

Body size and resource competition in New World bats: a test of spatial scaling laws

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Assembly rules based on body size characterize processes that determine community composition and structure. One prominent model proposes a spatial scaling law (SSL) that links body size with foraging behavior and predicts the minimum difference in body size that is necessary for species coexistence. Although this SSL is cited frequently, robust tests of its predictions are few, and its performance in these tests has been mixed. We used data on 34 well sampled bat assemblages from throughout the New World to test predictions of the SSL for 5 feeding guilds: aerial insectivores, frugivores, high-flying insectivores, gleaning animalivores, and nectarivores. Contrary to the model's predictions, body-size ratios of species of adjacent size did not decrease with increasing body size, the frequency distribution of sizes within a guild was not left-skewed, and the relationship between species richness and productivity was not modal with a long tail to the right. Body size alone appears insufficient to describe niche differentiation and species coexistence in New World bats, calling into question the broad applicability of this model of spatial scaling. Future studies of the SSL should identify the characteristics that predispose a community to be characterized well by such a model, rather than assuming it is a robust descriptor of communities regardless of taxon and other conditions.

A fundamental goal of ecology is to identify mechanisms that determine the structure and composition of communities. Although neutral models have been successful in describing some patterns of biodiversity, particularly at broad spatial scales (Hubbell 2001), many ecologists continue to consider niche differentiation critical to local coexistence of species (Chase and Leibold 2003). In that context, body size commonly is used as a surrogate or indicator of niche characteristics because it is associated strongly with many ecological attributes (Peters 1983), particularly those relating to resource use (Brown and Lieberman 1973, Maurer et al. 2004) or energetics (Kleiber 1932, West et al. 2003). As such, assembly rules based on body size frequently have been used to characterize processes that determine community composition and structure (Bowers and Brown 1982, Brown and Nicoletto 1991, Stevens and Willig 2000a, b).

In addition to imposing metabolic constraints, body size influences the foraging behaviour of species (Belovsky 1997, Ritchie 1998). One model that explicitly links this phenomenon to patterns of biodiversity and community structure is a spatial scaling law developed by Ritchie and Olff (1999; hereafter referred to as the SSL, following Cromsigt and Olff 2006). This model, grounded in fractal geometry, describes how species of different body sizes find food in patches that differ in size and resource concentration. It is based on the

premise that larger species detect only larger patches of food but can tolerate lower concentrations of resources (i.e. lower quality food items), compared to smaller species (Belovsky 1997, Ritchie 1998). This trade-off determines the subset of possible combinations of patch size and resource concentration that permits population growth to be positive for a species of a particular body size (i.e. its niche). For a species to persist regardless of the abundance of competitors, it must have an exclusive niche (a set of combinations of patch size and resource concentration used by no other species in the community) within which energetic benefits of resource intake at least equal energetic costs associated with metabolic expenditures. The SSL identifies the minimum difference in size between competitors that will produce exclusive niches that are sufficient for persistence of both species. This rule leads to several testable predictions regarding patterns of biodiversity relative to body size and productivity, and imposes an upper bound on local species richness, thereby providing a unifying framework for studies of biodiversity and community structure.

The promise of this particular scaling law is reflected in its pervasive citation in the literature during the last decade; it had generated 153 citations as of 21 May 2010 (ISI Web of Science). The SSL commonly is used to provide explanations or predictions for the form of patterns of diversity, body size, and productivity (Chase and Leibold

2002, Schweiger et al. 2005, Schreier et al. 2009), or as a conceptual basis for development of additional theory (Brown et al. 2002, Hambäck and Englund 2005).

Empirical assessments of the SSL have yielded mixed conclusions. Predictions were supported by size and diversity patterns of assemblages of several groups: grazing ungulates and grassland plants (Ritchie and Olff 1999, Anderson et al. 2004), vertebrate granivores in the Chihuahuan Desert (Ritchie and Olff 2004), vascular plants in the Great Basin Desert (Ritchie and Olff 2004), and carabid beetles (Sota et al. 2000). In contrast, parasites of marine fish (Rohde 2001) and of macropodid marsupials (Poulin et al. 2008) failed to conform to model expectations. The only experimental test of the SSL, which focused on four species of savanna grazers, found little support for its central premise. Contrary to predictions, the smallest species consistently chose plots with larger resource patches, whereas larger species showed no preference (Cromsigt and Olff 2006). Otherwise, rigorous empirical assessments of the SSL are lacking for most organisms, especially those in diverse tropical environments.

The SSL makes three testable predictions about body size and biodiversity (Ritchie and Olff 1999). First, body-size ratios of species of adjacent size (i.e. the ratio in size of larger species to size of smaller species) should decrease with increasing body size (i.e. larger-bodied species can be packed more densely into patch size-resource concentration space). Second, the frequency distribution of sizes within a community should be left-skewed and unimodal because larger species can be packed more densely than can smaller species (as per the first prediction), but the largest species are limited by the availability of patches of food that are large enough for them to perceive. Third, the relationship between species richness and productivity (i.e. resource abundance) should be unimodal with a long tail to the right.

New World bat communities represent a model system for evaluating the SSL. In the continental New World, the Order Chiroptera is relatively species rich, represented by over 250 species (Simmons 2005), as well as ecologically and phylogenetically diverse, comprising seven functional groups (Patterson et al. 2003) and 11 families (Wilson and Reeder 2005). Moreover, bats exhibit strong latitudinal (Willig and Selcer 1989, Stevens and Willig 2002) and elevational gradients (Patterson et al. 1998, McCain 2007) of diversity. Nonetheless, the structure of bat communities is highly variable in the extent to which they correspond to deterministic models based on the competitive exclusion principle (Willig 1986, Willig and Moulton 1989, Stevens and Willig 2000a, b). Herein, we test the three predictions of the SSL for each of 5 feeding guilds of bats spanning 34 different communities throughout the New World.

Methods

Characterization of feeding guilds

We gathered data from the literature regarding species composition of the bat fauna at each of 34 sites in the New World (Supplementary material Table S1). Each data set fulfilled the criteria established by Stevens and Willig

(2002) to maximize the likelihood that it represented a reasonably complete community of bat species that, because of spatial and temporal proximity, have the potential to interact.

We categorized species from each community into seven feeding guilds: aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, nectarivores, piscivores, and sanguinivores (Stevens and Willig 1999). We assigned species to guilds based on designations from the original description of the community or from other published dietary information (Wilson 1975, Gardner 1977). Because small sample size severely limits statistical power, we included a guild in analyses only if it contained at least five species. The piscivore and sanguinivore guilds never met this criterion; consequently, we used the remaining five guilds in analyses. We used mean body mass as an estimate of body size for each species. We obtained most of these measurements from Jones et al. (2003), but a few from museum specimens or other literature sources.

Statistical analyses

The SSL predicts that body size ratios should decrease with increasing body size (Ritchie and Olff 1999). The exact form of the decrease depends on values assigned to various model parameters. To test this prediction, we used Spearman's rank correlation (which detects a monotonic decline regardless of the exact form of the relationship) between the ratio of the untransformed body sizes of adjacent-sized species and the log-transformed size of the larger species in each species pair. To test the prediction that frequency distributions of body sizes of species are left-skewed, we estimated the third moment statistic, g_1 . A value of g_1 significantly less than 0 indicates an asymmetrical distribution with the mean less than the median (i.e. left skewness). To assess significance, we used the z-transformation of D'Agostino et al. (1990) and compared the resultant values to the standard normal distribution. Because this transformation is undefined at small sample sizes, we conducted this analysis only for combinations of guild and community for which species richness was ≥ 8 . For both the correlations and the assessment of skewness, we used one-tailed tests to increase the likelihood of detecting a pattern consistent with the predictions of the SSL. In addition to testing correlations and skewness for each combination of guild and site separately, we conducted a meta-analysis based on Fisher's test for combining probabilities (Sokal and Rohlf 1995) to evaluate whether the overall pattern for each guild was consistent with the first two predictions of the SSL.

To examine the third prediction of the SSL, we obtained estimates of net primary productivity (NPP) for each community from Imhoff et al. (2004a; <<http://sedac.ciesin.columbia.edu/es/hanpp.html>>). Estimates of NPP were taken from a global grid with cells of 0.25-degree resolution (Imhoff et al. 2004b). We corrected estimates of productivity for latitudinal changes in area of cells by dividing the number of grams of carbon fixed per year in each cell by the area of that cell, thereby generating an estimate of productivity on a km² basis. We visually assessed, for

each guild, whether the relationship between guild richness and productivity was unimodal with a long tail to the right as predicted by the SSL.

The SSL should be most applicable to communities that are strongly structured by a history of competitive interactions. Therefore, we predicted that model fit should be greatest for guilds in communities at tropical latitudes, where species richness is greatest. To test this, we conducted Spearman's rank correlation analyses between latitude and each of two variables: the correlation coefficient (r_s) between body size ratio and body size of the larger species, and the skewness coefficient (g_1) for each body size distribution. Because patterns of species richness in the tropics may be driven more by high productivity than by latitude per se (Hawkins et al. 2003), we also tested for a correlation between productivity and each of the two measures of model fit (r_s and g_1) for the body size predictions.

Results

Patterns of body size in the 34 bat communities did not support the predictions of the SSL. Of the 85 combinations of site and guild that met the sample size criterion, none exhibited a significant negative correlation between body size ratios and body size of the larger species in a species pair (Fig. 1A). In fact, only 30 of 85 rank correlation coefficients were negative, and only four of these approached significance (Supplementary material Table S2). Similarly, frequency distributions of body size were not significantly left-skewed for any guild at any community (Fig. 1B). Most (45 of 58) estimates of g_1 were positive, suggesting instead a right-skewed distribution of body sizes (Supplementary material, Table S3). Fisher's test confirmed the lack of support for the SSL, as the meta-analyses did not generate a significant result for any guild (Table 1).

The third prediction of the SSL, that the relationship between species richness and productivity should be unimodal and right-tailed, was inconsistent with observations from bat communities. The empirical relationship was neither strongly modal nor skewed to the right for any of the five guilds (Fig. 2). Instead, the extended tails of these relationships, if apparent, were to the left.

Associations between latitude or productivity and the degree to which observations were consistent with the first two predictions of the SSL were not consistent among guilds (Table 2). For aerial insectivores, measures of fit for both predictions 1 and 2 correlated negatively with latitude, suggesting that the SSL is more predictive of body size distributions of insectivores in communities that are more distant from the equator. For nectarivores, the correlation between body size and size ratio was positively correlated with latitude, suggesting that model fit decreased with increased distance from the equator. Productivity was significantly correlated with model fit in only two cases: negatively for nectarivores with respect to prediction 1 and positively for aerial insectivores with respect to prediction 2. For frugivores and gleaning animalivores, model fit was correlated with neither latitude nor productivity. Regardless, for each combination of guild and site, observations

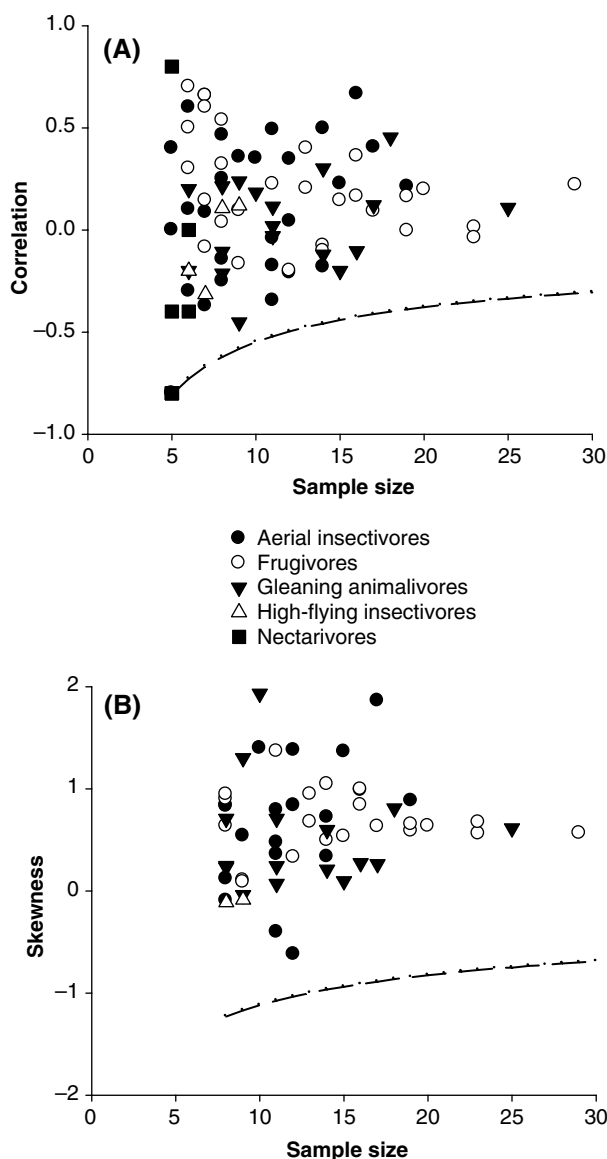


Figure 1. Results of individual tests of correlations between body size ratio and body size (A) and negative skewness of body size distributions (B). Black dashed lines separate regions of significance (below line) from non-significance (above line) of test statistics.

consistently differed from expectations under the SSL (Supplementary material Table S2, S3).

Discussion

Body size is an important ecological characteristic of organisms, and has long been associated with niche partitioning based on the concept of limiting similarity. Hence, the hypothesis that species richness is regulated largely by differences in body size among potential competitors is intuitively appealing, with a strong historical precedent. The SSL elegantly links biodiversity to foraging theory, and can be used to derive predictions about a wide variety of ecological phenomena, including responses of species richness to productivity or habitat fragmentation

Table 1. Results of a meta-analysis (Fisher's test for combining probabilities) that summarizes tests of two predictions of the SSL (negative correlation between body size ratio and the body size of the larger species, and negative skewness of body size distributions) for each guild, considering all sites simultaneously. A significant outcome indicates an overall pattern consistent with the SSL. Statistic mean indicates the average correlation coefficient (r_s) or skewness measure (g_1) observed for each feeding guild.

Feeding guild	Statistic mean	p	DF
Correlation			
Aerial insectivores	0.088	0.967	54
Frugivores	0.208	0.999	58
Gleaning animalivores	0.029	0.893	36
High-flying insectivores	-0.070	0.579	8
Nectarivores	-0.343	0.113	14
Skewness			
Aerial insectivores	0.543	0.999	58
Frugivores	0.711	0.999	42
Gleaning animalivores	0.465	0.999	32
High-flying insectivores	0.444	0.517	4

(Ritchie and Olff 1999). Nevertheless, our results provided no support for the model, with empirical patterns often opposite to those predicted by the SSL. Consequently, the SSL may be of more limited applicability than is typically assumed. Reasons for this are rooted in particular assumptions of the SSL and how they relate to mechanisms by which organisms partition niche space. First, the mechanism of the SSL reflects only some of the possible dimensions by which niche partitioning can occur. Second, the SSL requires that body sizes of guild members reflect strong, pervasive effects of resource competition. Third, the SSL does not consider the effects of variability in body size or perception.

Resource partitioning

The conceptual basis of the SSL is based on the assumption that body size mediates patch selection (Ritchie and Olff 1999). Because all species in a community are assumed to use similar resources (i.e. to be members of the same guild), body size is the sole predictor of patch selection and, therefore, the sole dimension of niche differentiation. Therefore, all individuals of a particular size must share the same niche. If body sizes of species are sufficiently different, each species will exploit an exclusive set of resource patches (i.e. the exclusive niche) that are too small for larger species and too low in resource concentration for smaller species. If differences in body size among species are small, exclusive niche space is also small, and coexistence is unlikely. In nature, however, multiple dimensions of niche differentiation are possible. In addition to choosing different patches (i.e. spatial niche partitioning), potential competitors can partition niche space by specializing on different resources (Futuyma and Moreno 1988) or by exploiting the same resources at different times (Pianka 1973). Bat guilds commonly exhibit such alternative means of niche partitioning. Bats have multiple complementary phenotypic characteristics (e.g. body size, cranial morphology, wing morphology, echolocation calls) that are important to

resource acquisition and processing, and these facilitate extensive dietary specialization.

For many species, partitioning of food resources probably cannot be characterized completely by a single measure such as body size because multiple phenotypic characters affect resource exploitation, and these characters may not be highly inter-correlated. In particular, most animals have an apparatus that imparts mobility and another that processes materials (food) obtained during foraging. In bats, wings provide mobility, echolocation facilitates movement as well as detection of food, and the cranium is responsible for much of the physical processing of food. With respect to all three of these trophic characteristics, a great deal of variation exists that places constraints on where bats can forage (Kalko 1998) and the types of foods that can be processed (Dumont 1999, Aguirre et al. 2003). For example, the shape of the wings and aspects of echolocation signal determine whether a species can forage in cluttered areas or must do so in more open spaces (Jones and Holderied 2007, Kalko et al. 2008). Similarly, differences in the shape of the cranium translate to different food processing abilities and, hence, different diets (Freeman 1979, Dumont 2004, Stevens 2005). The extensive variation in shape among bat species, as well as the separation of phenotypic characteristics related to locomotion, navigation, and food processing, may facilitate niche complementarity, thereby circumventing the effects of ecological processes such as competition on patterns of variation in body size.

Dietary specialization may also facilitate coexistence of species of similar body size. Under the SSL, resources (e.g. nutrients) are bound within patches of food (Ritchie and Olff 1999). The SSL does not consider variability in patch characteristics other than size that may allow coexistence of species of similar body size. For example, carbon is a resource that can be obtained from fruit. In nature, however, many plant species bear fruit, and therefore many different types of patches exist, irrespective of size. Bat species of similar body size can specialize on different forage species (i.e. type of patch), and thus coexist. Many examples of specialist syndromes exist in the Chiroptera, including moth and beetle specialists in aerial and high-flying insectivores (Freeman 1979); *Ficus* (Handley et al. 1991), *Piper* (Fleming 1988), and *Solanum* (Marinho-Filho 1991) specialists in frugivores; and numerous extreme pollination adaptations in nectarivores (Muchhala 2007). Even if two species have diets that contain the same food species, the potential for niche differentiation remains. Generalist herbivores, for example, often consume the same plant taxa, yet can maintain species-specific nutritional niches by consuming different amounts and ratios of proteins and carbohydrates (e.g. grasshoppers; Behmer and Joern 2008). This mechanism could facilitate coexistence of competing generalists regardless of body size. Similarly, temporal niche partitioning could occur between species with similar diets. Little empirical research supports this contention for bats (Castro-Arellano et al. 2009, Presley et al. 2009a, b), although temporal niche partitioning has been documented for rodents (Kotler et al. 1993, Castro-Arellano and Lacher 2009).

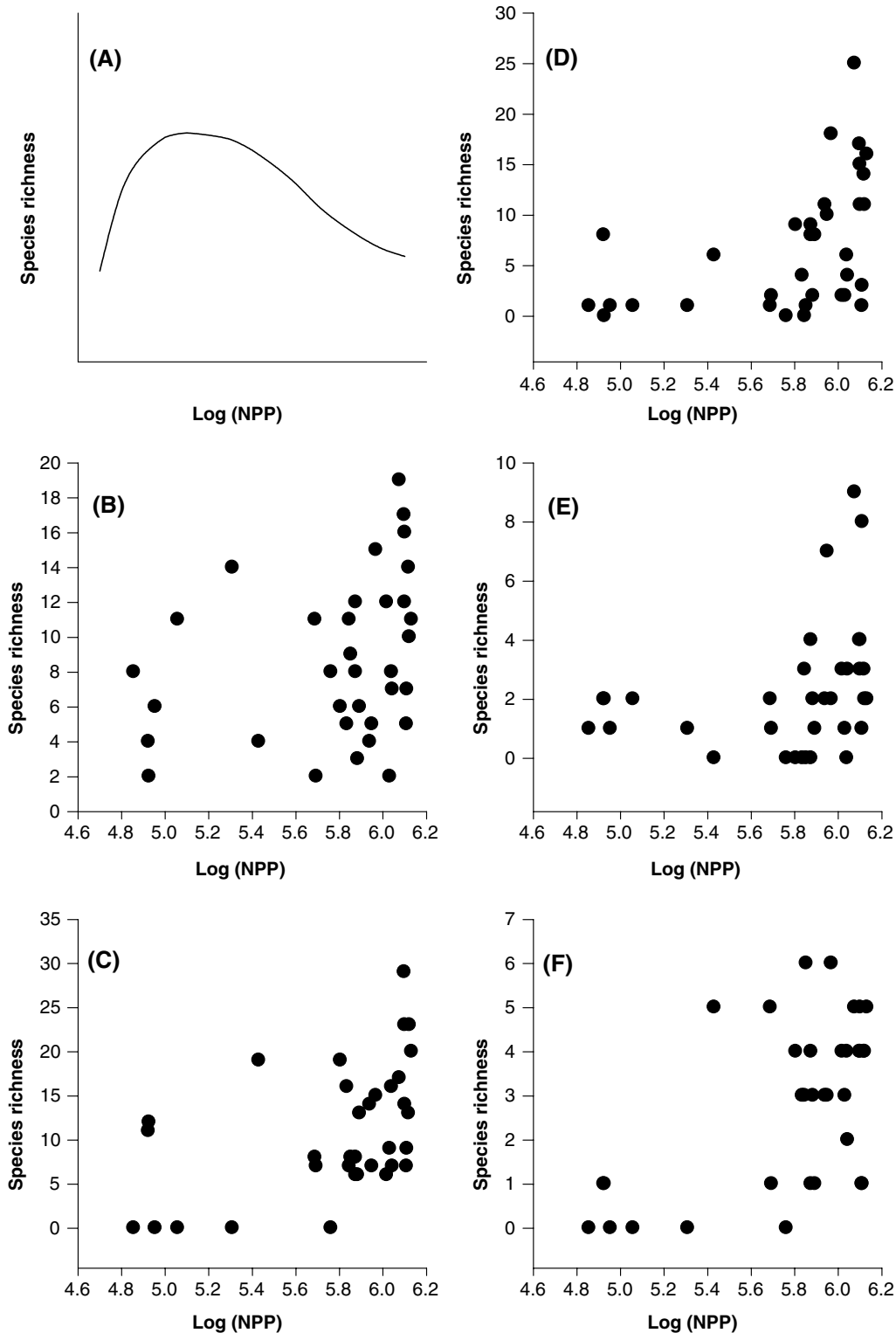


Figure 2. Species richness as a function of the log₁₀ of primary productivity (g of carbon yr⁻¹ km⁻²), as predicted by the SSL (A) and observed for aerial insectivores (B), frugivores (C), gleaning animalivores (D), high-flying insectivores (E), and nectarivores (F). Each point corresponds to a different community.

Importance of competition

For competition to produce detectable morphological patterns, such as those predicted by the SSL, certain conditions must be met. Competition must be sufficiently

intense to cause local extinction or character displacement, pervasive enough to affect most members of the guild, and the dominant structuring mechanism (Moulton and Pimm 1986). Such conditions are most likely to be met in stable, predictable environments. Hence, the SSL is implicitly an

Table 2. Spearman rank correlations (r_s) and associated significance levels (p) between latitude and the test statistics for two predictions of the SSL (prediction 1: body size ratios should decrease with increasing body size; prediction 2: body size distributions should be left-skewed). n is the number of sites at which the predictions were tested for each guild. Sample sizes are lower for prediction 2 than for prediction 1 because exact p -values for skewness could be identified using the method of D'Agostino et al. (1990) only if the number of species in a guild at a particular site was ≥ 8 . Correlations were estimated for 4 of the 5 guilds; high-flying insectivores were excluded because of low sample size (only 3 sites had $S \geq 5$, and only 2 had $S \geq 8$).

Guild	Prediction 1			Prediction 2		
	n	r_s	p	n	r_s	p
Aerial insectivores	27	-0.43	0.024	19	-0.65	0.003
Frugivores	29	-0.09	0.642	19	-0.18	0.430
Gleaning animalivores	18	0.42	0.083	16	0.33	0.217
Nectarivores	7	0.82	0.025	-	-	-

equilibrial model. Nevertheless, many conditions can conspire to prevent populations and communities from reaching equilibria, thereby enabling competitors to coexist regardless of body size. For example, the intensity of competition for resources may be reduced in some communities by a super-abundance of resources or by a reduction of population densities of superior competitors below equilibrium levels by predation (Paine 1966) or disturbance (Connell 1978). For most guilds of New World bats, however, super-abundant resources probably do not account for inconsistencies with the SSL, as model fit improved with increasing latitude or productivity only for aerial insectivores. In extreme cases, predation or disturbance can eliminate species, generating an unsaturated community and further disrupting morphological patterns that would be expected under strong competition.

In the context of the SSL, an unsaturated assemblage is one in which not all combinations of patch size and resource quality are included within the minimum exclusive niches of extant species. That is, ecological space could be further apportioned to accommodate more species. This situation was common for New World bats, as size ratios of pairs of adjacently-sized species of bat often increased with increasing body size. This may arise because of the extirpation of species (e.g. by competition, predation, or disturbance that is not mediated by body size) or by dispersal limitation that prevents species from reaching a site. The latter is unlikely for bats, given their high vagility, but may explain why guilds of less mobile organisms (e.g. parasites; Rohde 2001, Poulin et al. 2008) appear to be unsaturated.

In contrast to the effects of dispersal limitation, high mobility may also degrade patterns of body size predicted by the SSL. Mass effects (Mouquet and Loreau 2003) and rescue effects (Brown and Kodric-Brown 1977) are common and allow species to persist in communities as sink populations. For mobile organisms, frequent dispersal into a community can allow some species to remain present at a site over the long term, even when competitors of similar body size cause them to suffer non-positive growth rates. Mass effects enhance the persistence of bat species that would otherwise be eliminated by environmental (vegetation and climate) filters (Stevens et al. 2007), and a similar phenomenon may exist with respect to competitive interactions (Willig and Moulton 1989).

Variability and the SSL

Certain assumptions must be met for a patch foraging framework to characterize a community. For example, resources must be spatially distributed among patches of different size or resource concentration, and foragers must be able to distinguish suitable from unsuitable patches, and move between them. This accounts for the failure of the SSL to describe patterns of body size and diversity for diatoms, which do not forage in discrete patches of resources (Passy 2007). In particular, the SSL implicitly assumes that all individuals of a species have the same body size and all individuals of a particular body size perceive resources in the same manner at all times. The latter remains largely unexplored, but the scale at which a species perceives patches of resources can change depending on the pattern of distribution of those resources (McClure and Shipley 2009).

When species differ greatly in body size, variability in body size within a species probably is not a problem for the SSL because exclusive niche space remains extensive. Nevertheless, body size varies among individuals within a species, and when two species are similar in size, this often results in considerable overlap of body size distributions. If body size distributions routinely overlap, then the mechanism for niche partitioning proposed by the SSL fails. This situation is common within bat guilds, especially at species-rich sites. For example, of 17 species of aerial insectivores captured at Iquitos, Peru, all but two, *Lasiurus ega* and *Noctilio albiventris*, had adult body size distributions that overlapped with at least one other species (Fig. 3). No other species enjoyed any exclusive niche space based on body size alone. This is additionally problematic if one considers juveniles. Because juveniles are much smaller than are adults, body size distributions that include juveniles should overlap even more extensively than would those including only adults.

Conclusion

Our results, in combination with those of Rohde (2001) and Poulin et al. (2008), challenge the generality of the SSL and its utility for developing general theory regarding biodiversity. These observations are consistent with prior studies that suggest that competitive interactions are not strong structuring mechanisms for New World bats

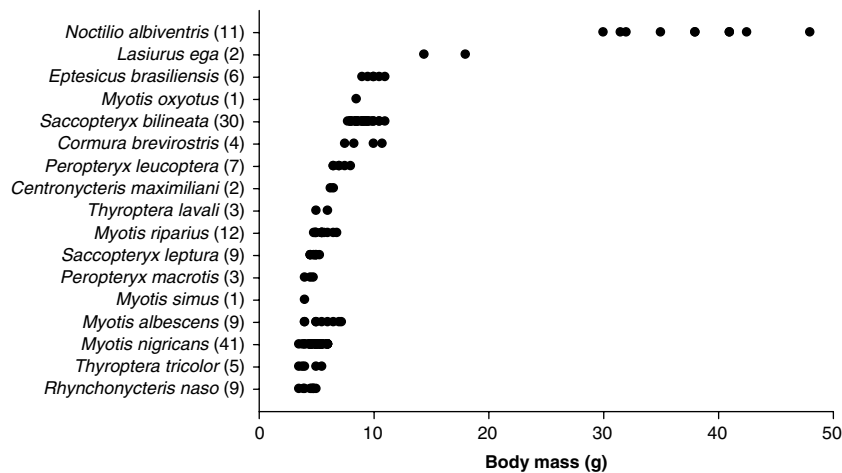


Figure 3. Body size (mass, g) of adult aerial insectivores (excluding pregnant females) captured at Iquitos, Peru. Each point represents an individual, except when multiple individuals of a species had the same mass. The total number of individuals per species is listed in parentheses after species names.

(Willig 1986, Willig and Moulton 1989, Willig et al. 1993, Stevens and Willig 2000a, b) or that patterns of body size alone are insufficient to account for coexistence of species (Simberloff and Boecklen 1981, Willig 1986, Dayan and Simberloff 2005). Hence, alternative mechanisms must be sought to account for patterns of species richness in bats. Future research regarding the SSL should focus on identifying the characteristics that predispose a community to be characterized well by such a model, rather than assuming it is a robust descriptor of communities independent of taxon or other considerations.

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