

Reports

Ecology, 80(8), 1999, pp. 2788–2792
© 1999 by the Ecological Society of America

GAPS IN MAMMALIAN BODY SIZE DISTRIBUTIONS REEXAMINED

EVAN SIEMANN¹ AND JAMES H. BROWN

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

Abstract. Holling suggested that discontinuities in the body size distributions among species of animals are a universal feature of terrestrial biomes. We compared the magnitudes of body size gaps of mammal communities of North America and Australia to those generated by a simple random null model. In most biomes, no gaps were significantly larger than random, so discontinuities in body size distributions are the exception, not the rule. We also made intra- and intercontinental comparisons of size distributions to test two alternative hypotheses: (1) Holling's Textural-Discontinuity Hypothesis, that body size distributions reflect structural characteristics of the habitat; and (2) the Core-Taxa Hypothesis, that body sizes reflect the distributions of widespread taxa. We found that the gaps in body size were similar in structurally dissimilar but adjacent biomes that shared the same or closely related species. We conclude that body size distributions of biomes are not highly discontinuous, and their structure reflects taxonomic constraints on body size.

Key words: *Australia; biogeography; biomes; body size; Core-Taxa Hypothesis; evolutionary constraints; gaps; geographical range; mammals; North America; Textural-Discontinuity Hypothesis.*

The lumpiness of body size distributions for animals in terrestrial ecosystems is clearly real and universal.

—Holling et al. (1996)

Holling (1992) suggested that discontinuities in landscapes should cause clumps and gaps in the distributions of body sizes among species within animal communities at large spatial scales, such as within biomes. His preliminary analyses raised the intriguing possibility that there are indeed such clumps and gaps, a possibility that has caused much excitement among ecologists (117 citations through January 1999, SciSearch).

In a reanalysis of Holling's data, Manly (1996) used clump detection methods to show that there are very few clumps in species' body size distributions that are typically unimodal or bimodal. However, even if the probability distribution does not exhibit multiple modes, there may still be gaps or discontinuities in the distribution of body sizes. Even randomly placed points cluster together just by chance, however, so purely random processes could generate the magnitudes of gaps seen in natural communities.

Manuscript received 12 November 1998 (originally submitted 5 February 1998); revised 17 February 1999; accepted 18 February 1999; final version received 16 March 1999.

¹ Present address: Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005 USA. E-mail: siemann@rice.edu

Regardless of the magnitudes of body size gaps, if a theory were able to predict the body sizes where they occur, it would give insight into the processes structuring animal communities at large spatial scales. The Textural-Discontinuity Hypothesis (Holling 1992) proposes that the clumps and gaps in body size distributions of mammals and birds in biomes reflect structural characteristics of the vegetation and landscape. Alternatively, the clumps and gaps could reflect the fact that certain species or closely related taxa of similar size are widely distributed across habitats and biomes within a continent (Holling 1992, Brown 1995). This is an elaboration of Holling's Historical Hypothesis (1992), in that it includes sharing of species among biomes as well as conservation of body sizes within higher taxa. Hereafter, we will refer to this as the Core-Taxa Hypothesis.

These two hypotheses make opposite predictions about the sizes at which the greatest species' body size gaps occur in different biome types and on different continents. The Textural-Discontinuity Hypothesis predicts that: (1) the greatest gaps should occur at similar body sizes in structurally similar biomes on different continents, but (2) at different sizes in structurally different biomes on the same continent. The Core-Taxa Hypothesis predicts just the opposite, that: (1) the greatest gaps should occur at different body sizes in structurally similar biomes on different continents, but

(2) at similar sizes in structurally different biomes on the same continent. Because Australia and North America do not share any native mammal species, but have several structurally similar biome types, they allow a clear test of these two hypotheses.

We used data on mammals of North America and Western Australia to test: (1) whether random processes can account for the magnitudes of gaps in body size distributions, (2) if the assumptions of the Core-Taxa Hypothesis are met in natural communities, and (3) whether the Textural-Discontinuity or Core-Taxa hypothesis better predicts the sizes at which the greatest body size gaps occur in intra- and intercontinental comparisons.

METHODS

Data for mammalian species in North American biomes were taken from Brown and Nicoletto (1991). These data are lists of the mammal species that occurred in each of 19 biomes prior to European settlement (excluding bats, marine mammals, and humans), and the average body mass of each of the 464 species. The number of species per biome ranged from 36 to 182. Data for mammalian species in Western Australia were taken from Burbidge and McKenzie (1989). These data are lists of all terrestrial mammal species (except humans; we also excluded the bats) that occurred in each of six areas prior to European settlement, together with the body masses of the 102 species. We combined some of the areas to create lists for four biomes (both Kimberley areas were combined, as were the Darling and Wheat areas). The number of species per biome ranged from 41 to 51. We also used the data for mammals in Holling (1992), but only in comparisons of gap magnitudes to random models. We did not remove bats from these lists, so as to keep our analyses comparable to Holling's original analyses. Including or removing bats gave similar results.

We wanted to estimate how many body size gaps in real biomes were significantly larger or smaller than expected in random biomes. For each real biome, we calculated the magnitudes of species body size gaps as $[\log(\text{mass}_{n+1}) - \log(\text{mass}_n)]$, where mass_n is the mass of the n th smallest species in the biome. The $S - 1$ gaps were sorted in descending order, gap_1 to gap_{S-1} (where S is the number of species in the biome). This two-point gap metric differed from the three-point gap metric used by Holling (1992): $[(\text{mass}_{n+1} - \text{mass}_{n-1}) / \text{mass}_n^\gamma]$, where γ is a taxon-specific constant fitted to the data a posteriori. The two-point log-transformed metric has the advantages of giving a more precise location, handling a geometric variable without arbitrary correction, and having a long tradition of use by ecologists and statisticians (e.g., Fisher 1940, Darling

1953, Barton and David 1956, Hutchinson 1959, Simberloff and Boecklen 1981).

We compared the magnitudes of the largest gaps within real biomes to those in biomes generated by a very simple random null model. For each real biome, we constructed 10 000 random biomes. Each random biome was defined by $S - 2$ random numbers drawn with uniform probability from the interval $\log(\text{mass}_1)$ to $\log(\text{mass}_S)$. Gap sizes were calculated (end points were the smallest and largest species) and sorted in the same manner as in real biomes. In order to determine the number of gaps in real biomes that were significantly larger or smaller than those in these random biomes, we performed a series of conditional tests. We first tested whether the largest real gap was different from the largest gap in the random biomes. To be liberal and allow a large number of gaps, we set the probability level, α , at 0.10 (i.e., a result was significant if the largest real gap was larger than the largest gap in ≥ 9500 of the random biomes, or the largest real gap was smaller than the largest gap in ≥ 9500 of the random biomes). If this first test was significant, we tested whether the second largest gap deviated from random expectations at the same α level. We continued these tests until we did not obtain a significant result. The number of significant gaps was taken as a measure of the number that could not be explained by random processes. We repeated these analyses with $\alpha = 0.20$.

The Core-Taxa Hypothesis requires that some species occur in many biomes and/or that closely related species of similar sizes do so. To determine the distributions of individual species, we calculated the mean and maximum number of biomes in which they occurred (separately for North America and Australia). To determine the similarity of body sizes within higher taxa, we performed two sequential (i.e., Type I ss) unbalanced ANOVAs, one for each continent. The response variable was $\log$ (body mass) and the predictors were taxonomic order followed by taxonomic family. We used the classification of Wilson and Reeder (1993), which recognizes several orders of marsupials in Australia.

In order to determine whether biome type or continent more strongly influences the sizes at which the greatest gaps occur, we first paired each Australian biome with the most structurally similar North American biome, based on the classification of Cox and Moore (1985). These pairings were: (1) Kimberley: Guerreran (Tropical Seasonal Forest), (2) Pastoral: Grasslands (Temperate Grasslands), (3) Desert: Sonoran Desert (Desert), (4) Darling-Wheat: Californian (Mediterranean). Including just these eight biomes, we used ANOVA to test the dependence on biome type (four levels) and continent (two levels) of the body size midpoint of the greatest gap. The North American biomes with-

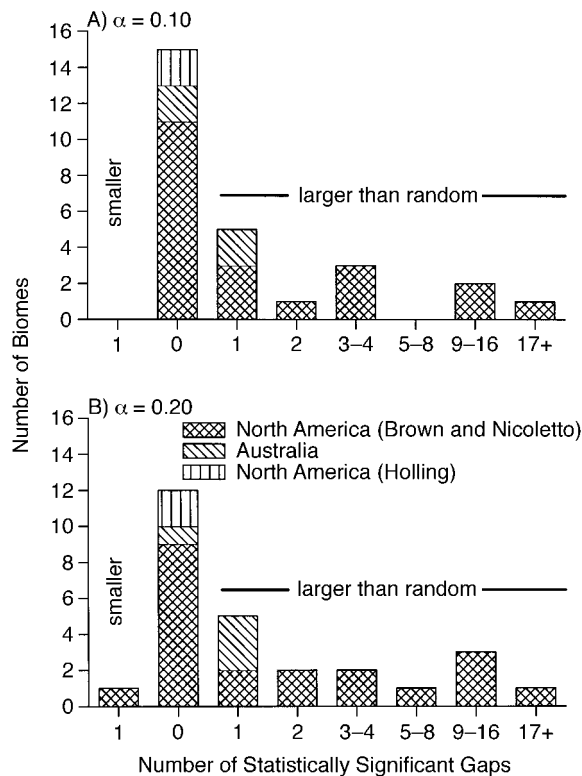


FIG. 1. Biomes classified by the number of body size gaps in the biome that were significantly larger or smaller than those in random communities at two different significance levels.

out Australian counterparts were omitted to simplify the analysis and provide tests of similar power. A second test used all 25 biomes and MANOVA to test whether the sizes at which the five largest gaps occurred depended on continent. MANOVAs with other numbers of gaps gave similar results.

RESULTS

For most biomes, few or no gaps were significantly larger and no gaps were significantly smaller than those in random communities (Fig. 1). At $\alpha = 0.10$, of the 21 North American biomes from Brown and Nicoletto (1991), 11 biomes had no significant gaps, three biomes had one, four had two or three, and only three had more than three significantly large gaps. At $\alpha = 0.20$, nine biomes had no significant gaps, six biomes had one to three, and five had more than three significantly large gaps, whereas a single biome had one gap that was significantly smaller than random. At both α levels, neither of Holling's communities had any significant gaps. At $\alpha = 0.10$ and $\alpha = 0.20$, two and three Australian biomes, respectively, had a single significantly large gap.

TABLE 1. Effect of taxonomy on average log species body mass in sequential ANOVAs. Overall F values are shown in the error rows.

Factor	df	Type I SS	MS	F	R^2 cum†
North America					
Order	9	364.9	40.54	223.81****	0.69
Family	20	83.9	4.19	23.15****	0.85
Error	434	78.6	0.18	85.43****	
Australia					
Order	5	66.9	13.40	58.36****	0.63
Family	7	17.1	2.44	10.64****	0.80
Error	89	20.4	0.22	30.52****	

**** $P < 0.0001$ for the significance test of parameter value from zero.

† Cumulative R^2 .

In North America, the average species occurred in 3.8 ± 3.9 biomes (mean ± 1 SD), with a range of 1–19 biomes. In Australia, the average species occurred in 1.8 ± 0.9 biomes, with a range of 1–4 biomes.

Body size was strongly and significantly constrained by taxonomy (Table 1). Over 60% of the variability in species body mass was explained by taxonomic order, both in North America and in Australia. Family explained an additional $\sim 15\%$ of the variability in body mass on each continent.

The size at which the greatest gap occurred in a biome depended significantly on continent, but was independent of biome structural type (ANOVA; Table 2). The sizes at which the five greatest gaps occurred in a biome depended significantly on continent (MANOVA; Wilks' lambda 0.22, $F_{5,19} = 13.68$, $P < 0.0001$).

DISCUSSION

A very simple null model of random body sizes was able to account for the magnitudes of nearly all of the largest gaps in species body size distributions in natural communities (Fig. 1). In fact, in the majority of biomes (15 of 27 at $\alpha = 0.10$, including both of Holling's; Fig. 1A), no gaps were significantly larger than those in random communities. These results, together with one gap smaller than random (at $\alpha = 0.20$; Fig. 1B) and Manly's (1996) demonstration that there are few modes (significant clumps in the distributions), suggest that

TABLE 2. Effects of biome type and continent on the size at which the greatest species body size gap occurred. Results are from an ANOVA (Type III ss). The overall F and P values are shown in the error row.

Factor	df	SS	MS	F	P
Continent	1	3.40	3.40	979.53	<0.0001
Biome	3	0.02	0.006	1.68	0.34
Error	3	0.01	0.003	246.14	0.0004

there is no general pattern of multiple gaps and clumps of body sizes in terrestrial mammal assemblages at the scale of biomes. There is no evidence of the clumpy-gappy pattern claimed by Holling. This result does not mean that landscape structure does not influence the sizes of mammals that occur in different biomes.

The magnitudes of the smallest gaps in natural communities also do not differ consistently from those in random communities. Hutchinson (1959) proposed that competition should place a limit on the similarity of body sizes of coexisting animal species. Simberloff and Boecklen (1981), using the same random model that we use here, found that the smallest gaps in natural communities usually were no different than those expected by chance, although there were significant results in both directions. We note, however, that our results do not directly address Hutchinson's hypothesis because: (1) the biomes that we analyzed are much larger and contain substantially more species than the small habitat patches that are most appropriate for assessing coexistence (Brown and Nicoletto 1991); and (2) the large assemblages of mammals analyzed here include many species that would not be expected to compete because they are in different trophic guilds (including both herbivores and carnivores). When analyses are restricted to members of the same guild that coexist in the same local habitats, some nonrandom patterns have been detected by others. For example, coexisting species of seed-eating desert rodents can be shown to have both more uniform distributions of sizes and fewer small gaps in the distributions than expected by chance (e.g., Simberloff and Boecklen 1981, Bowers and Brown 1982, Kelt and Brown, *in press*).

Even though the magnitudes of the largest gaps are easily accounted for by random processes, if the large gaps occur at predictable body sizes, they may still reflect processes that determine the structure of biotas at the scale of biomes. Indeed, gaps occurred at significantly similar body sizes for biomes on the same continent, both in the two-way ANOVA that considered only the greatest gap (Table 2), and in the MANOVA that considered multiple gaps simultaneously. On the other hand, structurally similar biomes in Australia and North America did not have their large gaps at similar body sizes (Table 2). These results do not support the Textural-Discontinuity Hypothesis, but are exactly what is predicted by the Core-Taxa Hypothesis. This hypothesis suggests that similarities in size distributions among biomes on the same continent are due largely to some combination of two phenomena: (1) taxonomic relatedness of species in different biomes, and (2) the occurrence of the same species across multiple biomes.

Our analyses suggest that both phenomena contribute to the observed similarities. Because, on average, spe-

cies occur in more than one biome and in biomes with dissimilar vegetation and landscape structures (reviewed in Brown et al. 1996), this sharing contributes to the observed similarities in body size distributions. Body size was strongly conserved within orders and families (Table 1), in agreement with evolutionary theory (e.g., Stanley 1973, Maurer et al. 1992, Brown et al. 1993) and empirical studies (e.g., Brown et al. 1993, Cadle and Greene 1993, Siemann et al. 1996, Siemann et al. 1999). Most orders are represented by at least one species in each biome, also contributing to the similarities in the size distributions across structurally different biomes on the same continent. In other words, there is considerable overlap, but also some turnover in the distribution of species from biome to biome, but the substituted species tend to be closely related members of the same families and orders, and therefore to be of similar body sizes. For example, the deer mouse (*Peromyscus maniculatus*) occurred in 19 of the 21 North American biomes, including ones with such dissimilar structure as Yukon Taiga, Sonoran Desert, Grasslands, and Tropical Season Forest; *Peromyscus truei* occurred in 10 of the 21 biomes (Brown and Nicoletto 1991).

There is growing evidence for the influence of regional processes on the structure of local communities (e.g., Cornell 1993, Ricklefs and Schluter 1993, Caley and Schluter 1997, Godfray and Hassell 1997, Roland and Taylor 1997). Our results suggest that the body size distributions at the scale of biomes are influenced by processes at continental scales, including the geographic ranges of species and the history of phylogenetic radiations. Our results do not support Holling's claims that these body size distributions have significantly larger gaps and clumps than expected by chance, or that they reflect a strong influence of biome-specific vegetation and landscape structure.

ACKNOWLEDGMENTS

We thank Ethan Decker, Morgan Ernest, Drew Kerkhoff, Bruce Milne, Carla Restrepo, and the Biological Complexity seminar at UNM for helpful discussions, Carla Restrepo for comments, Ron Christensen for statistical assistance, and the National Science Foundation for support (Sevilleta LTER grant DEB-9411976, Portal grant DEB-9707406).

LITERATURE CITED

- Barton, D. E., and F. N. David. 1956. Some notes on ordered random intervals. *Journal of the Royal Statistical Society, B* 18:79-94.
- Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391-400.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago, Illinois, USA.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* 142:573-584.
- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of

- species composition: body masses of North American land animals. *American Naturalist* **138**:1478–1512.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27**: 597–623.
- Burbidge, A. A., and N. L. McKenzie. 1989. Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**:143–198.
- Cadle, J. E., and H. W. Greene. 1993. Phylogenetic patterns: biogeography, and the ecological structure of Neotropical snake assemblages. Pages 281–293 in R. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Caley, M. J., and D. Schluter. 1997. The relationship between local and regional diversity. *Ecology* **78**:70–80.
- Cornell, H. V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. Pages 243–252 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Cox, C. B., and P. D. Moore. 1985. *Biogeography: an ecological and evolutionary approach*. Fourth edition. Blackwell Scientific, Oxford, UK.
- Darling, D. A. 1953. On a class of problems related to the random division of an interval. *Annals of Math and Statistics* **24**:239–253.
- Fisher, R. A. 1940. On the similarity of the distributions found for the test of significance in harmonic analysis, and in Steven's problem in geometric probability. *Annals of Eugenics* **10**:14–17.
- Godfray, H. C. J., and M. P. Hassell. 1997. Hosts and parasitoids in space. *Nature* **386**:660–661.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* **62**:447–502.
- Holling, C. S., G. Peterson, P. Marples, J. Sendzimir, K. Redford, L. Gunderson, and D. Lambert. 1996. Self-organization in ecosystems: lumpy geometries, periodicities and morphologies. Pages 346–384 in B. Walker and W. Steffen, editors. *Global change and terrestrial ecosystems*. Cambridge University Press, Cambridge, UK.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* **93**:145–159.
- Kelt, D. A., and J. H. Brown. *In press*. Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. In E. Weihr and P. A. Keddy, editors. *The search for assembly rules in ecological communities*. Cambridge University Press, Cambridge, UK.
- Manly, B. F. J. 1996. Are there clumps in body-size distributions? *Ecology* **77**:81–86.
- Maurer, B. A., J. A. Brown, and R. D. Rusler. 1992. The micro and macro in body size evolution. *Evolution* **46**:939–953.
- Ricklefs, R. E., and D. Schluter. 1993. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Roland, J., and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**:710–713.
- Siemann, E., D. Tilman, and J. Haarstad. 1996. Insect species diversity, abundance and body size relationships. *Nature* **380**:704–706.
- Siemann, E., D. Tilman, and J. Haarstad. 1999. Abundance, diversity and body size: patterns from a grassland arthropod community. *Journal of Animal Ecology*, *in press*.
- Simberloff, D., and W. Boecklen. 1981. Santa Rosalia reconsidered: size ratios and competition. *Evolution* **35**: 1206–1228.
- Stanley, S. M. 1973. An explanation for Cope's rule. *Evolution* **27**:1–26.
- Wilson, D. E., and D. M. Reeder. 1993. *Mammal species of the world*. Smithsonian Institution Press, Washington, D.C., USA.