CHAPTER 12

Trophic Strategies, Niche Partitioning, and Patterns of Ecological Organization

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Introduction

The tremendous variety of foods that bats exploit, coupled with the various foraging techniques and roosting structures they utilize, have led to remarkable levels of abundance and diversity. Here, we examine elements underlying ecological organization of bat. First, we review an enormous literature that describes and analyzes the principal trophic strategies of bats and the salient features of each type of resource. In doing so, we attempt to identify prevailing patterns of niche partitioning and to determine the special opportunities or constraints that appear to be associated with each feeding strategy. Bats respond to these opportunities and constraints at multiple levels of organization: individual variation, abundance and range limits of species, and the amalgamation of local assemblages into faunas. Where possible, we identify this kind of variation and its corollaries, but the mechanisms that underlie many ecological patterns involving bats mostly remain elusive.

The geographical context of assemblages also helps to shape their variation at broader spatial scales. We follow the discussion of resource partitioning and coexistence at local scales with analyses of latitudinal patterns. These analyses and accompanying discussion focus on gradients in local diversity and the role of character displacement in structuring them.

In the concluding remarks, we relate our findings to bat ecology and conservation. We also call attention to two research areas that appear particularly promising for further ecological research.

Conceptual Underpinnings and Terminology

Controversy surrounds the taxonomic, spatial, and temporal delineation of ecological communities. Most concepts of community involve a set of populations or species that is likely to interact through competitive, trophic, or mutualistic associations. These interactions occur among species that share temporal and spatial domains (Ricklefs 1979). In this expansive sense, a "com-

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Pp. 536 – 579 in Bat Ecology, (T. H. Kunz & M. B. Fenton, Eds.). Univ. Chicago Press, (2003).

munity" is the suite of all taxa that exist contemporaneously at a given place, or the biotic portion of an ecosystem. A community cannot be defined by taxonomic criteria (i.e., "bat communities") because communities must include both autotrophs and heterotrophs. So defined, few communities have been enumerated or studied because it is too costly, time consuming, and taxonomically challenging to do so in any but the simplest systems.

Ecologists commonly study subsets of ecological communities, often because their interests and expertise are circumscribed either by taxa (e.g., bats, birds, bacteria) or by processes (e.g., frugivory, carnivory, detritivory). Fauth et al. (1996) proposed a nomenclature for these subsets that is adopted here (fig. 12.1). An "assemblage" is a subset of the community defined only by taxonomic constraints. Thus, all mammalian (or avian or fungal) components of a community constitute assemblages. In contrast, a "guild" is a subset of the community defined by some type of functional characteristics (e.g., habitat, foraging mode, and diet [Root 1967, 1973]). To study all frugivores or all gleaning insectivores within a community is to target guilds. However, even these more limited groupings are difficult to study in nature. Few community ecologists study the structure or diverse interactions among all the mammals in an ecosystem or their composition and interactions among all insectivorous species (including, e.g., arthropods, amphibians, reptiles, birds, and mammals). Rather, they study components of the community stemming from cross-classifications based on both taxonomy and function (e.g., detritivorous insects, nectarivorous birds, granivorous mammals). These cross-classified groupings constitute "ensembles" (Fauth et al. 1996; fig. 12.1).

By this terminology, bat ecology is the ecological study of assemblages of chiropterans. Studies of frugivorous bats or insectivorous bats focus on ensembles. These distinctions are necessary because rejection or acceptance of hypotheses concerning community organization may depend on whether the research focused on ensembles or assemblages. For example, patterns of body size in frugivorous bats may be difficult to comprehend if interactions with other frugivorous animals such as birds are important but not addressed in a study's design. Indeed, emphasizing that frugivorous bats constitute an ensemble rather than a guild is a terminological reminder that other frugivores may exert significant impacts on the composition and structure of these interacting groups of bats, either through joint exploitation of resources (e.g., Palmeirim et al. 1989) or through territoriality (e.g., Miller 1962).

Logistics commonly force ecologists to study incomplete or heterogeneous collections of bat populations. Often, biologists study the composition and structure of bat faunas occupying geopolitical units (e.g., states, provinces, departments) or large islands (e.g., Puerto Rico). Such studies are unlikely to resolve hypotheses concerning community-level phenomena (Willig 1986). Included populations may never interact with one another, or interactions may

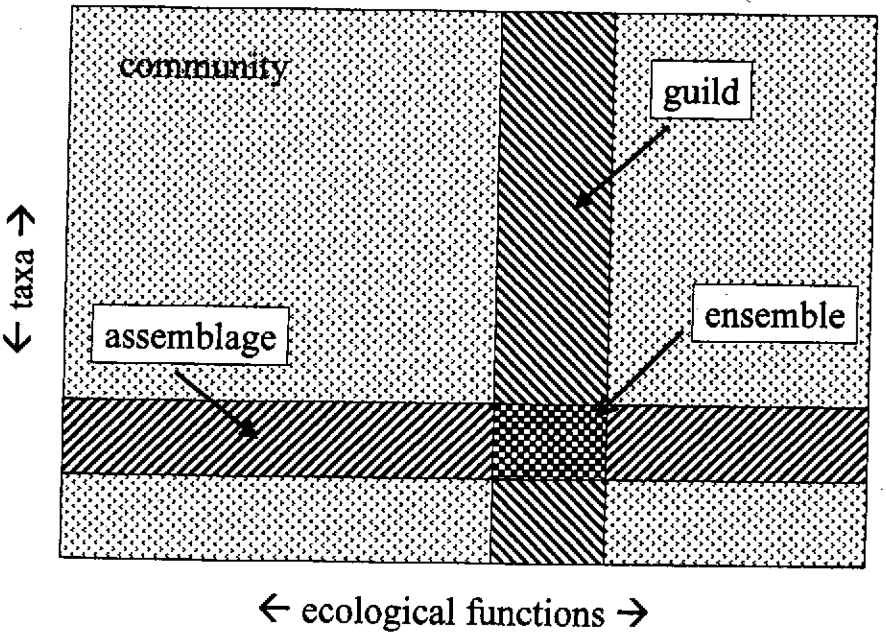


Figure 12.1. Conceptual partitions of an ecological community (after Fauth et al. 1996).

take place with excluded populations. The scale at which patterns are sought in the field should correspond to the spatial and temporal scales of mechanisms thought to produce them.

In some localities, bat diversity may be so great that sampling all elements becomes impractical. Myers and Wetzel (1983, fig. 3) documented the slow accumulation of bat species in the Chaco Boreal of Paraguay, which eventually reached an asymptote of 20 species after 60 nights of collecting. However, 28 species are thought to occur in the area. This problem is particularly important in studies of tropical assemblages, where whole segments of faunas often escape detection and monitoring. Besides necessitating certain types of sampling methodologies, such features may also dictate the choice of sampling units and scales of analysis (e.g., Patterson et al. 1998).

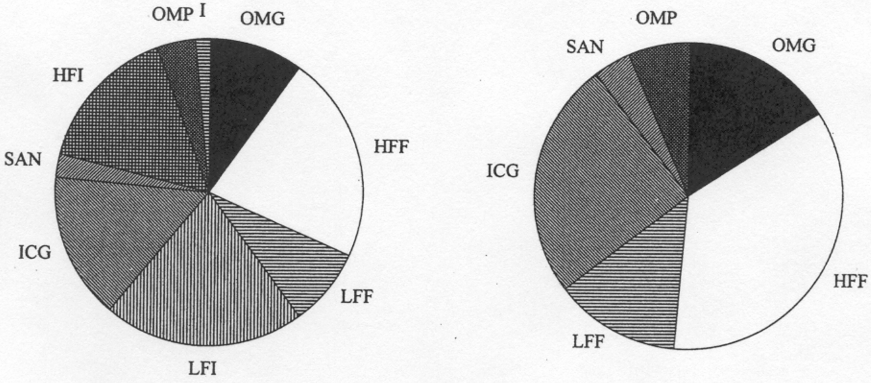
If mechanisms that transpire within communities (e.g., competition, predation, mutualism) are of interest, then communities or their subsets should be the focus of study. Although studies of broadly defined geographic units provide important information concerning biogeography, and may inform studies of community composition (e.g., Arita 1997), it is unclear how patterns and processes operating at a geographic level affect mechanisms of coexistence at local levels (Allen and Starr 1982). No single spatial or temporal scale is proper for studying communities and their component ensembles or assemblages. Rather, the guiding principle should be that the area is not so large, or the time so long, as to contain species with no likelihood of interacting. Similarly, the area should be sufficiently large and the time adequately expansive to contain all of the species whose interactions affect population dynamics.

Finally, it should be obvious from the foregoing that ecologists interested in studying bat assemblages at appropriate spatial and temporal scales are largely limited to observation and comparison, not experiment and manipulation. Experimental community ecology calls for replicated grids, controlled resource levels, and reciprocal-removal experiments that are practically impossible to use in studying bats. For example, each night while foraging, a nectarivorous bat (*Leptonycteris curasoae*) may travel dozens of kilometers, whereas a granivorous pocket mouse (*Chaetodipus baileyi*) foraging below it may move only dozens of meters. The wide-ranging behavior of bats often precludes elegant experimentation and decisive refutation of hypotheses. However, the diversity and importance of ecological roles played by bats in natural communities ensures that elucidating their ecological roles will constitute an important, even vital, step in ecological understanding and environmental management.

Bat Ensembles and Their Characteristics

There are many possible ways to classify coexisting bats that are most likely to interact with one another. Major food types, principal roosting habits, echolocation type, and flight strata have all been used singly or in combination to identify interacting bat ensembles (Findley 1993; Norberg and Rayner 1987; Patterson et al. 1996; Willig 1986). The suitability of these definitions differs widely with the assemblage and research goals under study. For example, those investigating aerial insectivores or the role of echolocation in foraging will prefer the trivariate "guild" classification of Kalko and coworkers (Kalko 1998), which is based on food, feeding method, and habitat structure. Because habitat structure represents an important avenue of resource partitioning among aerial insectivores, it is essential in any ecological classification of these bats (see below; Jones and Rydell, this volume; Norberg and Rayner 1987). However, a univariate classification based on food type alone may sometimes be adequate because bat carnivores, piscivores, sanguinivores, frugivores, nectarivores, and omnivores (as well as a few insectivores) all forage via gleaning in relatively confined spaces.

We use a broad classification of bat diets (Ferrarezzi and Amaral Gimenez 1996) to organize our discussion of bat ensembles. Herbivory and animalivory are treated as two main classes of trophic adaptation and behavior, with various subdivisions recognized within each. Subclasses of herbivory exploited by bats include frugivory, feeding predominantly or solely on fruits; nectarivory, feeding on nectar as well as on other floral products and parts, such



All bats

Phyllostomids only

Figure 12.2. Trophic diversity of bat assemblages in Andean foothills of Peru. Graphs represent 123 species of bats, and 76 species of phyllostomids, that inhabit forests at or below 1,000 m in the Manu National Park and Biosphere Reserve (data from tables I and II of Patterson et al. 1996). Trophic categories are *HFF,* high-flying frugivore; *HFI,* high-flying insectivore; *ICG,* insecti-carnivore; *I,* insecti-piscivore; *LFF,* low-flying frugivore; *LFI,* low-flying insectivore; *OMG,* omnivorous nectarivore; *OMP,* omnivorous predator; and *SAN,* sanguinivore. The phyllostomid radiation exploits nearly the full range of trophic procurement strategies utilized by Neotropical bats.

as pollen and petals; and folivory, consumption of leaves, including buds and other green parts of plants. Animalivory includes generalized insectivory, carnivory, piscivory, and sanguinivory (see also Francis 1990; Muñoz-Saba et al. 1995, 1997). Simmons and Conway (this volume) discuss the evolution of various feeding adaptations within Chiroptera. Figure 12.2 contains a classification of food habits among bats in exceptionally rich assemblages in southeastern Peru.

The utility of any dietary classification is limited by behavioral plasticity and individual variation. We are only now learning about components of variability, which may be highly deterministic. For example, species adapted to operate in closed habitats might exploit edge and open habitats, but those adapted to open habitats might have limited access to closed or edge habitats because of sensory prerequisites for navigating in "clutter" (Fenton 1990). Such attributes seem likely to structure interactions of bats in ways scarcely appreciated at present.

Although we have chosen food as a framework for considering ecological interactions among bats, a variety of additional ecological interactions help to shape bat behavior, ecology, and ultimately their integration into ecological assemblages. Predation surely has pervasive effects on bat ecology, possibly limiting the extent of the chiropteran radiations (Rydell and Speakman 1995). Modern bats are almost exclusively nocturnal—the ecological diversity of species with this habit would seem to invalidate alternative explanations based on resource limitation or hyperthermia during daylight flight. Competition with birds is an unlikely explanation for nocturnal habits because most groups of aerial-feeding birds evolved after bats had adapted to night hunting. Because bats do not become diurnal on small islands lacking predators (e.g., *Nyctalus* on the Azores), other factors may also be operational (Speakman 1995).

Predation serves to limit bat foraging ranges, activity periods, and courtship displays (Fenton 1995). It affects social behavior and interactions, including the adoption of feeding roosts, alternation of day roosts, and emergence behavior (Kunz and Lumsden, this volume). In South Africa, small colonies of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) utilize roost switching and unpredictable "burst" emergence to foil predators (Fenton et al. 1985; see also Acharya 1992; Morrison 1980). Roosting in large colonies decreases the risk of predator attack on any one individual (Fenton et al. 1994). Bats emerging from roosts show the evasive behavior patterns predicted by the selfish-herd principle (Fenton 1995). Morrison (1980) noted that *Artibeus lituratus* and *Vampyrodes caraccioli* change roost sites on almost a daily basis, but roosts are not shifted to minimize distance to fruiting trees. Sit-and-wait predators such as owls seem to be attracted to fruiting trees, and use of remote feeding roosts may reflect the importance of predation (Morrison 1980). Bats often suspend or greatly reduce feeding passes to fruiting trees during periods of bright moonlight. Some phyllostomids, including *Artibeus lituratus* and *Carollia perspicillata,* quickly investigate alarm calls issued by other bats, including members of other species (Ryan et al. 1985).

Although roosting behavior can evolve in response to predation, other pressures may also affect it. Many bats are found in characteristic roosting associations with other species (Kunz 1982; Kunz and Lumsden, this volume), which may influence the survival or persistence of codependent species (Campanhã and Fowler 1993). Some roosting associations comprise species belonging to two or more trophic ensembles (Wohlgenant 1994). In addition, bats that depend on plants for roosts may indirectly depend on other bat species that pollinate their flowers or disperse their seeds. Such interactions seem particularly obvious in the sequence of species recolonizing Krakatau (Whitaker and Jones 1994), with *Cynopterus sphinx* as an important disperser of pioneer plants used by later colonists (Kunz 1996). Obviously, none of these ecological interactions are anticipated in our trophic-based classification. We urge biologists to ensure that the classification they employ in analyzing their own data is meaningfully related to known patterns of resource exploitation.

Animalivory

Arthropods

Most bats in temperate zones exploit arthropods, but tropical bats have strikingly diversified trophic habits. Therefore, it is surprising to many that arthropod consumers also can dominate tropical communities. Francis (1990) determined that insectivorous species made up 75%–87% of the bat fauna and 88%–93% of the individuals inhabiting the understory of lowland dipterocarp rainforest in Malaysia, even though his samples were strongly biased toward capturing frugivores. Almost two-thirds of the 78 bat species at Paracou, French Guiana, depend on insects ("aerial insectivores"+"gleaning animalivores" = 64%; Simmons and Voss 1998), and aerial insectivores may constitute 30%–50% of the species (but less of the biomass) in local assemblages in the Neotropics (Kalko 1998). Heller and Volleth (1995) concluded that the richest ensembles of insectivorous bats are roughly equivalent in number in the New and Old Worlds.

Insectivorous bats are usually subdivided by foraging method into aerial insectivores (those capturing insects on the wing during flight) and foliage gleaners (those flying slowly over substrates and taking prey from them). Foraging in different microhabitats often exposes organisms to novel prey distributions (e.g., taxonomic composition and size spectra) and entails different demands on sensory and locomotory systems. Findley (1993) classified insectivorous bats based on foraging station: sallying and gleaning, forest and clearing, water surface, and open air (see also Decher 1997). Kalko et al. (1996) divided aerial insectivores into three groups (calling these "guilds") based on whether the foraging space is uncluttered, background cluttered, or highly cluttered. Simmons and Geisler (1998) inferred that insectivorous foraging strategies of bats evolved sequentially, from gleaning stationary prey from a perch, to using perches to hunt stationary and flying prey, and finally to aerial hawking.

The ecological relationships and interactions of arthropod-feeding bats are still poorly understood, in part owing to the methodological challenges that must be overcome to study them. Many insectivorous species fly high above the ground and are difficult to capture in mist nets, so that they are apt to be underrepresented in inventory or ecological studies (Patterson et al. 1996; Kalko 1998). The echolocation calls of others are so quiet that they can only be monitored by remote sensing equipment at a few meters distance (Fenton et al. 1992). In addition, many insectivorous bats are known to exhibit high degrees of ecological specialization and niche subdivision (see below). Despite this, much progress has been made since 1982, when an important review concluded: "A consideration of the available literature [on insectivorous bats] provides no convincing evidence that bats specialize by the timing of activity, diet, use of habitat, foraging strategy or morphology. . . . There is still no clear picture of how sympatric insectivorous bats partition food resources, or if, indeed, they do" (Fenton 1982, 280).

The biophysics of echolocation appears to constrain body size in bats (Jones 1996). In turn, body size can influence call frequency and respiration rates (Jones 1999). To exploit the resources represented by nocturnal flying insects, bats must use high-frequency sounds to give strong echoes from small targets, and they must be small in order to produce ultrasound. In addition, wingbeat frequency decreases as body size increases, and aerial insectivores typically produce no more than one pulse per wingbeat. Larger insectivorous species might not produce echolocation calls at a rate sufficient to capture enough insects. These biophysical relationships explain why ecomorphological classifications of bats also separate them into groupings based on echolocation calls (e.g., Habersetzer 1986). In addition, Bogdanowicz et al. (1999) showed that the dominant frequencies of bat echolocation calls can be correlated with the incidence of different moths in their diets, but that this relationship holds only for low duty-cycle echolocators (Vespertilionidae and Molossidae), not for species of high duty-cycle bats (Rhinolophidae and Hipposideridae).

Norberg and Rayner (1987) showed that insectivorous bats exhibit highly diversified morphologies and correspondingly distinctive flight and foraging behaviors. In general, bats that hawk high-flying insects have small pointed wings, making them agile, fast, and cost-efficient flyers. Gleaners and bats hunting for insects in vegetation have very short and rounded wing tips on short, broad wings, making them highly maneuverable during slow flight. Insectivorous species that forage in open areas often have longer wings, and hence lower cost of transport, than those flying in cluttered environments. Adaptive variation in wing morphology was also correlated with corresponding echolocation call structure. Insectivorous bats that differ in body size and wing shape often choose different foraging habitats and harvest different subsets of food resources (e.g., Saunders and Barclay 1992). Analyzing Indian bat assemblages, Habersetzer (1986) determined that differences in echolocation call structure were correlated with differences in wing morphology but provided clearer separation of coexisting species. Heller and Helversen (1989) and Kingston et al. (2000) documented partitioning of frequency calls by rhinolopid bats.

Bats that take prey from surfaces often take different taxa than those hunting airborne targets, and such foraging differences may determine both the taxonomic identity of prey species and their energetic values (Fenton 1995). Gleaners frequently use prey-generated sound to locate prey (Belwood and Morris 1987; Fiedler 1979; LaVal and LaVal 1980), whereas hunters of flying insects often rely on echolocation. Gleaning insectivores generally have more restricted geographic ranges than do aerial foragers (Arita et al. 1997). Humphrey et al. (1983) studied surface-gleaning bats in Panama, and found that gleaning omnivores exploited resources differentiated by combinations of food type, food size, and vertical and horizontal foraging habitat. Five types of food constituted important niche differences for guild members, but beetles formed an important part of the diet for all insect gleaners (see also Kalko et al. 1999).

There is now compelling evidence to indicate that insectivorous bats are especially sensitive to deforestation and other forms of habitat disturbance in both the Neotropics (Brosset et al. 1996; dos Reis and Muller 1995; Fenton et al. 1992) and the Paleotropics (Zubaid 1993). For example, Wilson et al. (1996) determined that taxa such as Emballonuridae, insectivorous Phyllostominae, Thyropteridae, Furipteridae, and Vespertilionidae are all more abundant in undisturbed than in disturbed forests in Peru. Similar patterns, perhaps not quite so sharply developed, also characterize temperate regions (Eichstadt 1997; Law et al. 1999). This special vulnerability presumably derives from altered resource distributions in modified or converted forests (Fenton et al. 1992). In contrast, light or moderate levels of disturbance may actually increase the number of pteropodid species living in Philippine rainforests (Utzurrum 1998) or the abundance of carolline phyllostomids living in Neotropical forests (Wilson et al. 1996), provided that forest structure and composition remain essentially intact.

Differential habitat use may be a principal avenue of resource partitioning by insectivorous bats. McKenzie and colleagues (McKenzie and Rolfe 1986, McKenzie and Start 1989) characterized the structure of bat ensembles in mangrove communities in Australia using aerodynamic attributes. They found almost no overlap among flight morphologies of species that foraged in a given stand of mangroves. Morphological differences could be tied to differences in both vertical stratum and foraging microhabitats (also true of *Myotis myotis* and *M. blythii* where they occur in sympatry; Arlettaz and Perrin 1995). Differential abundance of arthropods in different habitat patches and strata may ultimately account for the morphological differentiation of bats, such as beetle-feeding and moth-feeding molossids (Findley and Black 1983, Freeman 1979).

In upland rainforest in Queensland, use of space by insectivorous bats was predictable from their ecomorphologies (Crome and Richards 1988). Bats were divisible into closed-canopy specialists (low aspect ratio and wing loading), gap specialists (high aspect ratios and wing loadings), and gap incorporators (intermediate). No patterns in assemblage structure were correlated with gap age, suggesting that the exclusion of gap species in the course of ecological successions is a slow process.

Kalko (1995) examined the echolocation calls produced by Neotropical Emballonuridae, finding them highly structured with respect to habitat. *Diclidurus* and *Peropteryx* spp. exploited open, uncluttered space with low frequency, shallow modulated echolocation calls. *Saccopteryx bilineata, S. leptura,* and *Cormura brevirostris* used medium-frequency echolocation signals in "cluttered habitats" filled by vegetation. Foraging within a meter or two of small forest streams, *Rhynchonycteris naso* used high-frequency echolocation signals similar in structure to those of noctilionid bats (that also forage in similar situations). Parallel structure may exist for vespertilionids and molossids but not phyllostomids, which represented the largest and most diverse group in terms of diet, yet emitted rather uniform signals.

Horizontal segregation may characterize north temperate bat ensembles, which are often dominated by maneuverable, relatively slow-flying species (Arlettaz 1999). Although some species hovered in complex, structurally diverse habitats where insect density and diversity appeared high, most were open-air foragers incapable of very slow or hovering flight. The latter species foraged on the wing over large areas. Terrestrial foragers (i.e., *Antrozous pallidus*) and over-water foragers (i.e., *Myotis yumanensis*) constituted separate trophic classes (see also Black 1974). Habitat generalists, such as *Lasiurus cinereus semotus* in Hawaii, may use different flight speeds and echolocation frequencies to forage in open versus cluttered habitats (Jacobs 1999), enabling the bats to capture a different spectrum of prey body sizes in each habitat.

In Neotropical communities, vertical stratification may be more important in organizing interactions. Handley (1967) was among the first to substantiate this hypothesis, comparing the relative capture success of nets placed on the ground and in the canopy of Amazonian forest near Belém, Brazil. He encountered generally higher capture rates in the canopy nets. The species that were taken solely in the canopy nets were, without exception, poorly known, supposedly uncommon, and irregularly distributed. In this instance, vertical stratification of flight activity has faunistic as well as ecological implications.

In Panama, food is limiting at some periods of the year, and flight activity of insectivorous species is vertically stratified (Bonaccorso 1979). *Mimon crenulatum*, *Trachops cirrhosus*, and *Tonatia sylvicola* were netted significantly more often near the ground than at subcanopy level, whereas *Tonatia saurophila* generally was captured at subcanopy level. Vertical segregation of potential competitors is accompanied by some horizontal or macrohabitat segregation, with the partial displacement of *Trachops* to creek forest and *Tonatia sylvicola* to forest patches between creeks. Finally, some evidence suggested that species with similar feeding habits are active at different times (Bonaccorso 1979; see also Ascorra et al. 1996).

Eichstadt (1997) studied resource partitioning by eight sympatric species in Europe, all roosting together within a 30-ha forest. Three groups were evident, based on diet choice: several opportunists taking small flying insects, a flightless beetle specialist (*Myotis myotis*), and a moth specialist (*Plecotus auritus*). Differences existed between opportunist and specialist species in habitat use. Opportunistic species foraged together on superabundant resources over wetlands and lakes, whereas specialists foraged on defensible resources in territories close to their roosts. Because opportunists feed on abundant prey that is not depleted greatly by feeding activities, defense is impractical or too costly.

Eichstadt (1997) found species differences in temporal activity periods, with long-distance commuters leaving day-roost areas first. However, it is questionable whether such differences enabled the bats to exploit different resources. Extended studies of foraging by *Lasiurus cinereus* and *L. borealis* at streetlights revealed no consistent evidence of temporal partitioning (Hickey et al. 1996). Over 3 yr, the food niche of larger *L. cinereus* (25–35 g) was consistently broader than for *L. borealis* (7–13 g). Niche overlap varied among years and was highest when resources were unusually low.

Behavioral opportunism is responsible for some of these shifts. Husar (1976) studied the diets of *Myotis evotis* and *M. auriculus* in New Mexico and documented that the diets of bats are highly labile. Although exploiting highly similar diets in allopatry, these two species are more specialized where their ranges overlap, *M. evotis* relying more heavily on beetles and *M. auriculus* on moths. Furthermore, each species exhibits sexual differences in foods taken in allopatry but not sympatry.

Other Animal Foods

Animalivorous (or carnivorous) bats include members of three families: Nycteridae, Megadermatidae, and Phyllostomidae. They exploit a variety of other organisms as food, but arthropods remain an important component (Norberg and Fenton 1988). Because they sometimes carry heavy loads, they tend to be heavy, with low aspect ratios and low relative wing loadings (Norberg and Fenton 1988). Nevertheless, they otherwise resemble other arthropod-feeding species that forage by perching, hunting, and gleaning (Norberg and Rayner 1987) and sometimes supplement their diets with fruit (Ferrarezzi and Amaral Gimenez 1996). Fenton et al. (1990) found that *Nycteris grandis* fed primarily on frogs, bats, and arthropods and occasionally took birds and fish. Lack of carnassial teeth and long handling times for larger prey (Fenton et al. 1983) may limit exploitation of carnivory by bats.

Although fishing bats also consume small vertebrates, fishing bats forage differently and do not fly in clutter (Norberg and Fenton 1988). All piscivorous bats supplement their diets with arthropods, either aquatic or nonaquatic insects caught on the water surface or else crustaceans (Ferrarezzi and Amaral Gimenez 1996). Piscivores forage over long stretches of open water, selecting for very long wings (low flight power and cost of transport) with long rounded tips for control and stability (Norberg and Rayner 1987).

Finally, blood feeding or sanguinivory is the most specialized diet exploited by bats, necessitating all sorts of correlated adaptations. However, even vampire bats supplement their diets with insects (Ferrarezzi and Amaral Gimenez 1996). The ecological mechanisms facilitating coexistence of the three living species are known, but the origins of sanguinivory itself remain speculative (reviewed in Schutt 1998). The fossil record, representing only members of the genus *Desmodus*, sheds little light on transformation series (Freeman 2000). Preliminary data suggest that *Desmodus rotundus* prefers mammalian prey and the other two vampire species prefer birds (see Gardner 1977; Greenhall and Schmidt 1988; Greenhall and Schutt 1996). In addition, the two bird feeders may be distinguished by roosting sites: *Diaemus youngi* prefers tree cavities, whereas *Diphylla ecaudata* roosts in caves, as does *Desmodus* (Dalquest 1955; Uieda 1993).

Herbivory

Over half of the world's living bat species use plants exclusively or opportunistically as resources for food and/or shelter (Kunz 1996). Roughly a third visit plants for nectar, pollen, or fruit (Fleming 1993). We recognize the following subdivisions: frugivory, feeding predominantly or solely on fruits; nectarivory, feeding on nectar as well as other floral products and parts, such as pollen and petals; and folivory, consumption of leaves, buds, and other green parts of plants (Ferrarezzi and Amaral Gimenez 1996). Omnivorous species also exploit diets partly comprising vegetal material (usually fruits and/or flowers).

Herbivory by bats has involved a host of morphological adaptations (Kunz and Ingalls 1994), developed over more than 50 million years of evolutionary association (Marshall 1983). These have included novel dental features (for microchiropterans, cf. Ferrarezzi and Amaral Gimenez 1996) to crush fruit, not triturate chitinous exoskeletons (Andersen 1908). Compared to insectivorous relatives, herbivorous species possess structurally complex stomachs (Forman 1990) that are more specialized and compartmentalized (Perrin and Hughes 1992). Herbivorous species are also distinguished by relatively large brains, apparently an aid in locating and exploiting rich but highly dispersed food resources (Eisenberg and Wilson 1978). "Brainy" herbivorous bats are sharply distinguished from insectivorous species, which have smaller-than-expected brains because of constraints on body mass imposed by requirements for highly maneuverable flight. Neurobiology of bats is treated in far greater detail in Baron et al. (1996), with ecological patterns of brain morphology in bats detailed in the third volume.

Most herbivorous bats are members of the Pteropodidae and Phyllostomidae, whose evolutionary radiations have taken place independently and in geographic isolation. The Pteropodidae are exclusively Old World in distribution, whereas the Phyllostomidae are practically confined to the Neotropics. Although the Pteropodidae are predominantly herbivorous, with major radiations of nectarivorous and frugivorous species, the phyllostomids employ both of these strategies (Gardner 1977; Wilson 1973), as well as a number of others (see Kalko et al. 1996; Patterson et al. 1996).

The differential success and radiations of the Pteropodidae and Phyllostomidae may be partly attributed to differences in their sensory systems (Heller and Volleth 1995). Although phylogenetic relationships among "yangochiropteran" families remain poorly understood, there is strong support for a group containing the Neotropical endemic families Noctilionidae, Mormoopidae, and Phyllostomidae (Simmons 1998) and the New Zealand endemic

Mystacina (Kirsch et al. 1998). All these taxa depend to varying degrees on echolocation, as do the potential sister clades of this group, whereas this ability is limited in Pteropodidae to some cave-roosting *Rousettus*. Perhaps in consequence, the number of coexisting phyllostomids exceeds the number of syntopic pteropodids in most tropical lowland forest sites. Differences between groups are especially marked in the understory ensemble, where a premium is placed on the ability to fly amid structural complexity (Francis 1994; Heller and Volleth 1995; Kingston et al. 2000; Zubaid 1994).

The diversity of herbivorous bats is highest in the tropics. Although few studies have documented annual cycles of tropical bat ensembles, the importance of annual variation can be gleaned from studies of vegetation. Most tropical shrubs and trees produce leaves and flowers in bursts, with seasonal variation in production of leaves, flowers, and fruits as adaptations to biotic or abiotic factors (van Schaik et al. 1993). Whereas abiotic factors promote synchronous responses by a flora, biotic factors can select for either clumping or staggering of events. Competition for food resources typically leads to staggered exploitation patterns, whereas predation often leads to synchronized activities, as individuals and groups respond to external predation threats (in this way resembling many abiotic factors, such as seasonal rains or cold periods that produce flora-wide responses). In seasonally dry forests, many plants concentrate leafing and flowering at the onset of the rainy season with synchronous fruiting (an adaptation that reduces seedling mortality at the start of the following dry season).

At the level of the forest community, phenological variation leads to dietary switching by primary consumers, as well as to seasonal breeding, range changes, migration, or aestivation (van Schaik et al. 1993). Certain plant products—keystone resources—act as mainstays of the primary consumer community during periods of resource scarcity. "Nomadism [as a response of vertebrates to seasonal or local resource scarcity] may be more prevalent in bats than is currently realized" (van Schaik et al. 1993, 370). Patchiness of tropical trees and the enhanced vagility of flight may explain the numerical predominance of very rare bat species in many local ensembles (cf. Handley et al. 1991). Apparent segregation of male and female *Otopteropus cartilagonodus* along elevational gradients in the Philippines (Ruedas et al. 1994) represents a solution to intraspecific competition that is available only to highly vagile species.

In turn, bats are particularly important in maintenance of tropical forests because (1) conspecific trees are often spatially isolated and dioecious; (2) the longevity of tree species, together with intense pressure from competitors, predators, and pathogens, places a premium on genetic recombination; (3) both tree species and their pollinators are highly diverse; and (4) biotic pollinators are more important than they are in temperate regions (Bawa 1990).

Nectar and Pollen

Radiations of bats to exploit the nectar and pollen produced by flowering plants have taken place in both the Old World (Pteropodidae: "macroglossines") and New World (Phyllostomidae: Glossophaginae, Lonchophyllinae, and Brachyphyllinae). Nectarivorous species are distinguished by their greatly elongated heads and tongues, representing extremes in both categories for the chiropteran radiations. Kitchener et al. (1990) showed correlations between tongue morphology (including details of tip morphology as well as overall tongue length) and dietary breadth for the six common species of nectarivorous pteropodids on Lombok, Indonesia.

The number of plant species pollinated by bats and the number of bat species involved as pollen vectors are not known for any tropical wet forest. Bats encompassed nearly 4% of 52 animal species pollinating woody canopy plants at La Selva (Costa Rica), and the same fraction of 220 pollinators of subcanopy and understory plants there (Bawa 1990). Pollination by vertebrates is more important in the tropics than in the temperate zone. However, along elevational gradients within the tropics, pollination by hummingbirds actually increases from lowland tropical forest into montane tropical forests (Bawa 1990), and nectarivores make up proportionally larger fractions of bat faunas ascending elevational gradients in Peru (Patterson et al. 1996) and Venezuela (Soriano et al. 1999). Although flowers may receive a wide range of visitors, only one or two—often members of the same order—act as effective vectors (Bawa 1990; Helversen and Winter, this volume). For plants, bats may be more expensive energetically than other pollinators, but these energetic costs are offset by the wide distribution given pollen by widely foraging bats (Start and Marshall 1976). Bat pollination is found in many plant families but is particularly common or well studied among the Bombacaceae (Bawa 1990).

Start and Marshall (1976) described a West Malaysian ensemble containing three species. *Eonycteris spelaea* roosts in caves, travels considerable distances to feed, forages in flocks, and obtains food from diverse, scattered, seasonally flowering sources. In contrast, *Macroglossus minimus* and *M. sobrinus* roost singly or in well-spaced groups close to food sources (*Sonneratia* sp. and *Musa* sp., respectively), and forage individually on sources that flower aseasonally. Heithaus et al. (1975) studied plant-visiting bats in Guanacaste, Costa Rica, where floral resources varied seasonally. Although most species were nectarivorous periodically, only *Glossophaga soricina* maintained this diet during periods of nectar scarcity (see Helversen and Winter, this volume).

Fruit resources were more uniformly abundant throughout the year and consequently were more finely divided by bat species. If competition for food has structured this bat assemblage, fruit has been more important than nectar and pollen in controlling diversity. However, flowering times of plant species were staggered, suggesting competition among bat-pollinated species

(Heithaus et al. 1975). Asynchronous peaks of flowering for different species of plants in the diet of *Glossophaga longirostris* allow plant species to use the same seed disperser and pollinator without suffering interspecific competition for such "services" (Soriano et al. 1991).

At a finer scale, *Artibeus jamaicensis, Sturnira lilium, Phyllostomus discolor,* and *G. soricina* all pollinated *Bauhinia* flowers at Guanacaste (Heithaus et al. 1974). Spatial partitioning of *Bauhinia* flowers is considerable and perhaps is the dominant form of resource partitioning (Fischer 1992; Heithaus et al. 1974). Malaysian nectarivorous bats also partition resources spatially, maintaining the effectiveness of this strategy by trapline foraging and territorial defense. Patterns of visitation at *Musa* and *Oroxylum* are typical of trapline foragers (Gould 1978). The phyllostomid *Lonchophylla bokermanni* is also a trapliner, habitually foraging in open habitats for *Encholirium glaziovii,* a ground-dwelling bromeliad (Sazima et al. 1989). Although other flower-visiting bats occur in southeastern Brazil and are not mechanically precluded from exploiting this bromeliad, none seems to compete with *L. bokermanni.* However, this strategy is not universally used by nectarivorous species—visits to *Parkia* flowers by Old World pteropodids are more frequent and opportunistic than in these other plants and sometimes involve agonistic interactions among would-be pollinators (Gould 1978).

Temporal partitioning of nectar and pollen resources appears less common than spatial partitioning. Heithaus et al. (1974) suggested that vertical and temporal differentiation may enhance spatial partitioning. *Phyllostomus discolor* began foraging earlier in the evening and confined its visits to flowers >2.5 m aboveground. This could leave more nectar later in the evening for *G. soricina* and *Anoura caudifer* in flowers below this level because an individual bat does not exhaust the nectar supply of a flower on a given visit. In some situations, however, little advantage may be gained by such refined resource partitioning: on the island of Curaçao, *Leptonycteris curasoae* and *G. longirostris* are the principal pollinators of at least two of three columnar cacti that grow on the island (Petit 1997). Fully 85%–91% of dietary samples contained seeds and pollen of cacti. Parturition and lactation in both species are timed to correspond to peaks in the seasonal phenology of the two abundant species of cactus.

Nectarivorous bats sometimes forage in cohesive but unorganized flocks to search for resources more efficiently and to exploit them more thoroughly (Howell 1979). Communal feeding in *Leptonycteris* permits intermittent communal roosting, in turn leading to more efficient digestion (via shared thermoregulatory costs on cold desert nights). By following "leader" bats from a depleted resource patch without individually confirming its depletion, all bats save energy, and these savings are enhanced because only lead bats appear to use echolocation.

Anthropogenic extinctions of birds have increased the importance of bats as dispersers of large-seeded fruits and reduced the guild of pollinators and dispersers of small-seeded fruits (Rainey et al. 1995). Resource defense, more common among megachiropteran frugivores than among microchiropterans, may structure patterns of pollination and seed dispersal as bat density and movements are determined by local resource abundance and behavioral responses to them (Richards 1995). Where plants depend on a single species of bats for pollination, such as insular populations of *Ceiba pentandra* pollinated by *Pteropus,* behavioral responses such as establishment of feeding territories, can structure patterns of plant reproduction (Elmqvist et al. 1992).

The ecological limits of nectarivory are difficult to specify. For example, Muñoz-Saba et al. (1997) determined that *Artibeus jamaicensis, A. lituratus, A. obscurus, G. soricina, Carollia perspicillata, Sturnira lilium, Uroderma bilobatum,* and *U. magnirostrum* all forage on nectar and pollen in the Serrania La Macarena. Collectively, their diet is 83% fruit, 8% insects, and 9% pollen and nectar. In addition to pollen from plants obviously adapted for chiropteran pollination, these bat species also carried pollen grains of Compositae, Myrtaceae, Gramineae, and Euphorbiaceae. Valiente-Banuet et al. (1996) documented some pollen from an abundant cactus, *Neobuxbaumia,* on *A. jamaicensis* but showed that *Leptonycteris* and *Choeronycteris* were the plant's only pollinators. An even more diverse array of visitors (including various birds and all three bats) disperses its seeds.

In certain areas, terrestrial mammals rival or exceed the importance of bats as pollinators. Despite a diversity of potential bat pollinators, several Amazonian tree species are evidently pollinated by nonvolant mammals, including *Ceiba, Ochroma,* and *Quararibea* (all Bombacaceae [Janson et al. 1981]). Elsewhere, *Banksia* flowers are visited by two Australian marsupials, *Petaurus breviceps* and *Antechinus stuartii* (Goldingay et al. 1991). Both species of marsupial depart with pollen loads comparable to those of nectar-feeding birds.

Fruits

Terborgh (1986) estimated that frugivorous species represent 80% of the mammalian and avian biomass at Cocha Cashu, Peru, and frugivorous bats tend to dominate assemblages in lowland Neotropical forests (Kalko 1998 and references therein). Depending on habitat, 50% to >90% of the species of tropical shrubs and trees rely on fruit-eating vertebrates to disperse their seeds (Howe and Smallwood 1982). Seeds of Araceae, Guttoferae, Hypericaceae, Moraceae, Piperaceae, and Solanaceae were recovered from the feces of 15 species of frugivorous phyllostomids from Loreto, Peru (Ascorra and Wilson 1992), and Ascorra et al. (1996) demonstrated comparable diversity of seeds dispersed by bats in Madre de Dios, Peru. The dispersion of tropical plants is every bit as much a consequence of the foraging, dietary, and home-range patterns of frugivores as the latter are a product of the former.

At the same time, despite comparable diversity of insectivorous species, the understory of dipterocarp forests in Southeast Asia supports relatively few species of obligate frugivores, at least in nonmasting years (Francis 1990). Some Asian frugivores are astonishingly catholic in their habits. Tan et al. (1998) documented fruits of 54 plant species, leaves of 14 species, and flower parts of four species in the diets of *Cynopterus brachyotis* in secondary habitats in Malaysia. Opportunities for partitioning resources in the company of such trophic generalists appear limited.

Marshall (1985) reviewed feeding habits of pteropodid bats throughout the Old World and concluded that their food tends to be conspicuous, clumped spatially and temporally, and abundant and easily harvested within these clumps. Consequently, there is no need to specialize on food resources as insectivorous species must do, and there is time for complex mating behaviors such as lekking, an activity unknown in insectivorous species. In addition, flock foraging is possible, even advantageous, in harvesting clumped resources.

In addition, species of pteropodid frugivores tend to be wider-ranging than their phyllostomid counterparts, as shown by comparisons of mean ranges and maximum movements of 14 species of Asian and African pteropodids and six species of phyllostomids (Heideman and Heaney 1989). Whether these are real taxonomic differences or are instead related to the body sizes, group sizes, and/or resource distributions of each situation remain unknown.

Fleming and Williams (1990) showed that at least 28 species of vertebrates (15 diurnal, 13 nocturnal) eat *Cecropia peltata* fruit in a Costa Rican tropical dry forest. An equal amount of fruit is removed day and night. Owing to gentler treatment of ingested seeds, bats and birds were more effective dispersers of this species than were monkeys. Digestion by *Carollia* has either no effect (e.g., *Piper, Chlorophora,* and *Muntingia*) or a positive effect (*Cecropia* and *Solanum*) on seed germination (Fleming 1988; see also Iudica and Bonaccorso [1997] for *Sturnira lilium*).

Bats tend to be wasteful seed dispersers, often defecating in dark areas with little opportunity for subsequent germination; they are probably more efficient at dispersing pollen than seeds (Fleming and Sosa 1994). However, given the large numbers of seeds ingested by individual bats, their density in the forest, and the length of the fruiting season, bats are highly successful at dispersing seeds (Fleming 1988). In the Old World, pteropodids ingest small seeds and transport them substantial distances; larger seeds are frequently carried with fruits to feeding roosts, farther than is practicable for avian frugivores. Only the large pteropodids are capable of dispersing the largest seeds (Kunz 1996).

Fruit resources in some tropical forests are present and more or less uniformly abundant throughout the year, so that fruits may be more finely divided by bat species than are floral resources. Mean size of fruit and its variance can be positively correlated with body size of bats (Heithaus et al. 1975), and species may specialize on the types of fruits eaten, provided that their phenology makes them available throughout the year. Marinho-Filho (1991) documented the seasonal abundance and phenology of *Piper* and *Solanum*, which are principal dietary components of *Carollia* and *Sturnira*, respectively, and are implicated in the coexistence of these species. Kalko et al. (1996) described the characteristics of figs eaten by frugivorous bats in the New and Old World tropics. Experiments by Rieger and Jakob (1988) in Costa Rica suggest that olfactory cues are also used in foraging decisions by phyllostomid frugivores.

Fruit and seed characteristics may serve as the basis of fruit choice (and hence resource partitioning), as shown by Gautier-Hion et al. (1985; also see Dumont, this volume; Muller and dos Reis 1992). Size-dependent partitioning of fruit resources by bats may affect the spatial distribution of the trees on which they feed. Utzurrum (1995) documented differences in fruit handling by Philippine bats. Large bats (>150 g) consume resources on the spot, producing splats and ejecta directly beneath the source tree. Smaller bats use feeding roosts in the immediate vicinity of, but not directly beneath, the focal feeding tree. Clumps of seeds found beneath these roost trees were mixed, producing a more heterogeneous pattern of seed scattering than would be expected if all bats behaved the same. Their importance as seed dispersers is confirmed by seed germination tests, in which gut-passed seeds (splats) of *Ficus chrysolepis* show higher percentages of germination than do seeds from fruits or ejecta (Utzurrum 1995).

In Amazonian Brazil, Handley (1967) noted reciprocal abundance patterns of two common species of *Artibeus* in the canopy and at ground level. *Artibeus lituratus* is usually captured far less frequently on the ground than its congener *A. jamaicensis*. However, *A. lituratus* dominated canopy samples. Ascorra et al. (1996) devoted substantial effort to aerial sampling, presenting the number of captures—recorded on the ground as well as in elevated nets of various heights—for 50 bat species in Manu, Peru (see also Simmons and Voss 1998). Among primarily frugivorous species, only *Chiroderma trinitatum* and *C. villosum* were captured solely in aerial nets (Ascorra et al. 1996), and both are taken in nets on the ground in that region (B. Patterson and S. Solari, personal observation). However, several frugivores and omnivores (e.g., *A. lituratus* and *Phyllostomus hastatus*) were more commonly taken in elevated nets, indicating vertically stratified activity patterns (Ascorra et al. 1996; Simmons and Voss 1998).

Vertical stratification of forest-inhabiting bats in lowland rainforest of Luzon, Philippines, was documented by Ingle (1993). She found that pteropodids made up 95% of captures in subcanopy nets (placed 3–16 m aboveground in natural forest gaps) but only 25% of bat captures in nets placed 0–3 m aboveground. Megabats appeared to be substantially more active in the subcanopy, and this may coincide with the vertical distribution of their food. In dipterocarp rainforest in Malaysia, Francis (1994; see also Zubaid 1994) also documented differential use of vertical space by bats. Nets on the ground in primary forests captured only two individual bats, whereas subcanopy nets captured bats at rates up to 100 times those on the ground. Diversity indices calculated from samples also showed a positive correlation with height above the ground. None of the species captured on the ground was restricted to that level, practically the inverse of patterns known from the Neotropics. Both of the common ground species were also found in the subcanopy.

Weak vertical stratification of Paleotropical pteropodids relative to Neotropical phyllostomids may reflect more fruit resources in the canopy of dipterocarp forests (e.g., Fleming 1988) but might also reflect the more limited ability of pteropodids to navigate in cluttered understory habitats (Francis 1994; Zubaid 1994). Certainly, Neotropical frugivores that feed on canopy plants often fly near the ground (Ascorra et al. 1996), perhaps to avoid predators or to reach roosting sites. Vertical stratification of flight activity undoubtedly contributes to our conceptions of relative abundance because the latter are fashioned from capture or ultrasonic recordings. Given the vulnerability of bats to human-induced changes in habitat quality and structure, either directly through clear-cutting or indirectly through pollution, far more work is needed.

Folivory

Bats chew leaves of at least 44 species of plants in 23 different families (Kunz and Diaz 1995). At least 17 species of Old World pteropodids and four plant-visiting bats in the Neotropics are known to feed on leaves, although none depends exclusively on them (Kunz and Ingalls 1994). Feeding on leaves involves mastication, swallowing liquids, and expelling fibrous residue (spats) (Lowry 1989). The digestive tracts of Old World fruit bats are designed for a largely liquid diet and rapid gut passage, and so require little if any modification for a leaf diet (Kunz and Ingalls 1994). In addition, plant-visiting bats are preadapted in having longer stomachs and intestines than do their insectivorous counterparts. Longer guts of plant-visiting bats offer added surface area for absorbing protein from the ingested fruits and leaves (Tedman and Hall 1985). The principal contribution of folivory to coexistence of bat species may be in supplementing the nutrient value of herbivorous diets, which are otherwise inadequate for bats in terms of mineral nutrients or proteins (Rajamani et al. 1999; Ruby et al. 2000).

Clearly, evolutionary diversification has resulted in bat species occupying a variety of ecological niches. As a consequence, members of the Chiroptera provide a diversity of ecological services (e.g., seed dispersal, flower pollination) that may be important to the overall composition, structure, and function of ecosystems. Nonetheless, natural selection, operating within the context of local environments and historical constraints, has produced considerable taxonomic and functional heterogeneity at the level of local bat assemblages. Indeed, much of the theoretical and empirical research pertinent to contemporary community ecology has focused on identifying recurrent patterns in local assemblages and identifying their underlying mechanistic bases. In the past, patterns of bat species composition within assemblages often were explained in light of such prevailing ecological theory, but research on bats lagged behind other taxonomic subdisciplines of ecology, such as those focusing on birds, rodents, or plants. In the past few decades, bat ecologists have begun to make rapid strides in documenting patterns and exploring their mechanistic bases. In the sections that follow, we rely heavily on the work of empirical bat ecologists to refine our understanding of both pattern and process as it relates to chiropteran components of local assemblages.

Broad-Scale Patterns in the Organization of Local Bat Assemblages and Ensembles

For 25 yr, ecologists have argued whether ecological assemblages are equilibrial and structured by deterministic processes or nonequilibrial and assembled by stochastic processes (Cody and Diamond 1975; Diamond and Case 1986; Gee and Giller 1987; Kikkawa and Anderson 1986; Polis 1991; Ricklefs and Schluter 1993; Strong et al. 1984). Although competition, predation, and mutualism have all been championed as mechanisms determining the formation and structure of local assemblages, evidence for the hegemony of one mechanism, or even for equilibrial conditions, is controversial. In part, the failure to find a dominant factor may be a consequence of spatial variation in environmental characteristics (e.g., temperature, precipitation, or insolation), which prevents any particular mechanism from operating with equal efficacy in all locations. Indeed, as the discipline of ecology has matured as a science, the search for a dominant mechanism structuring communities has been replaced with the deeper goal of understanding the environmental or evolutionary contexts in which equilibrial communities are most likely (Pickett et al. 1994).

While the controversy concerning the mechanistic basis of community organization has waxed and waned, bat ecologists intensively sampled the composition of bats in many local assemblages throughout the New World (fig. 12.3; table 12.1). We examined spatial variation in the biodiversity of assemblages and ensembles of bats at numerous sites ranging from 42° N latitude to 24° S latitude (Stevens and Willig, unpublished data), selected for analysis those that met certain spatial and temporal criteria: (1) each site must represent a single biome, with reasonable evidence to suggest sampling has been adequate to uncover potentially interacting bat species (i.e., sampling based on multiple sites within an area <1,000 km^2); (2) sampling must have been undertaken on a regular basis in all seasons during which bats are active;

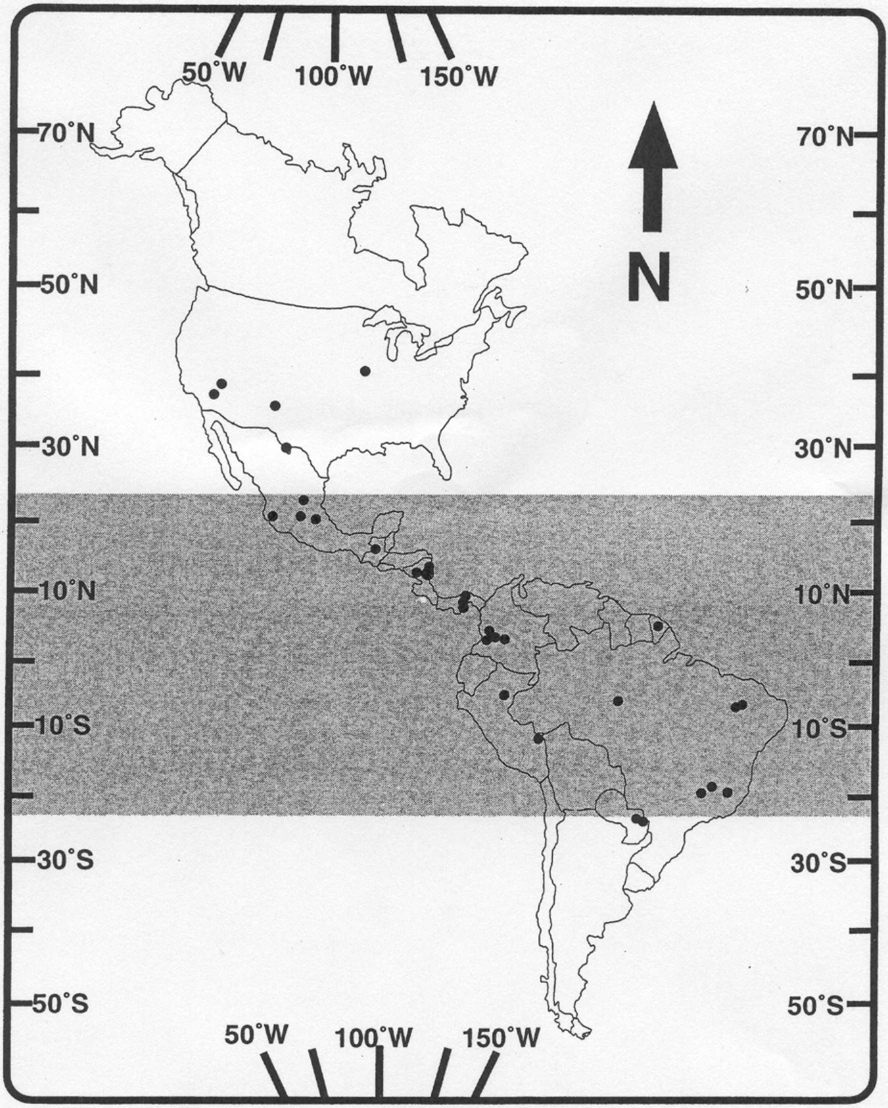


Figure 12.3. Map indicating the location of 32 bat assemblages (table 12.1) for which comparable and reliable data on species richness are available in the New World. The shaded region encompasses the tropics. Modified from Stevens and Willig (unpublished).

Table 12.1. Environmental characteristics of each of 32 bat assemblages used to evaluate patterns of diversity

Community	Latitude	Longitude	Habitat	References
Iowa, USA*	42.25°N	93.00°W	Temperate riparian	Kunz 1973
California, USA*	36.50°N	117.25°W	Temperate desert	Supernant 1977
Nevada, USA	36.20°N	115.20°W	Temperate desert	O'Farrell and Bradley 1970
New Mexico, USA	34.87°N	107.35°W	Temperate desert	Black 1974
Big Bend Ranch, USA	29.75°N	103.75°W	Temperate desert	Yancey 1996
Queretaro, Mexico	21.12°N	99.33°W	Montane tropical forest	Navarro and L.-Paniagua 1995
Manantlan, Mexico	19.33°N	104.00°W	Montane tropical forest	Iniguez Davalos 1993
Ixtapan del Oro, Mexico	19.25°N	100.16°W	Montane tropical forest	Alvarez and Alvarez-Castaneda 1996
Los Tuxtlas, Mexico	18.42°N	95.00°W	Wet tropical forest	Estrada et al. 1993
Chiapas, Mexico*	16.10°N	95.00°W	Wet tropical forest	Medellin 1993
Guanacaste-1, Costa Rica*	9.47°N	85.15°W	Wet tropical forest	LaVal and Fitch 1977
Guanacaste-2, Costa Rica*	9.47°N	85.15°W	Wet tropical forest	Fleming et al. 1972
Puntarenas, Costa Rica*	10.00°N	84.75°W	Montane tropical forest	LaVal and Fitch 1977
Heredia, Costa Rica*	10.5°N	83.75°W	Wet tropical forest	LaVal and Fitch 1977
Sherman, Panama*	9.33°N	79.95°W	Wet tropical forest	Fleming et al. 1972
Rodman, Panama*	8.95°N	79.62°W	Dry tropical forest	Fleming et al. 1972
BCI, Panama*	9.17°N	79.80°W	Wet tropical	Handley et al. 1991
Paroucou, French Guiana	5.27°N	52.92°W	Wet tropical forest	Simmons and Voss 1998
Hormiguero, Colombia	4.00°N	76.00°W	Wet tropical forest	Thomas 1972
Zabelitas, Colombia*	4.00°N	76.50°W	Wet tropical forest	Thomas 1972
Marcarena, Colombia	3.25°N	73.92°W	Wet tropical forest	Sanchez-Palomino et al. 1993
Manaus, Brazil	3.00°N	60.00°W	Wet tropical forest	dos Reis 1984
Pance, Colombia*	3.00°N	76.00°W	Montane tropical forest	Thomas 1972
Jenero Herrera, Peru*	4.92°S	73.75°W	Wet tropical forest	Ascorra et al., personal communication
Edaphic Cerrado, Brazil*	7.23°S	39.38°W	Tropical woodland-savannah	Willig 1982
Caatinga, Brazil*	7.58°S	39.66°W	Dry tropical forest	Willig 1982
Manu, Peru	11.93°S	71.28°W	Wet tropical forest	Ascorra et al. 1996
Linhares, Brazil	19.01°S	40.30°W	Wet semitropical forest	Peracchi and Albuquerque 1993
Panga, Brazil	19.25°S	48.38°W	Wet semitropical forest	Pedro and Taddei 1997
Minas Gerais, Brazil	19.83°S	41.83°W	Wet semitropical forest	Moura de Souza Aguiar 1994
Rio Verde, Paraguay	23.00°S	56.12°W	Dry semitropical forest	Stevens and Willig 2002
Mbaracayu, Paraguay	24.00°S	55.50°W	Wet semitropical forest	Stevens and Willig 2002

*Denotes the 15 communities analyzed by Stevens and Willig (1999, 2000a, 2000b).

(3) data must be gathered within a 1–5-yr period, raising the likelihood of including rare species and diminishing the likelihood of sampling species that do not interact because of temporal turnover; and (4) finally, a site was included in analyses only if empirical collector's curves (numbers of species as a function of number of individuals) for that site revealed that the observed species richness had reached an asymptote. Although each criterion is somewhat

subjective, collectively they increase the likelihood that the species present at the 32 sites potentially interact.

Gradients of Biodiversity

Four indices were used to characterize the nature of biodiversity at each site (Magurran 1988). Species richness (S) is simply the number of different species. Species dominance, as estimated by the Berger-Parker index (BP), is the proportional abundance of the species with the highest number of captures. Species diversity as estimated by the Shannon-Weiner index (H'), is sensitive to both S and the equitability with which individuals are apportioned among species, and is given by

$$\mathrm{H}' = - \quad p_i(\log p_i),$$

where p_i is the proportional abundance of species i, and the summation is over all S species in the assemblage. Species evenness (E), as estimated by Pielou's ratio (Pielou 1969), is given by

$$E = \frac{H'}{H_{\max}} = \frac{H'}{\log S}.$$

This equation reflects the degree to which the diversity of a community is at its maximum, given the number of species that it contains. Assemblages with high evenness have an equitable distribution of individuals among species, whereas assemblages with low evenness are characterized by heterogeneity in the proportional abundances of species.

Bat assemblages ranged in richness by almost an order of magnitude, from <10 species in more temperate latitudes to almost 80 species in tropical latitudes. As expected, based on biogeographic studies of latitudinal gradients of diversity (Willig and Sandlin 1991; Willig and Selcer 1989), species richness of an assemblage increased significantly ($P < 0.001$) toward the tropics (fig. 12.4A). In contrast, neither species dominance (fig. 12.4B) nor species evenness (fig. 12.4C), exhibited a significant latitudinal gradient ($P > 0.118$). Mostly as a consequence of its richness component, species diversity significantly increased ($P = 0.003$) toward the tropics (fig. 12.4D).

In part, species richness of a local assemblage of bats is related to the regional richness of bats (fig. 12.5A). Indeed, species richness of an assemblage is associated positively with the number of species whose geographic ranges overlap the location of a site ($P < 0.001$). Moreover, as the regional richness of the bat fauna increases, so does the variation in the number of species that coexist in a local assemblage. As a consequence, only a third of the variation in the richness of a local assemblage is accounted for by variation in its regional richness ($r^2 = 0.376$).

Although primary gradients of temperature, precipitation, and insolation

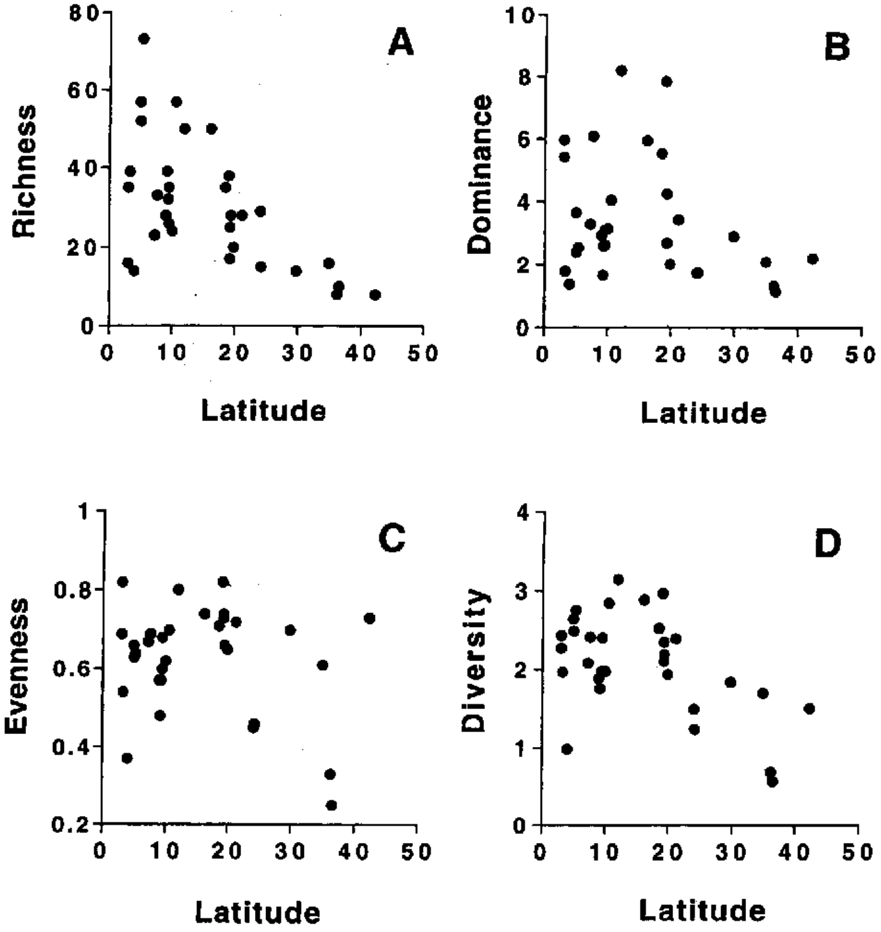


Figure 12.4. Latitudinal gradients in species richness (*A*), dominance (*B*), evenness (*C*), and diversity (*D*) based on 32 assemblages in the New World (see fig. 12.1 and table 12.1). The relationship between richness and latitude, as well as between diversity and latitude is significant, with tropical regions supporting higher biodiversity. Modified from Stevens and Willig (unpublished).

are related to gradients of latitude, other biogeographic factors (e.g., mountain ranges, ocean currents, edaphic features, distance) create spatial heterogeneity in environmental characteristics that are independent of latitude but affect species richness as well. Neighboring but strongly differentiated Amazonia and the caatinga in central Brazil are a case in point. Clearly, not all tropical assemblages should be expected to be equally species rich as a consequence. In fact, tropical regions might be expected to be most variable in bat species richness at the local level (cf. Janzen 1967). In general, tropical latitudes support a

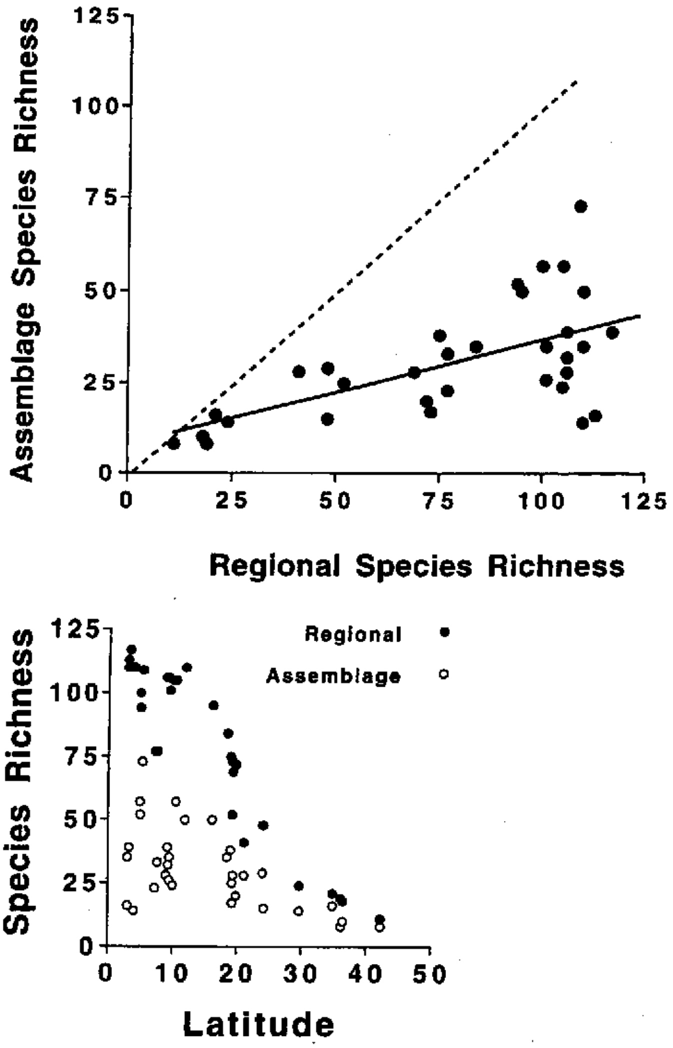


Figure 12.5. *A*, Graphic representation of the association between species richness of local assemblages and the species richness of regional faunas (defined by the number of species ranges that intercept the geographic location of the assemblage). The *solid line* represents the best-fit line from regression analysis, whereas the *dashed line* represents the upper boundary of assemblage richness based on the geographic ranges of species. As regional richness increases, local assemblages contain proportionally fewer of the possible species, suggesting a gradient in ecological filters. *B*, Latitudinal gradients in local (assemblage) and regional richness. The regional gradient is stronger (steeper slope and higher r^2) than the local gradient, mostly as a consequence of greater variation among assemblages at tropical latitudes. Modified from Stevens and Willig (unpublished).

greater number of life zones or plant formations than do cool temperate or boreal regions (Holdridge 1967). The primary environmental mechanisms that drive the latitudinal increase in species richness toward the tropics (i.e., solar irradiance, temperature, stress, or variability), may similarly be the ones that affect the greater variability in the tropics (i.e., the mean and variation in critical environmental characters are positively correlated).

Ecomorphological Structure

Morphologies of species evolve as a consequence of natural selection, so differences in size and shape should be adaptive with respect to ecological function (Peters 1983; Swartz et al., this volume). Morphology can be quantified more easily than direct ecological measures, such as reproductive power (Brown et al. 1996), reproductive stress (Clarke 1995; Palmer and Strobeck 1986), or ecological overlap (MacArthur and Levins 1967; Schoener 1974). It is also possible to use powerful statistical analyses to analyze morphological characters because, after log transformation, they frequently have normal distributions and homogeneous variances (Ricklefs and Travis 1980).

Morphological variation often provides considerable insight into ecological variation within and among species for animals in general (Blackburn et al. 1993; Dayan and Simberloff 1994; Fa and Purvis 1997; Hespenheide 1973) and for bats in particular (Findley and Black 1983; Freeman 1981, 1984, 1988, 1992; Swartz et al., this volume). Consequently, morphological patterns have been used to approximate the underlying ecological patterns in many bat faunas (e.g., Aldridge and Rautenbach 1987; Fenton 1972; Findley 1973 1976; Findley and Black 1983; McNab 1971; Schum 1984; Tamsitt 1967; Willig 1982 1986; Willig and Moulton 1989), despite the many simplifying assumptions that this approach entails.

In general, assemblages of closely related bat species typically comprise a relatively large number of specialists with invariant attributes clustered tightly around a centroid, whereas a smaller number of distinctive, variable species occupy more distant, peripheral niches (Findley 1976; Findley and Black 1983; Fleming 1986). Increases in species richness are facilitated by increasing the size of the total morphological hypervolume occupied by the assemblage, as well as by increases in the degree of species packing within constituent ensembles. Findley (1976), for example, compared three tropical bat faunas and found them to be essentially alike in packing, dispersion, and average degree of morphological overlap. In a study of ensembles of insectivorous-carnivorous bats from the New World, Schum (1984) found that species packing (i.e., distances between nearest neighbors in ecomorphological space) increased with increasing species richness. Moreover, Findley (1993) noted that a negative exponential relationship best described the decrease in mean nearest-neighbor distances with increasing species richness in those ensembles, suggesting limits on the degree of packing or similarity that can be accomplished within an ensemble.

Alternatively, novel ensembles may be accumulating within assemblages along species richness and latitudinal gradients. Stevens and Willig (2000b) presented evidence for this based on 15 assemblages from the New World (table 12.1). The number of ensembles per assemblage ranged from one in Iowa, to seven in Chiapas, Sherman, Barro Colorado Island, edaphic Cerrado, and Caatinga communities. Moreover, as the species richness of an assemblage increased, the number of constituent ensembles increased as well (Spearman's $r_s = 0.52$, $P = 0.023$). The ecomorphological characteristics of species in the different ensembles are quite distinctive (Stevens and Willig 1999, fig. 1). The addition of ensembles explains why increases in species richness consistently enlarge the ecomorphological hypervolume of the resultant assemblage.

Size Assortment and Character Displacement

The degree to which morphological patterns within assmblages are the product of biotic interactions or any other mechanism is unclear. Indeed, the similarity in structure between real ensembles or assemblages and those generated by random selection of species from regional species pools has been noted for over a quarter century (Ricklefs and Travis 1980; Van Valen 1973). This observation applies equally well to bat faunas (Fleming 1986; Schum 1984; Willig and Moulton 1989). Nonetheless, comprehensive or broad-scale evaluation of the degree to which ecomorphological patterns are a consequence of deterministic patterns have only recently been realized for bat assemblages and ensembles.

Morphological Structure and Competition

In a recent study, Stevens and Willig (1999) extended powerful simulation approaches (Moulton and Pimm 1987; Willig and Moulton 1989) to assess the ubiquity of deterministic structure for 15 sites throughout North, Central, and South America (table 12.1). They evaluated the degree to which morphological overdispersion—an indication of competitively induced structure (Hutchinson 1959; MacArthur and Levins 1967)—characterized each of five ensembles of bats (aerial insectivores, frugivores, gleaning animalivores, molossid insectivores, and nectarivores). If species that are morphologically alike jointly consume limiting resources, they should experience interspecific competition. If sufficiently intense, these interactions should favor divergence between competitors, resulting in character displacement. Alternatively, local extinction might characterize species not sufficiently distant from nearest neighbors in ecomorphological space. In either scenario, ecomorphological distances between species should be larger than expected by chance. Similarly, the distances between species would be more homogenous than expected by chance alone as a result of the elimination or displacement of nearest neighbors that exceed some degree of limiting similarity. In summary, ecological equilibria should occur within an ensemble when competitive interactions are minimized by hyperdispersed morphological patterns, leading to similar ecomorphological distances between nearest neighbors.

Overdispersion in at least one bat ensemble was detected at 10 of 15 sites in the New World. Similarly, overdispersion for at least one site was detected for four of five ensembles. Although overdispersed ecomorphological patterns exist in bat ensembles, they are not a common characteristic of the structure. Indeed, no conspicuous pattern existed as to which sites or ensembles exhibited overdispersion. Consequently, Stevens and Willig (1999) conducted a meta-analysis, combining results for all ensembles within an assemblage or combining results for all sites at which an ensemble occurs in the New World. Three of 15 assemblages (California, Guanacaste, and Heredia) exhibited larger distances between nearest neighbors than expected by chance alone. Similarly, three of 15 assemblages exhibited less variable distances between nearest neighbors than expected by chance alone (i.e., Sherman, Barro Colorado Island, and Caatinga).

Finally, the aerial insectivore and frugivore ensembles exhibited structure consistent with a competitive mechanism, based on larger and less variable distances, respectively, between nearest neighbors. Environmental factors such as spatial heterogeneity and climatic variability, or taxon-specific factors such as high mobility (enhancing the likelihood of the rescue effect, sensu Brown and Kodric-Brown 1977), may countermand mechanisms associated with deterministic processes, such that overdispersion is at best a transitory outcome of the effect of competitive interactions on ecomorphological structure.

Density Compensation and Competition

Competitive interactions can act as agents of natural selection in one of two general ways. Competition can cause the morphological evolution of populations via character displacement. Alternatively, competition can contribute to the local extinction of populations of species that exceed the limits of similarity that a local environment can support. However, competition may not be sufficiently intense to cause the local extinction of species but may alter the abundances of local populations of interacting species.

Indeed, it is a general principle in population biology that species that experience more competitive pressure should exhibit lower abundances (Lotka 1932; Volterra 1931) and that the consequence of competitive interactions at equilibrium need not be exclusion or local extinction. If morphological similarity is a surrogate for ecological similarity, then those species that are most dissimilar from other species in an ensemble should experience the least competitive pressure and enjoy the highest abundance, all other things being equal. This phenomenon is known as density compensation (Crowell 1962; Hawkins and MacMahon 1989; Root 1973). As a result, the abundance of a species and its morphological separation from competitors should have a positive association, and the magnitude of the association should be greater than produced by stochastic processes.

A simulation model (Stevens and Willig 2000a) was used to assess whether density compensation affects ensemble structure. The model can also be used to determine whether the competitive effects producing density compensation are mediated by interactions between nearest neighbors or are more diffuse in nature. The model was applied to data for five ensembles in 15 bat assemblages occurring throughout the New World (fig. 12.3; table 12.1). Nonrandom associations between abundance and morphological distance were detected in five assemblages (Guanacaste, Sherman, Barro Colorado Island, Peru, and edaphic Cerrado) and in three feeding guilds (aerial insectivores, gleaning animalivores, and frugivores). Nonetheless, no assemblage was strongly structured in all its constituent ensembles, and no ensemble was deterministically structured across most locations. There was no pattern as to which sites or which ensembles consistently evinced signs of density compensation.

A meta-analysis of the data suggests that gleaning animalivores are most affected by interactions between nearest neighbors, and the assemblage at Sherman exhibits a strong pattern of density compensation in all constituent ensembles from both diffuse and near-neighbor perspectives. Moreover, the likelihood of significant deterministic structure was unrelated to the number of species in an ensemble or to the number of species in the assemblage from which the ensemble was obtained (Stevens and Willig 2000b).

Methodological Constraints

Understanding pattern and process at the level of local assemblages is predicated on accurate estimation of attributes such as species composition and density. As a result, all assemblage-level research suffers from a number of constraints and biases related to sampling methodologies and effort, and this is particularly true for studies of bats. Characteristics related to temporal (nocturnal activity), spatial (vertical stratification), and sensory (ultrasonic communication) activities of bats make it difficult to detect their presence and estimate their abundance, compared to the situation for many other groups of animals or plants. As a consequence, we have been careful to utilize rigorous criteria in selecting bat assemblages for analysis. Nonetheless, we have likely underestimated species richness and excluded rare species from our representations of local assemblages.

We cannot evaluate, per se, the accuracy of estimates used in the previous broad-scale analyses of bat assemblages. To do so would require knowledge of the actual taxonomic composition and species densities at local sites. If we had such "parametric information," we (as well as the original authors) could have used it in analyses. Thus, caution should be applied in accepting patterns and process as real in ecological studies at the assemblage level. Nonetheless, resampling methodologies or jackknife procedures can be used to assess the degree to which detected patterns are predicated on sampling effort alone. Initial sensitivity analyses that focus on attributes of diversity (species richness, species evenness, species dominance, and species diversity) with sampling effort suggest such patterns may be quite robust for bat assemblages.

The essence of resampling methodologies or jackknife procedures is that it is easier and more accurate to predict the effects of sampling at lower levels of effort than it is to extrapolate to more intense levels of effort. For each of 32 bat assemblages (table 12.1), Stevens and Willig (2001) evaluated the extent to which sampling intensity affected the detection of latitudinal gradients in 15 different indexes of species richness, evenness, dominance, or diversity. Regardless of index, the statistical association between latitude and an index of biodiversity was insensitive to sampling effort to about 50% of the original effort. For example, based on all data at each site, the correlation between species richness and latitude was approximately −0.59 and significant ($P < 0.05$). Incremental reductions in sampling (5% steps) to 50% of the original effort gradually decreased the average correlation to −0.58, but all simulated correlations remained significant.

In a similar fashion, the correlation between Hill's index of evenness and latitude based on all the data at each site was approximately 0.11 and nonsignificant at $\Delta = 0.05$. The correlation gradually decreased with reductions in sampling effort, but at 50% of the original sampling intensity, the correlation remained 0.11 with all simulated correlations not significant. Although variation in the magnitude of the simulated correlations generally increased with decreasing sampling intensity, decisions of significance or nonsignificance were unaffected for the most part. If simulations to lower levels of effort provide insight to the patterns that would be detected with greater effort, then the gradients in diversity, which we detected, are reasonably robust and unlikely to be altered appreciably by increased effort at the local level.

Additional application of these numerical techniques to other measures of pattern at the assemblage level represents an exciting area of future research. Equally important, as new technologies become refined (e.g., bat detectors) or the application of canopy netting becomes prevalent, more accurate estimations of assemblage composition and abundance may be forthcoming. Thereafter, comparison of patterns based on ground netting to those based on combined approaches will provide deeper insight to the spatial and temporal dynamics of bat assemblages.

Overview and Prospectus

Bat species achieve remarkable degrees of local diversity and regional abundance that are enabled by their ability to exploit extensive home ranges (e.g., Handley et al. 1991). In some regions, individuals of up to 100 species of bats may have at least partially overlapping home ranges (e.g., Patterson et al. 1996; Simmons and Voss 1998). No other group of mammals in the 230-million-year history of the group has approached this degree of alpha diversity. Flight (or more precisely the enhanced vagility it provides) is fundamental to this ecological overlap. Lacking flight and thus being more confined to given locales, terrestrial mammals must satisfy their ecological requirements within a smaller spatial "footprint," leading to finer-grained (sensu Levins 1968), less specialized patterns of resource utilization. As shown in the preceding survey, most trophic groupings of bats rely to some degree on exploitation of diffuse resources. In areas where diversity is greatest—the tropics—partitioning of resources may involve a combination of spatial, temporal, and food-specific factors. The ability of bats to move quickly and efficiently over considerable distances in search of food, roosts, and mates has permitted such extensive and refined partitioning of resources.

Ecological resource partitioning sustains bat diversity at high levels but also leaves them vulnerable to rapid endangerment and extinction in a human-dominated world. As humans convert an ever-greater fraction of natural habitats, all kinds of organisms are affected (Willig and Walker 1999), but three groupings are especially vulnerable to landscape changes. First, those with small geographic ranges may find their entire ranges denuded and may be left without appropriate habitats. Second, species that are highly specialized in terms of food preferences or ecological requirements may be vulnerable to the disappearance of these resources or conditions, even if the habitat in which they live remains largely unaltered by human activity. Finally, even species with large geographic ranges can be vulnerable to anthropogenic modification of the landscape if they exploit decidedly diffuse resources.

It has been argued that the great diversity of tropical forests is built on the highly dispersed distributions of many plant species (Condit et al. 2000). To exploit these dispersed species requires adaptations to and reliance on diffuse resources. Bats, more than any other group of terrestrial mammals, excel in the efficient exploitation of diffuse resources. However, as tropical forests become fragmented, the commuting costs while foraging necessarily increase as bats traverse increasingly large, unsuitable matrix habitats.

Even though the high vagility associated with flight allows bats to exploit fragments, seemingly protecting them from the effects of deforestation, their reliance on already-diffuse resources leaves bats highly vulnerable, as increasingly distant resources become too expensive to harvest. Sadly, the same phenomenon applies to some bats in the temperate zone, where bat species constitute disproportionate fractions of the endangered species lists for Europe and North America. Temperate-zone bats are often doomed by their specialized roosting habits, which make disruptions of breeding or hibernation cycles all-too-common—often lethal—occurrences. Tropical bats, in contrast,

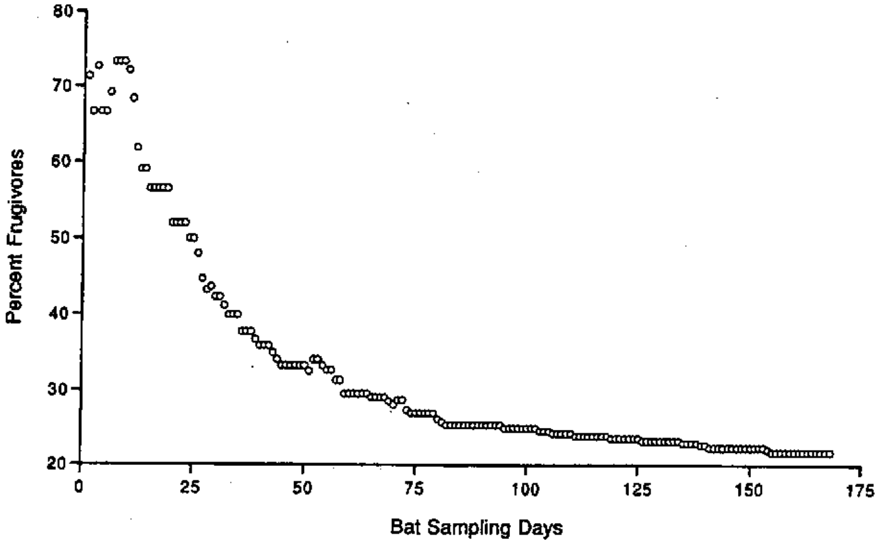


Figure 12.6. Differential capture success for different bat ensembles is well known. Differential accumulation of bats at Paracou, French Guiana, produces remarkably different estimations of the diversity and community importance of frugivores, depending on the sampling intensity employed (Simmons and Voss 1998, fig. 77). Greater sampling efforts over realistic spatial and temporal scales will be necessary to understand all tropical communities. However, bat ecologists must be especially committed to this effort, given the vagility, elusiveness, and ecological diversity of bats.

particularly insectivorous species, respond to habitat conversion with reductions in both species richness and abundance (Brosset et al. 1996; Estrada et al. 1993; Vaughan and Hill 1996; Wilson et al. 1996). Some, like many phyllostomines, appear well suited to serve as "indicator species," indexing by their presence and abundance the quality of habitat remaining in a region (e.g., Fenton et al. 1992).

Because bats are far ranging, nocturnal, and operate in a perceptual realm organized mostly by sound rather than sight (except in pteropodids), they are often difficult to sample. Most ecological studies of bats have targeted only part of an assemblage—few have targeted guilds or ensembles. Assemblage-wide inferences from such incomplete samples can lead to serious misconceptions. Figure 12.6 (from Simmons and Voss 1998, fig. 77) illustrates that the proportion of species that are frugivores in a Neotropical bat fauna decreases monotonically with sampling, from a predominating 70% after a week of sampling to an asymptotic value of 22%. Although it is customary to ascribe patterns such as these to the different perceptual abilities of bats or to the flight strata that they utilize, differential apparency to sampling is also tied to the diffuse space-use patterns under discussion.

Finally, Kalko (1998) observed that future studies of bat "communities" (assemblages by our definition) should combine macroecological and mechanistic studies. Our review concurs that far more progress has been made in assembling macroecological patterns than in testing the mechanisms thought to produce them. Certainly, the large spatial scale needed for such tests offers a powerful explanation for these trends. Kalko's discussion emphasized the methodological challenges to be overcome in order to understand the ecological interactions of tropical bat diversity. Although all are important, we would emphasize one: ecologists must be prepared to compare, contrast, and ultimately integrate ecological patterns of bats with those shown by other taxonomic groups. Comparisons of gross macroecological patterns have been revealing (Graham 1990; Patterson et al. 1998), but we need to go further.

Comparisons must extend to the level of resource partitioning and species-abundance patterns if we are to understand their mechanistic basis. Only a few comparative studies exist (e.g., Gorchov et al. 1995; Palmeirim et al. 1989), but efforts underway in Panama by Kalko, Robinson, and von Staden (Kalko 1998), in Peru by Patterson, Stotz, Solari, and Hodgkison, and in Malaysia by Kingston, Jones, Zubaid, and Kunz (Kingston et al. 2000) promise to extend them. Only when bat ensembles can be placed into a community-wide context will bat studies take their rightful place in ecology's pantheon.

Acknowledgments

We are grateful to two anonymous reviewers as well as to Tom Kunz, Jodi Sedlock, and Sergio Solari for their help and insights in developing more balanced and complete references to the enormous literature on ecological interactions of bats. We thank Tom Kunz and Brock Fenton for their invitation to participate in this important undertaking and for their comments on the text.

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