

## ON THE SCALING OF HABITAT SPECIFICITY WITH BODY SIZE

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**Abstract.** Larger species tend to occupy more habitats, but a theoretical framework for the pattern is lacking. I modified the continuous-time logistic equation of population growth in two ways to allow for such a habitat-based theoretical framework. First, I separated birth rate from death rate. Second, I included two new terms in the equation: (1) an explicit spatial variable for habitat quality that reflects the match between a habitat and a population (species–habitat match), and (2) a demand/supply function that depends on the ratio between the energy used by all populations occurring in a habitat, and energy available in that habitat. Energy was used as a common currency to overcome differences between species of different body sizes as well as to overcome differences caused by disproportional intra- and interspecific effects. Allometric relations were used to characterize parameter values that correlate with body size, such as metabolic rate, birth rate, and death rate. The analytical solution of the equation for carrying capacity shows that, for a population to have a positive carrying capacity, its ratio of death rate to birth rate should be less than its match to the habitat it occupies. Literature-based body-size-dependent birth and death rates of Eutherian mammals show that the death-rate:birth-rate ratio decreases with body size. Combining the analytical solution and the death-rate:birth-rate ratio reveals that habitat generality should positively scale with body size. I used this model to simulate simple spatially explicit landscapes having diverse habitats and combinations of species of various body sizes. Using realistic parameters, the model generates results that are consistent with field observations. Thus, one can focus on specific processes to explore macroecological questions.

**Key words:** allometry; body size and habitat specificity; demand/supply function; energy; habitat; logistic equation; macroecology; range–abundance distribution; scaling; species–habitat match.

### INTRODUCTION

Species-diversity patterns of body size (e.g., Brown and Maurer 1986, 1989, Damuth 1987, Nee et al. 1991, Holling 1992, Blackburn et al. 1993, Siemann et al. 1996) have been studied repeatedly as a way to understand general rules of community ecology. The spatial scale of the pattern and the diversity of the body sizes involved make them subjects for landscape ecology and allometry.

Landscape ecology (Forman and Godron 1986, Turner 1989, Hansson et al. 1995, Pickett and Cadenasso 1995) recognizes that the configuration of the physical environment heavily affects the abundance and distribution of species. This is because a species is not a single homogeneous group of individuals, but rather a collection of populations, each behaving with its own

dynamics in a local environment (Hanski and Gilpin 1997). As a result, the ability of a particular species to inhabit a large area, which is actually a mixture of habitats, depends on how well its populations perform in (or matches to) the set of existing habitats. From a species perspective, local processes within each habitat (e.g., competition with other species' populations on habitat-specific shared resources) may result in populations having different fitnesses in the different habitats they occupy. Hence, the study of large-scale pattern of species diversity must take into account the occurrence and quality of different habitats in the landscape (Fahrig and Paloheimo 1988). This suggests that we should explicitly consider how well different species' populations do in each habitat in the heterogeneous structure of a landscape (i.e., the match between each population and each habitat).

Allometric relationships between body size and biological variables, such as home range and metabolic rate (Peters 1983, Schmidt-Nielsen 1984, Calder 1996), have two powerful features that make them attractive for use in ecological studies. First, ecologists can an-

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alyze processes and functions performed by species of different body sizes in an unbiased fashion by taking into account the ways different species respond to a particular variable (West et al. 1997). Second, allometric relationships usually explain a very large proportion of the observed variance (in many cases >90%). Therefore, although allometric relationships are not cause-and-effect, they suggest that, at least indirectly, body size is a major factor in ecological processes and patterns. Furthermore, we know allometric constants for many taxa, especially vertebrates. Consequently, allometry may help us focus on general rules rather than particular cases (see Yodzis and Innes' [1992] "plausible" model).

In this paper I present a model that incorporates an explicit consideration of spatial heterogeneity and allometric relations into the logistic equation of population dynamics. Using realistic body-size-based parameter values, the new model reveals a relationship between habitat specificity and body size. This model opens new directions and opportunities for studying large-scale body-size-dependent species diversity patterns.

#### THE MODEL

I modified the logistic equation of population dynamics to include both spatial heterogeneity and allometric considerations. To represent spatial heterogeneity explicitly (i.e., the effect of different habitats on the species), I include a term in the equation that indicates how well a species' population performs in a particular habitat (hereafter, species-habitat match, or  $f_m$ ). Allometric considerations are included so that known allometric relationships from field data may be used (e.g., separating species-specific birth and death rates from a single intrinsic rate of increase). I also introduce a carrying-capacity-like feedback function that uses a species-specific metabolic rate (hereafter, demand/supply function;  $f_s$ ) which is defined below. Population growth is given by the following equation:

$$\frac{dN_i}{dt} = f_m b_{0i} N_i (1 - f_s) - d_{0i} N_i (1 + f_s) \quad (1)$$

where  $N_i$  is the size of population  $i$ ,  $b_{0i}$  is population  $i$ 's maximal per capita birth rate, and  $d_{0i}$  is population  $i$ 's minimal per capita death rate.

I separated the intrinsic rate of increase into its original components, birth and death rates, because modeling a sink population ( $r < 0$ ) in an overcrowded habitat ( $[1 - f_s] < 0$ ) may otherwise artificially result in an increasing population. As mentioned above, having independent birth and death rates also allow us to use body-size-dependent values from the literature (Peters 1983, Calder 1996). For Eutherian mammals, per capita

birth rate approximately correlates with body size to the power of  $-0.33$  (i.e.,  $b \approx M^{-0.33}$ , where  $M$  is body size;  $n = 23$ ,  $r^2 = 0.98$ ; Western 1979), while per capita death rate approximately correlates with body size to the power of  $-0.56$  (i.e.,  $d \approx M^{-0.56}$ ;  $n = 27$ ,  $r^2 = 0.71$ ; Calder [1996], using data from Sacher [1978]; to my knowledge these coefficient values are the best available). Although some attempts have been made in these studies to get density-independent parameters, they are definitely not purely density independent. However, as expected, per capita birth rate is higher than per capita death rate. Additionally, the fact that these coefficients may include some density dependence suggests that any general allometric relationship derived from the above coefficients should be at worst an underestimation of the relationship between body size and habitat specificity. This is because pure density independence should result in a higher exponent for per capita birth rate and a lower exponent for per capita death rate.

The species-habitat match,  $f_m$ , ranges between 0 and 1. The value 0 indicates no match at all (i.e., a population of that species in that habitat cannot persist), while 1 indicates a perfect match (i.e., a population of that species in that habitat can experience its maximal growth). It may be calculated empirically if the major factors limiting particular organisms in real-system habitats are known. However, in this paper, I will use an arbitrary set of species-habitat matches representing a wide range of values. This is possible because whether a species-habitat match is calculated in a sophisticated way, taken from an empirical measurement, or assumed, it enters into the population growth equation as a single value. (The equations mentioned in this paper, together with others, are used in a process-based, multispecies, object-oriented landscape simulation model called SHALOM (Ziv 1998). In this model, the species-habitat match is calculated by a function built on the overlap between a temperature-precipitation bi-normal niche space of a species and a temperature-precipitation bi-uniform habitat space of the habitat that the species occupies. The number obtained represents how well individuals of a particular population are suited to a particular habitat, given the population's species identity and the patch's habitat type.) Therefore, as long as it has a value between 0 and 1 and accurately represents the system under study, the way the species-habitat match is calculated does not affect the outcomes of the model. For the rest of this paper, I also assume that the species mentioned here perceive habitat quality in a similar way, and thus have shared preferences (Rosenzweig 1991).

The demand/supply function uses allometric relationships and relies on energy as a common currency. Although I do not explore the effects of interspecific

competition and changing energy supply in this paper, I introduce the extended form of the new expression, which allows one to treat multiple species simultaneously, to demonstrate the powerful potential of the use of allometry and energy. This is consistent with the purpose of this paper in highlighting the importance of allometric relationships and habitat-specific quality in studying large-scale patterns in heterogeneous environments.

In general, instead of taking the ratio between population size and carrying capacity, the demand/supply function takes the ratio between the energy used by populations of different species and the energy available in the habitat. We can estimate energy per time unit used by an individual for maintenance and activity from its field metabolic rate (e.g., Nagy 1987). Metabolic rate is body-size dependent. The energy consumed by a particular species per unit time is its per capita metabolic rate multiplied by its population size (see also Brown and Maurer 1986). The total energy consumed by all species (populations) in a community per unit time is the sum of all species' metabolic rates. The energy available in a habitat per unit time (hereafter, energy supply; e.g., Kilojoules per year) is given by the habitat's productivity (e.g., Kilojoules per year per square meter) multiplied by the area of that habitat (Wright et al. 1993). The following demand/supply equation gives the ratio between the two energy rates:

$$f_s = \sum_{k=1}^R \sum_{i=1}^S \frac{(RU_{ki}E_{M_i}N_i)}{P_k A} \quad (2)$$

where  $k$  and  $R$  are a resource and number of resources, respectively,  $i$  and  $S$  are a population and number of populations, respectively,  $RU_{ki}$  is the proportion of population  $i$ 's diet that is resource  $k$ ,  $E_{M_i}$  is the per capita metabolic rate of population  $i$  given its body size  $M$ ,  $P_k$  is the proportional productivity of resource  $k$  in terms of energy, and  $A$  is area. The use of multiple resources allows for the inclusion of resource partitioning as a mechanism of coexistence between species (e.g., MacArthur 1965, Schoener 1974). Note that a ratio of 1 between the energy used by populations of different species in a habitat and the energy available in that habitat indicates that populations are in equilibrium with the resources. At this point, death will still be happening by processes other than a lack of resources. Carrying capacity is reached when the actual birth rate equals the actual death rate (see below).

There are two additional advantages to the use of energy as a common currency in the demand/supply function. First, it allows both intraspecific and interspecific effects to take place simultaneously without assuming a specific relationship between the two. Second, it does not require an arbitrary value for carrying

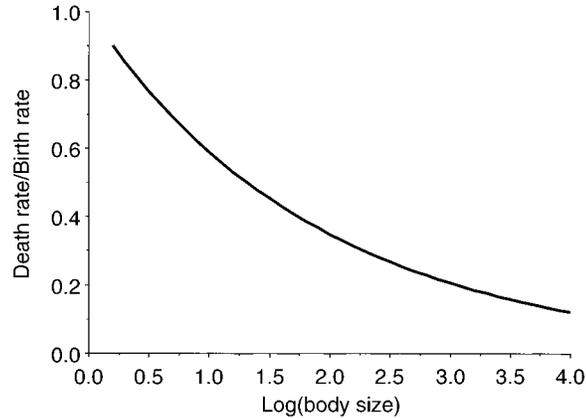


FIG. 1. Body-size-dependent death-rate:birth-rate ratio ( $d_0/b_0$ ) of Eutherian mammals. Birth rate is calculated as  $b_0 = M^{-0.33}$ . Death rate is calculated as  $d_0 = M^{-0.56}$ . Death-rate:birth-rate ratio decreases with body size.

capacity. Rather, population size at equilibrium with no interspecific competitors and predators, or carrying capacity ( $K_i$ ), emerges from the model given the species consumption and the productivity of a habitat.

We can solve Eq. 1 analytically for carrying capacity of a population  $i$  in a patch,  $K_i$ :

$$K_i = \frac{\left(\frac{b_0 f_m}{d_0} - 1\right)}{\left(\frac{b_0}{d_0} + 1\right) \left(\frac{E_{M_i}}{PA}\right)} \quad (3)$$

$K_i$  has units of individuals because  $E_{M_i}$  is the per capita metabolic rate of population  $i$ . The denominator of Eq. 3 always has a positive value. This means that whether or not a particular population has a positive carrying capacity depends on the numerator. A population has a positive carrying capacity if and only if  $(b_0/d_0) f_m > 1$ . Putting it differently,  $d_0/b_0$  must be less than  $f_m$ . Hence, for a population to have a positive carrying capacity in a habitat, its death rate-to-birth rate ratio should be less than its match to the habitat it occupies. Note that although negative carrying capacity is practically impossible, we can use it to characterize sink populations. In other words, the more negative the carrying capacity, the higher the immigration needed to rescue the population from extinction.

## RESULTS

I used the above mammalian coefficients for the per capita body-size-dependent birth and death rates to explore the relationship between habitat specificity and body size more closely. Interestingly, the mammalian death-rate:birth-rate ratio decreases with body size (Fig. 1). Therefore, the threshold of the match between

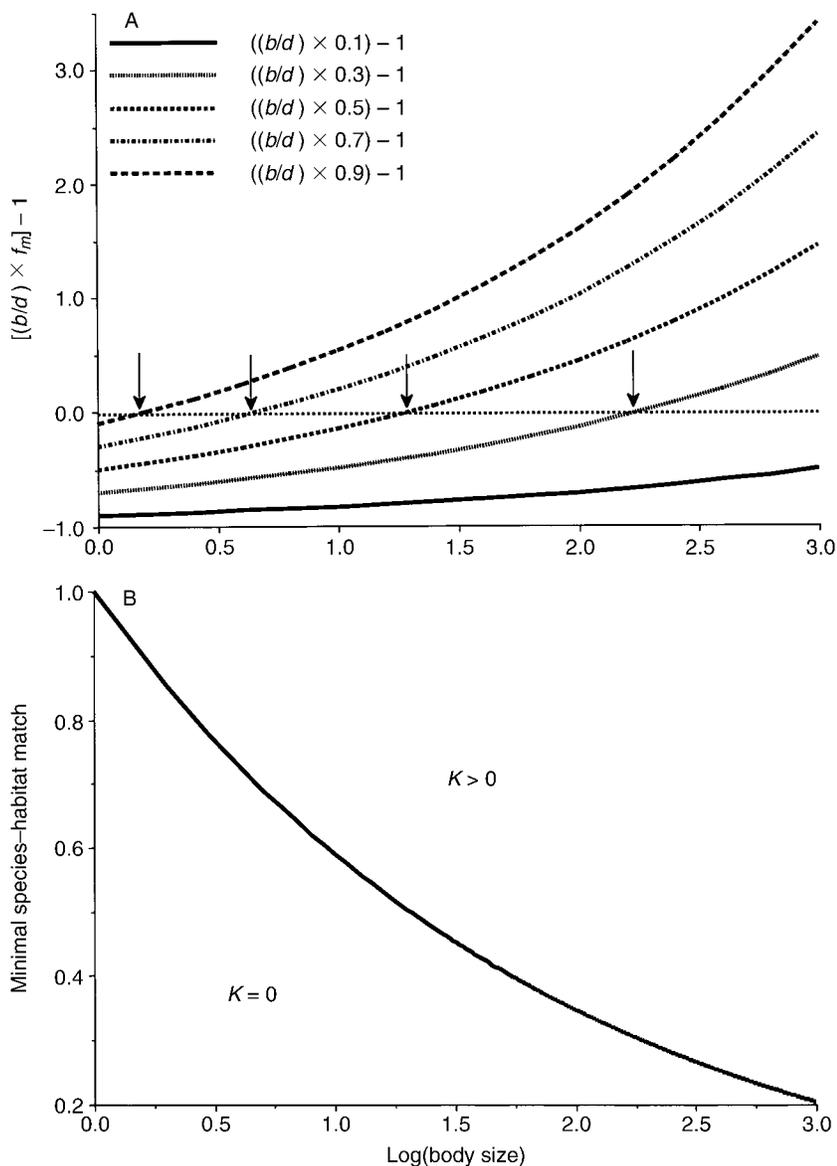


FIG. 2. The effect of the species-habitat match on the persistence of populations. (A) The value of the numerator term  $(b_0 \times f_m/d_0 - 1)$  increases with body size. The different lines represent habitats with different species-habitat matches. The higher the match, the better a population does with respect to the value of the numerator term, which in turn should be reflected by a higher population size. Values of the numerator term that are higher than zero indicate that the population has a positive carrying capacity in a habitat with the particular species-habitat match. Each arrow in the graph indicates the minimal body size needed to have a ratio of death rate to birth rate higher than the particular species-habitat match. (B) The minimal species-habitat match needed for a population to persist in a habitat decreases with body size. The larger the species, the lower the species-habitat match it needs to persist.

a species and a habitat below which a population cannot deterministically persist is lower for larger species (Fig. 2A). Hence, smaller mammals must match their habitats more precisely in order to survive in them (Fig. 2B). This result has an important implication regarding the distribution of species of different body sizes in

habitats of different qualities: larger species should be able to persist (as a source population) in a higher diversity of habitat types. Smaller species should be habitat specialists, while larger species should be habitat generalists.

To demonstrate this point, I calculated the carrying

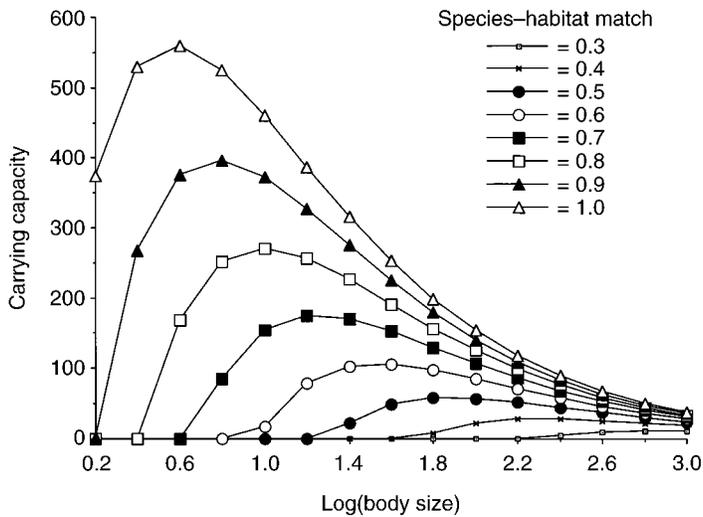


FIG. 3. The larger the species, the more habitats it can occupy. Smaller species can persist only in the better-quality habitats (i.e., higher species-habitat matches), while larger species can also persist in the lower-quality habitats. Carrying capacities were calculated using a fixed energy supply of 41.84 MJ/yr per habitat. Metabolic rate,  $E_M$ , was calculated with the equation:  $E_M = M^{0.75}$ , where  $M$  is body size (see *The model*).

capacities of species with different body sizes in a variety of habitats having different species-habitat matches. For each habitat type, I used the same species-habitat match for all species, implying that species do not differ in the ecological needs that determine their match with the habitat. Fig. 3 shows the carrying capacities of different species in different habitats. Larger species occupy a larger set of habitats (i.e., habitat specificity negatively scales with body size). Within each species, subpopulations have a higher carrying capacity in habitats with a higher species-habitat match. The distribution of carrying capacities of the different species in a particular habitat changes from a right-skewed unimodal curve to a monotonically increasing one. This change depends on the quality of the habitat, represented by the species-habitat match. In general, Fig. 3 is consistent with what we see in nature: although smaller species are not present in all habitats, they are more abundant than large ones in those habitats that both occupy. Altogether, these results suggest that larger species should be more abundant than smaller species in lower quality habitats, while smaller species should be more abundant in higher quality habitats. In other words, larger species should have a relative advantage in lower quality habitats, while smaller species should have an advantage in the highest quality habitats. This suggests that species of different body sizes may have different habitats in which they do better according to the way body size affects different parameters, such as demographic and metabolic rates.

#### DISCUSSION

The results of this paper do not imply that the relationship between body size and habitat specificity,

suggested here for Eutherian mammals, represents an evolutionary process or trend. The values for the allometric birth, death, and metabolic rates already take into account the evolutionary processes that shaped these values. Therefore, the results represent the ecological pattern we expect to see given the body-size relationships. Additionally, these results do not imply that larger species should occupy a higher diversity of habitats because of some intrinsic factors (e.g., physiology) that affect their particular birth and death rate values. It is equally possible that extrinsic pressures, such as a higher probability of survival of species with a higher birth-rate:death-rate ratio, shape the observed allometric relationships. Hence, processes such as stochastic extinction and migration may still play a role in shaping the observed values. For example, Brown and Maurer (1986) concluded that larger species should have larger geographic ranges to compensate for their low local densities. The purpose of this discussion is not to invoke any evolutionary scenario, but rather to emphasize that we should distinguish between the pattern observed and the cause for that pattern. In addition, the Results and Discussion of this paper refer to Eutherian mammals due to the allometric values taken for the birth, death, and metabolic rates. Although it is likely that the qualitative result of the model should also hold for other taxa, it is my recommendation to test it specifically for each additional taxon.

The prediction that habitat specificity scales with body size relies on the assumption that the modeled species (in this case, Eutherian mammals) do not differ in the ecological needs that determine their match with the habitat (i.e., that all species perceive habitat quality in similar terms). In reality, different species may be affected by different factors in similar habitats. Hence,

the scaling of habitat specificity with body size should be taken as a general predicted trend characterized by a high variability of the observed data. Additionally, we should expect different taxa within the general trend to be different from each other. For example, given major ecological differences between bats, small rodents, and shrews, large differences would be expected between the habitat specificity of similar-sized species belonging to different taxa. Similarly, we should expect to find high similarity in the scaling of habitat specificity with body size among closely related species and species belonging to the same ecological guild. However, the many significant allometric relationships found for Eutherian mammals suggest that the allometric relationship predicted here may also hold. Most importantly, the between- and within-taxa variability in the body-size-dependent habitat specificity requires careful observational studies to test the sensitivity of the general pattern to differences between taxa.

The model presented here gives a theoretical framework for the known relationship between body size and habitat generality. However, it also opens new directions. One direction is the use of the model by field biologists. All parameters and variables of the model are measurable. Field biologists who work on a particular system can insert their landscape information, such as species' body size, habitat productivity, and a system-specific measure of how each species is suited to the set of existing habitats, into the model. The latter can take any form that will best represent the particular system.

Another direction is using the model to explore how specific processes (e.g., energy use and species-habitat match) affect body-size patterns. The model is simple enough that one can easily simulate only one parameter, leaving all the others constant. For example, it can be asked how changes in productivity may affect species diversity patterns by comparing body-size distribution in habitats differing in their productivity. We may also explore how differences between habitat qualities determine the overall species diversity in a landscape composed of those habitats. Furthermore, elsewhere (Ziv 1998), I have used an extensive version of this model to explore not only how habitat composition, but also competition, stochasticity, and dispersal affect species diversity and community organization.

The model's result regarding body-size-dependent habitat specificity can easily be expanded to the relationship between geographical range and body size. Regardless of whether there is a landscape that shows a randomly, center-to-edge decrease in habitat quality, or even a uniform distribution of habitats of different qualities in a landscape, larger species should have wider geographical ranges due to their ability to persist in a greater diversity of habitats. For the same reason,

larger species should occupy more sites than smaller species. In light of the conditions in which these results have been obtained, we can consider the two biologically related hypotheses that have been used to explain the positive correlation between geographical range and species abundance: metapopulation dynamics (Hanski 1982) and resource tolerance (Brown 1984).

The metapopulation dynamics hypothesis states that populations of higher abundance are more likely to escape extinction on and to recolonize vacant patches, which in turn, would promote higher persistence in patches at the periphery where patchiness tends to occur. The present results contrast with this hypothesis in that neither stochastic extinction nor migration processes were included in the above calculations of the carrying capacities. Furthermore, if we consider larger species, we see lower population sizes (e.g., Lawton 1991) as well as wider geographical ranges (Brown and Maurer 1986). This is inconsistent with the explanation that a large geographical range is caused by a high species abundance. Therefore, although species abundance is positively correlated with geographical range, they do not necessarily represent a cause-and-effect relationship.

The resource-tolerance hypothesis states that "those species that can tolerate conditions and acquire sufficient resources so as to attain high densities in some places, should also be able to occur (albeit often at lower densities) in many other sites over a relatively large area" (Brown 1984). In the present work, the implicit similarity of the different species' ecological needs does not address the resource-tolerance hypothesis. However, similar to the resource-tolerance hypothesis, the present finding suggests that higher species abundance may come from a third process related to the one determining the distribution of species in a landscape, such as the relationship between body size and habitat specificity. This conclusion supports Brown's statement (1984) that on a larger spatial scale the suitability of environmental conditions plays an important role in determining the distributions of species and, in turn, their abundances (see also Venier and Fahrig 1996, Holt et al. 1997).

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