body-size distributions should be explored, including a global assessment of phylogenetic constraints. Importantly, bats represent ideal organisms to test contentions of Brown et al. (1993) concerning the association of body-size evolution and life-history evolution. The range of masses in the Chiroptera (1,200 g Pteropus vampyrus to the 2 g Craseonycteris thonglongyai) spans the proposed optimal size (100 g) for mammals and includes many small (<20 g) taxa; moreover, phylogenies in the group are reasonably well known (see Jones and Purvis 1997). However, the preliminary assessment is that bats do not adhere to the predictions of theory based on reproductive power, and future research is required to see if alternative models (Charnov 1993; Kozlowski and Weiner 1997) are generally more applicable to the association between body mass and life-history characteristics in bats.

Overview

Although macroecological patterns for bats differ from many general mammalian patterns concerning body mass and abundance, they represent exemplars of the latitudinal gradient of richness. To understand the ubiquity of such patterns, future efforts should concentrate on the application of standardized macroecological methodologies to bat distributions in Africa, Australia, and Eurasia and on intercontinental comparisons. Equally important, research concerning bats is woefully lacking concerning elevational gradients of richness, range size, body size or abundance on all continents and, as such, represent ripe areas of exploration for future study. Indeed, the contradictory
elevational patterns observed for richness and range size highlight the need for a larger number of studies at various latitudes on all continents.

For both elevational and latitudinal analyses, comparison of observed patterns with those produced by appropriate null models, and the design of quantitative analyses to tease apart various competing mechanistic hypotheses should be the emphasis of research in the future (see Hofer et al. 1999). Comparative studies with small mammals such as rodents and marsupials, or with other volant taxa, provide one avenue to explore the mechanistic bases of pattern. Alternatively, the application of analytical models incorporating phylogenetic information is apt to prove fruitful in virtually all macroecological studies of bats.

Clearly, the comparative method has revolutionized the way in which ecologists approach correlative studies like those that dominate macroecological research. Indeed, phylogenetic contingency shapes numerous phenotypic attributes important to the ecological characteristics of all organisms. However, Brown et al. (1996) make an important point: the increasingly popular approach of removing variation among species that is related to phylogenetic relationships may stymie progress in identifying recurrent patterns and understanding their mechanistic bases. Although the analysis of "phylogeny-free" residual variation removes the effect of sharing a common ancestor, it also removes the variation due to the ecology of the common ancestor as well. Ecological and phylogenetic relationships evolve together and are confounded in various ways. To the extent that this is true, phylogenetic variation cannot be removed without compromising ecological understanding. We do not advocate the suspension of comparing ecological phenomena in the context of phylogenies. Rather, we suggest that future research should explore novel ways of analyzing these two important and interrelated processes in a manner that will avoid the "either/or" interpretations of current methodologies (see Brown 1994).

Given the reasonably stable state of bat alpha taxonomy compared to many groups of plants or animals, and the growing information concerning accurate range-size distributions throughout the world, the early part of the current decade should see increasingly strong contributions by bat biologists to the study of macroecology. As ecological studies of bats at the community level increase, and as technologies for assessing bat abundance improve, broader understanding of the scale dependence of associations among range size, population density, and body mass should be forthcoming as well, from both latitudinal and elevational perspectives.

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**Literature Cited**


