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Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials

S. Kathleen Lyons and Michael R. Willig

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Controversy surrounds the existence and causes of latitudinal gradients in range size, as well as the methodologies for detecting them. We show that results based on traditional methods used to evaluate Rapoport's Rule (i.e., a positive correlation between range size and latitude) for New World bats and marsupials are conflicting and subject to problems associated with statistical independence and mathematical bias. To avoid these shortcomings, we used simulation models to assess the degree to which latitudinal patterns are a product of stochastic or deterministic processes. Two different kinds of simulations were used to generate range sizes. The simulations differed in the kinds of spatial constraints that were incorporated into random algorithms. The first model randomly produced upper and lower latitudinal limits, without any spatial constraint except that species ranges were entirely within the continental New World. To reflect aspects of empirical latitudinal gradients of diversity, the second model incorporated the constraint that the set of randomly generated ranges had a distribution of mid-latitudes or most-distal points that corresponded exactly to the distribution of mid-latitudes or most-distal points in each taxon. The correlation between latitudinal range size and latitude was calculated separately for each taxon. Random distributions of correlation coefficients were generated from 1000 simulations for each taxon. When mid-latitude was used as a descriptor, New World bats and marsupials had ranges that are smaller in the tropics and larger in the temperate zone than would be expected by chance alone. In contrast, when most-distal point was used as a descriptor, relationships were consistently indistinguishable from those produced by stochastic processes.

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Ecologists and biogeographers have searched for an explanation for gradients of species richness since Simpson (1964) first quantified the tendency for mammalian species richness to increase from high to low latitudes (Pianka 1966, Huston 1979, Terborgh 1985, Stevens 1989, Kaufman 1995, Rosenzweig 1995). An increasingly popular explanation involves the way in which the range size of species changes with latitude. North American taxa, including trees, marine mollusks, fishes, and reptiles and amphibians, exhibit a pattern of de-

creasing range size with decreasing latitude (Stevens 1989). North American mammals also follow this pattern (Stevens 1989, Pagel et al. 1991). Because Rapoport (1975) first noted the correlation between range size and latitude, Stevens (1989) termed this pattern Rapoport's Rule. The rule (Stevens 1989: 240) states that "when the latitudinal extent of the geographical range of organisms occurring at a given latitude is plotted against latitude, a simple positive correlation is found".

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Considerable controversy surrounds the universality of Rapoport's Rule (Gaston and Williams 1996, Gotelli and Graves 1996). Although Rapoport's Rule has been detected in a variety of taxa in North America (Stevens 1989, Pagel et al. 1991, France 1992), Rohde et al. (1993) and Rohde and Heap (1996) showed that Rapoport's Rule does not hold for marine teleosts below 25–35°N latitude. Data from Australian mammals (Smith et al. 1994) and from eastern Pacific molluscan provinces (Roy et al. 1994) do not adhere to Rapoport's Rule either. Moreover, taxonomic differences (Ruggiero 1994) exist in the degree to which mammalian taxa adhere to Rapoport's Rule in South America (support: Chiroptera, Primates, Carnivora; against: Endentata, Marsupalia, Artiodactyla, and Histicognathi). Finally, Colwell and Hurtt (1994) showed that a Rapoport effect may be caused by a sampling bias and may have no biological significance.

Part of the difficulty of assessing Rapoport's Rule may derive from the diversity of ways in which it has been quantified and the inherent biases or statistical problems associated with those methods. Rapoport's (1982) original contention was based on the distributions of mammals in North America and three orders of birds (Falconiformes, Coraciaformes, and Piciformes) in Asia. In both situations, he determined that subspecies with the largest range occurred at geographic positions farthest from the equator compared to other conspecific subspecies. More microendemic species or subspecies (range < 10 000 km²) occurred at lower latitudes. Subsequent research has focused on the ranges of species rather than of subspecies, and may be categorized into one of three quantitative approaches: Stevens' Method (Stevens 1989), Mid-point Method (Rohde et al. 1993), and Most-distal Point Method (Pagel et al. 1991).

Stevens' Method involves calculation of the average latitudinal extent of all species within each of a series of latitudinal bands, and determining the correlation between average range size and latitude. Because most species occur in more than one latitudinal band, data are not independent, and levels of significance from statistical analyses are not accurate (Rohde et al. 1993). Moreover, conclusions based on this method may be quite sensitive to the way in which data are categorized. For example, Rohde et al. (1993) and Roy et al. (1994) could not produce the same latitudinal patterns of range size as did Stevens (1989), even though all three analyses were based on the same data source (for fish, Lee et al. 1980, for mollusks, Rehder 1981). The Mid-point Method avoids the statistical problems associated with non-random data by categorizing a species by the median latitude within its geographic range, and calculating the relationship between latitudinal extent of a species range and its mid-latitude. Similarly, the Most-distal Point Method categorizes a species by the latitude within its range that is farthest from the equator,

and calculating the relationship between range size of a species and the most-distal latitude within that range.

Although previous analyses based on mid-latitude or most-distal point are not subject to the criticisms concerning independence, they do suffer from methodological biases (Lyons 1994, 1995). They fail to consider that range size is not independent of latitude, regardless of the method used to measure it. Consequently, correlations between range size and latitudinal descriptors (Pagel et al. 1991, France 1992, Rohde et al. 1993, Letcher and Harvey 1994, Smith et al. 1994, Blackburn and Gaston 1996, Hughes et al. 1996, Rohde and Heap 1996) may be mathematical artifacts rather than a product of biogeographic factors.

Consider a hypothetical range with a mid-latitude at the equator (Fig. 1, closed circle). That range poten-

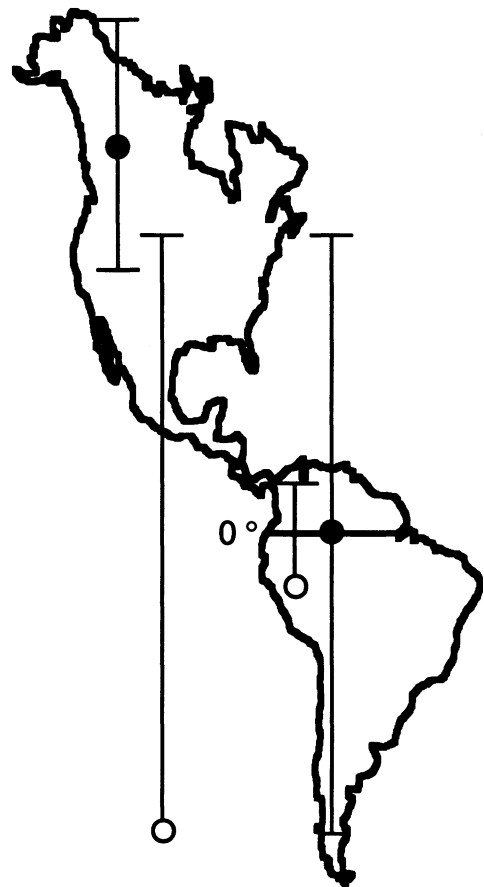


Fig. 1. Hypothetical ranges (vertical lines) illustrate the bias in mid-latitude (solid circles) and most-distal point (open circles). If a range is centered at the equator, it has the potential to have a large range. If a range is centered in a temperate zone, it will be restricted. By chance alone, a negative correlation is induced between mid-latitude and range size. If the most-distal point of a range is in the tropics, it must have a small range. If the most-distal point of a range is in the temperate zone, it has the potential to have a large range. By chance alone, a positive correlation is induced between most-distal point and range size (see text for further discussion).

tially extends throughout all of North and South America. However, a species whose mid-latitude is in a temperate zone must have a restricted range. A range with a mid-latitude at 55°N can extend in a northern direction only to the tip of the continent. Because a range must be symmetrical around its mid-latitude, this constrains the extent of that range in a southern direction. By definition, species with ranges centered at higher latitudes are restricted in the size these ranges can possess. This artifact inflates, by chance alone, the likelihood of a negative correlation between mid-latitude and area (Blackburn and Gaston 1996). Conversely, the correlation between range size and most-distal point tends to be positive by chance alone (Hughes et al. 1996). Consider a species with a most-distal point at 5°S latitude (Fig. 1, open circle). By definition, the most it can extend above the equator is 5°. This constrains the range of such a species to be small. In contrast, a range with a most-distal point near the equator will be small and less variable, whereas ranges with more temperate most-distal points will be large and more variable. This biases correlation coefficients, enhancing the likelihood that they will be positive in the absence of biological causation.

Blackburn and Gaston (1996) addressed some of these problems by eliminating species whose range boundaries were defined by continental edges (i.e. hard boundaries *sensu* Pielou 1977, Colwell and Hurtt 1994); however, they failed to address problems associated with soft boundaries (e.g., temperature tolerances, orographic barriers). Moreover, removing species with a particular type of range causes other types of biases and should be done with caution. Blackburn and Gaston (1996) used geographic range size rather than the latitudinal extent employed by this study, and as a consequence, the associated biases of the two methods are different. Comparison of results based on these different methods is tenuous and may not be germane to issues of latitudinal range per se. The only way to truly remove biases associated with patterns in range size is via simulation analyses.

A second problem with most previous studies of the latitudinal gradient in range size (for exceptions, see Rohde et al. 1993, Colwell and Hurtt 1994, Smith et al. 1994, Hughes et al. 1996, Blackburn and Gaston 1996) is that they have not considered a taxon's distribution throughout an entire land mass. Moreover, Colwell and Hurtt (1994) did not test their models with empirical data. In other studies in the New World, species with ranges that extend into South America were excluded from some analyses (Rapoport 1975, 1982, Stevens 1989, Pagel et al. 1991, France 1992), whereas taxa from North America were excluded from others (Ruggiero 1994). Without corroborative evidence for latitu-

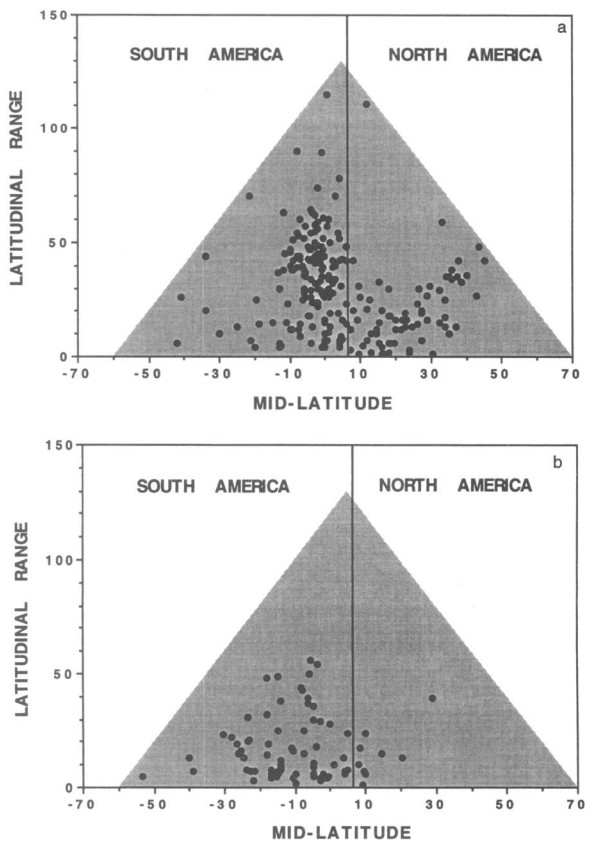
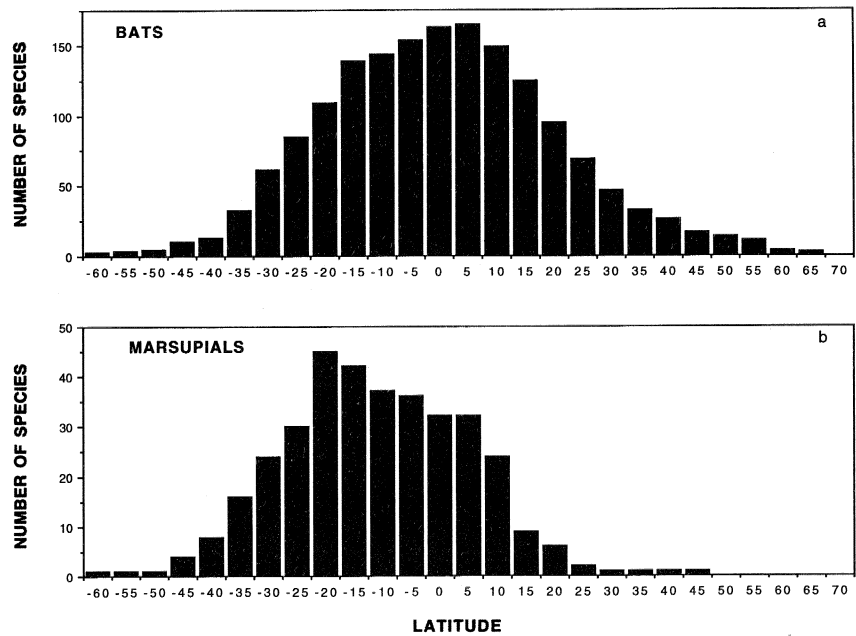


Fig. 2. Graphical representation of the relationship between latitudinal range size and mid-latitude for New World bats (a) and for New World marsupials (b). The vertical line represents the isthmus of Panama. Negative values for mid-latitude represent the southern hemisphere and positive values represent the northern hemisphere. The shaded area represents the range of coordinates geometrically possible as described in text.

dinal trends in both continents, generalizations may be biased or limited (see Willig and Selcer 1989, Willig and Sandlin 1991, Willig and Gannon 1997). For example, if patterns of range size found in North America are not recapitulated in South America, then observed "latitudinal" trends may not be a consequence of latitude per se, rather they could be caused by unique aspects of North America (e.g., geography, physiography, evolutionary history), or conversely, hidden in South America because of its unique characteristics. North American bats (right of Fig. 2a) evince a pattern of decreasing latitudinal range size with decreasing latitude. Ostensibly, these data support Rapoport's Rule. However, inclusion of South America (left of Fig. 2a) shows that this is not the case in general; mean range size and its variability are greater at the equator (mean = 34.71°, SD = 18.95°, minimum = 1°, maximum = 115°). Based on this methodology, bats do not adhere to Rapoport's Rule throughout the Western Hemisphere.

Fig. 3. Graphical representation of the relationship between number of species and latitude for bats (a) and marsupials (b) in the New World. Negative values for mid-latitude represent the southern hemisphere and positive values represent the northern hemisphere.



Bats and marsupials

Bats and marsupials are appropriate groups for evaluating Rapoport's Rule; both show strong latitudinal gradients in species richness (Fig. 3; Willig and Selcer 1989, Willig and Sandlin 1991, Willig and Gannon 1997). If Rapoport's Rule significantly contributes to latitudinal gradients in species richness, then both groups likely should exhibit gradients of range size with respect to latitude (Lyons 1995). Moreover, because of the ecological and evolutionary disparity between them, bats and marsupials are ideal for comparative purposes. Like Brown et al. (1996), we appreciate the importance of phylogenetic constraints on patterns of latitudinal range size, and concur that phylogenetic analyses "are neither necessary nor sufficient to address all of the interesting questions".

Our objectives are to determine and compare latitudinal patterns of range size in New World bats and marsupials based on a variety of quantitative approaches. In addition, we develop protocols that are not subject to mathematical bias or problems associated with statistical independence. Consequently, we identify deterministic patterns that are distinguishable from those produced by chance, and thereby evaluate the veracity of Rapoport's Rule.

Methods and materials

Distribution maps for bat species were prepared using Hall (1981) for North and Central America, and Koopman (1982) for South America. Distribution maps for marsupials were prepared using Hall (1981) for North

and Central America, and Streilein (1982) for South America. Eisenberg (1989) and Redford and Eisenberg (1992) were referenced to update and modify bat and marsupial distributions in South America. All distributions were prepared using equal area projection maps.

Range maps were digitized and processed in a GIS (geographic information system) program (MAP II). Latitudinal range size, mid-latitude, and most-distal point were calculated for the range of each species. Correlation coefficients describing the association between each type of range size and latitudinal descriptors were calculated separately for each taxon using Pearson product-moment algorithms (SPSS 1990).

To adjust statistical tests to account for inherent biases in mid-latitude and most-distal point, simulation analyses were conducted wherein random ranges were generated using programs written in Microsoft Quick-BASIC (1988). Two different types of simulations were conducted for each taxon in which latitudinal ranges were generated by stochastic processes along with corresponding mid-latitudes and most-distal points. In the random simulations, ranges were generated by randomly determining an upper and lower latitudinal boundary. In the pseudo-random simulations, ranges were constructed to have a distribution of mid-latitudes or most-distal points that corresponded *exactly* to the distribution of mid-latitudes or most-distal points from each taxon.

In each simulation, 82 ranges were calculated for marsupials or 244 ranges for bats, corresponding to the number of New World species in each taxon. These data then were used to calculate correlation coefficients between range size and mid-latitude or between range

size and most-distal point. This entire process was repeated 1000 times for each combination of latitudinal descriptor and taxon to create random distributions of correlation coefficients. Actual correlation coefficients were compared to corresponding distributions. If the observed correlation coefficient occurred in the lower 2.5% of the random distribution, a significant negative relation existed between range size and latitude; conversely, a significant positive relation existed if the observed correlation coefficient occurred in the upper 2.5% of the random distribution (i.e., two-tailed test, $\alpha = 0.05$).

Because of the nature of the correlation coefficient, significance in previous analyses could be due to variation in variables (range size and latitudinal descriptors) or due to the slope of the corresponding best-fit least squares line. The equation for the correlation coefficient (r) may be written as:

$$r = m \frac{S_x}{S_y}$$

where m is the slope, S_x is the standard deviation of the latitudinal variable, and S_y is the standard deviation of range size. Without knowing the contribution of each component, interpretation of results is difficult. Consequently, additional analyses were conducted to clarify causes of significant results. Analyses were identical to previous simulations, except that they produced distributions of standard deviations of the latitudinal variable (x), standard deviations of range size (y), and slopes based on 500 iterations.

Levels of significance from simulation analyses can be affected by the number of iterations involved in producing probability density functions; determination of robust estimates of significance is complex and controversial (Noreen 1989, Manly 1991). We consider the number of simulations used in our analyses (i.e., 500 or 1000) to be adequate for three reasons. First, the distribution of all of our simulated results were symmetrical, approximated normality in most situations, and spanned the same range of values when the number of simulations doubled from 500 to 1000. Second, test statistics were either far in a tail of the probability density function ($P < 0.002$) when significant, or near the median outcome when non-significant. Additional simulation might lead to more accurate levels of significance, but would unlikely change conclusions concerning significance or non-significance. Finally, as a test of the robustness of our analyses, we performed the random simulation of latitudinal range size of bats 10 000 times for each mid-latitude and most-distal point. In both cases, statistical conclusions were unaffected by an increase in the number of simulations; in fact, the p -values were identical.

For comparative purposes, actual ranges for marsupials and bats were analyzed using methods employed

by Stevens (1989), the Mid-point Method advocated by Rohde et al. (1993), and the Most-distal Point Method used by Pagel et al. (1991). To avoid problems associated with a lack of independence in mean latitudinal range size as assessed by Stevens' Method, we calculated the percent of each species latitudinal range that occurs within a latitudinal band. We then display the mean percentage of all species' ranges that occur within a band as a function of latitude. This eliminates the repeated appearance of the total range size of a particular species in the means for every latitudinal band in which it occurs. Although the same species can contribute data to different latitudes, the source of those data derives from different populations or individuals, minimizing the effects of non-independence. Nonetheless, all analyses, except those involving simulations, will be subject to critiques related to the autocorrelated nature of contiguous species ranges. If a Rapoport effect is in operation, then mean percentages should be largest in the tropics and progressively smaller toward the poles.

Results

As would be expected of highly volant species, the average latitudinal range size of bats was much greater than that of marsupials (Bats, mean = 58.50, SE = 4.75; Marsupials, mean = 9.00, SE = 0.63). Latitudinal range size of bats spanned over two orders of magnitude (1° to 115°) and was highly skewed to the right, with over 90% of the range sizes less than 60° in extent. Similarly, latitudinal range size of marsupials spanned approximately 1.5 orders of magnitude (1° to 56°) and was skewed to the right, with approximately 80% of the ranges less than 30° in extent.

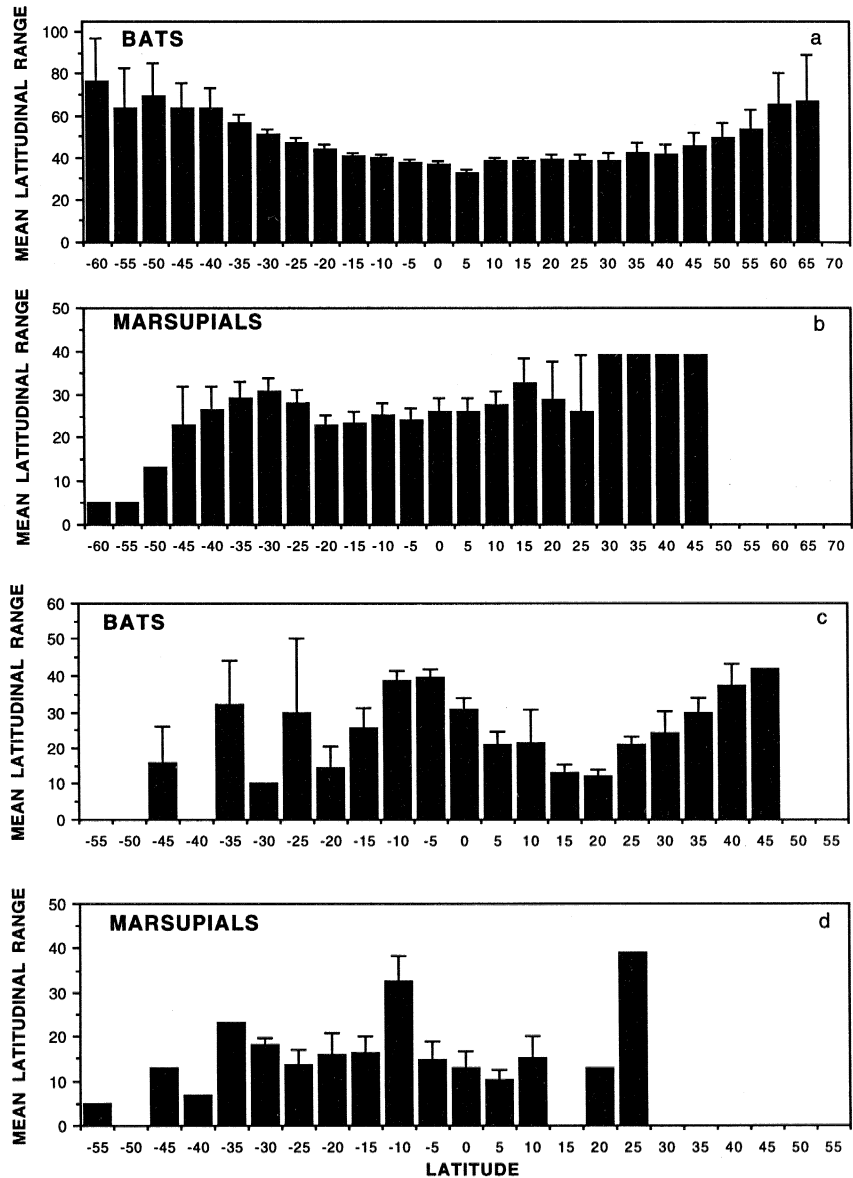
Empirical patterns

Latitudinal patterns of range size depend on methodological approach. Moreover, patterns in North America are not consistently recapitulated in South America, and the range sizes of bats and marsupials do not exhibit the same relationship with latitude, even when based on the same methodology.

Stevens' Method

Mean latitudinal range size increased with increasing latitude for bats regardless of continent (Fig. 4a). This pattern is consistent with that predicted by Rapoport's Rule. In contrast, marsupials evinced no clear pattern (Fig. 4b). Ironically, the largest mean latitudinal ranges occurred in northern North America and the smallest mean latitudinal ranges occurred in southern South America; this is not consistent with predictions from Rapoport's Rule. When mean percentage of each spe-

Fig. 4. Graphical representation of the relationship in the New World between mean latitudinal range size and latitude for bats and marsupials using Stevens' (a, b) method (Stevens 1989) and the mid-point (c, d) method (Rohde et al., 1993). Negative values for mid-latitude represent latitudes in the southern hemisphere and positive values represent latitudes in the northern hemisphere. Standard error of mean latitudinal range size in each latitudinal band is represented by vertical lines. Bands without standard errors had only one species.



cies range that occurs within a latitudinal band is plotted against latitude, patterns fairly consistent with Rapoport's Rule emerge for both bats and marsupials (Fig. 5). However, the pattern for marsupials is skewed in the direction of South America.

Mid-point Method

Mean latitudinal range size did not exhibit a clear or consistent pattern for bats or marsupials (Fig. 4c, d). For North American bats (i.e., those species whose latitudinal mid-points are in North America), range size decreases with decreasing latitude; however, for South American bats, this is not the case. For marsupials, mean range size is similar at all latitudes, with two

noteworthy exceptions. The mean size of ranges of marsupials whose latitudinal mid-points occur at 10° S latitude is larger than those centered at all other latitudes, with the exception of *Didelphis virginiana*, whose center occurs at 25° N latitude. The latitudinal patterns for bats and marsupials are not consistent with Rapoport's Rule when analyzed with the Mid-point Method. Moreover, the pattern reflects the mathematical biases of mid-latitude when each species is represented individually (Fig. 2, shaded regions) in a plot of range size versus mid-latitude. All species occur below a pair of lines that intersect at the latitude halfway between continental extremes (i.e., 8° N latitude) at a range size of 128° (i.e., the total latitudinal extent of the

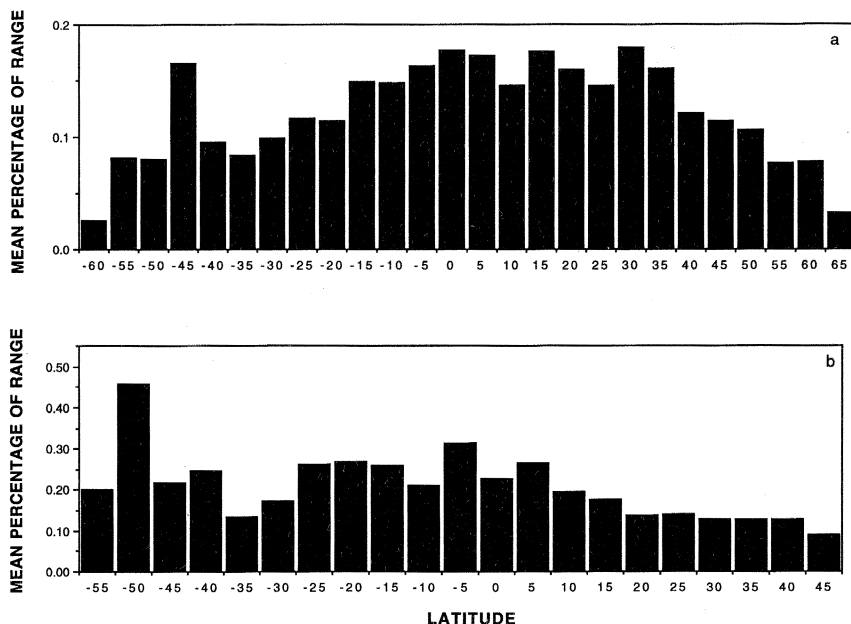


Fig. 5. Graphical representation of the relationship between mean percentage of a species range contained within a 5° band and latitude for New World bat species (a) and marsupial species (b). Negative values for latitude represent the southern hemisphere and positive values represent the northern hemisphere.

New World) and terminate at the continental extremes (i.e., 72° N latitude and 56° S latitude) with a range size of 0°.

Most-distal Point Method

Without exception, latitudinal range sizes, when plotted against most-distal point, occur below each of two lines with x -intercepts at the equator, and slopes of 2 and -2 (Fig. 6, shaded regions). This pattern is consistent with Rapoport's Rule if most-distal points are appropriate designators of tropical versus temperate affinities. At the same time, such a pattern is reflective of the mathematical bias associated with most-distal point. A species with a most-distal point at X° cannot have a range greater than $2X^\circ$.

Simulation analyses

Correlation coefficients

Simulation analyses remove the mathematical biases associated with mid-latitude and most-distal point, thereby facilitating a statistical assessment of patterns of range size. The biases are illustrated by the fact that all randomly generated correlation coefficients were positive for simulations involving most-distal point, whereas all randomly generated correlation coefficients were negative for simulations involving mid-latitude. Regardless of method (random or pseudo-random) or taxon (bats or marsupials), the relationship between most-distal point and range size never differed from that expected by chance alone (Fig. 7a–d). In contrast, detection of a relationship between range size and mid-latitude was taxon- and method-dependent (Fig.

7e–h). A significant positive relationship was detected between latitudinal range size and mid-latitude in all cases (Fig. 7e, f, h), except for ranges that were generated by the pseudo-random model for bats (Fig. 7g).

Components of correlation coefficients

Additional simulations for S_y , S_x and m were performed for mid-latitude because overall results pertaining to r were usually significant; these simulations facilitated interpretation of relationships between range size and latitude (Table 1). In all cases, variability in range size (S_y) was significantly smaller than expected by chance alone. The variability in mid-latitude (S_x) was constrained by the pseudo-random model to be exactly the same as those in bats and marsupials, as a consequence no additional simulations were conducted. Based on the random model, variability in mid-latitude was significantly smaller than expected by chance for bats and marsupials. The slope of the relationship between range size and mid-latitude (m) was more positive than expected by chance in all cases, except for bats in the pseudo-random simulations.

Discussion

Macroecology, the discipline that involves quantifying patterns in geographic ranges and understanding the processes which give rise to them, has emerged as a dynamic area of evolutionary biology (Brown 1995), despite relatively modest origins as areography (Rapoport 1982). Indeed, Brown et al. (1996) suggested that comparative studies of the size, shape, boundaries, and

internal structure of geographic ranges should significantly contribute to an understanding of the ecological and historical mechanisms responsible for the distribution of species. More specifically, geographic variation with regard to historical factors (Rapoport 1975, 1982), biotic interactions (Rosenzweig 1975, Rapoport 1975, 1982), and climate (Stevens 1989, Letcher and Harvey 1994) have been proposed as factors affecting latitudinal gradients in the size of species ranges. Nonetheless, empirical patterns that require biological explanation must be distinguished from those primarily affected by stochastic processes (Gotelli and Graves 1996). Rather than a mandate to search for a dominant deterministic cause, the universality of a pattern may be a consequence of the ubiquity of chance events, or the consequence of many factors, each with a small additive effect, acting in concert (Willig and Lyons unpubl.). We are the first to evaluate the manner in which the range sizes of mammalian taxa vary with latitude throughout North and South America, and to assess the degree to

which such hemispheric patterns may be a consequence of stochastic processes.

Hemispheric patterns of the manner in which range size differs with latitude provide only superficial and, at best, partial support for the existence of Rapoport's Rule. All of these patterns could be the consequence of stochastic processes and all suffer from mathematical biases. Nevertheless, questions concerning the form and significance of latitudinal patterns in range size have merit, especially if range size affects or is affected by the number of species found in tropical or temperate zones. Although mathematical complications associated with latitudinal descriptors for range size can obscure the biological significance of the observed patterns, alternative quantitative approaches circumvent this problem.

What makes a species tropical?

Perceived patterns in range size depend on the criteria used to describe the latitudinal affiliation of species. In some sense, mid-latitude of a species range may represent the optimal conditions or the geographic center of its evolutionary origin. In many instances (Brown 1995, Brown et al. 1995), the higher densities enjoyed by species in the central portions of their ranges attest to this. Alternatively, the most-distal point in a species distribution may reflect its physiological tolerance with regard to climatic variation or stress. Climatic variability has been proposed as an explanation for latitudinal gradients in range size. Species able to withstand high climatic variability may be more likely to have large ranges, and species that cannot will have narrower geographic extents (Stevens 1989, Letcher and Harvey 1994). Both kinds of characteristics (mid-latitude and most-distal point) may affect the ability of species to disperse to and exist within different latitudinal domains, and examination of patterns with regard to each should provide different insights into biological mechanisms.

Random simulations

Latitudinal patterns in range size are no different than those produced by stochastic processes when species are classified by the most-distal point in their distribution (Fig. 7a–b). The degree of climatic variability or stress which a species can tolerate, as estimated by most-distal point, is not associated with range size beyond the constraints imposed by the bounded nature of the New World. In fact, the correlation coefficient between range size and latitude occurred close to the modal values that would obtain if chance alone determined the location of the boundaries of species distributions. Hence, there is no need to ascribe a critical role for climatic

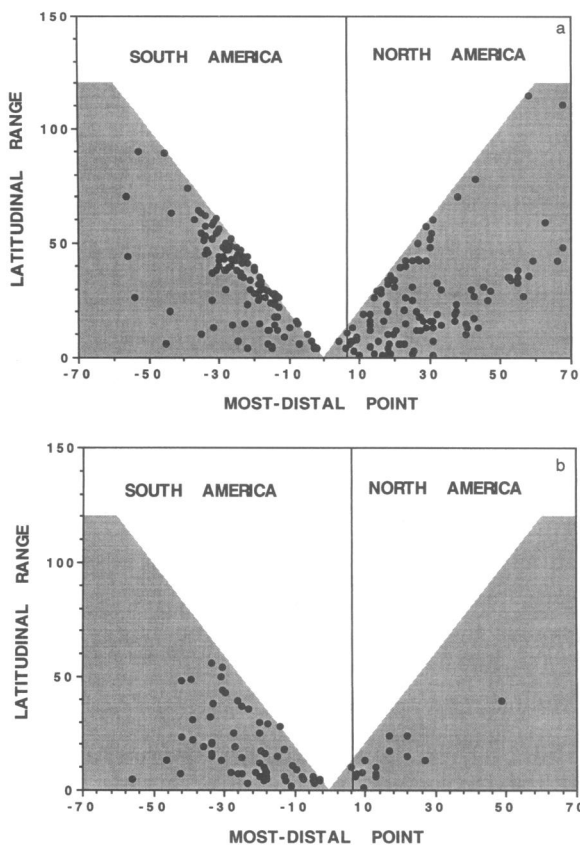


Fig. 6. Graphical representation of the relationship between latitudinal range size and most-distal point for New World bat species (a) and marsupial species (b). The vertical line represents the isthmus of Panama. Negative values for mid-latitude represent the southern hemisphere and positive values represent the northern hemisphere. The shaded area represents the range of coordinates geometrically possible as described in text.

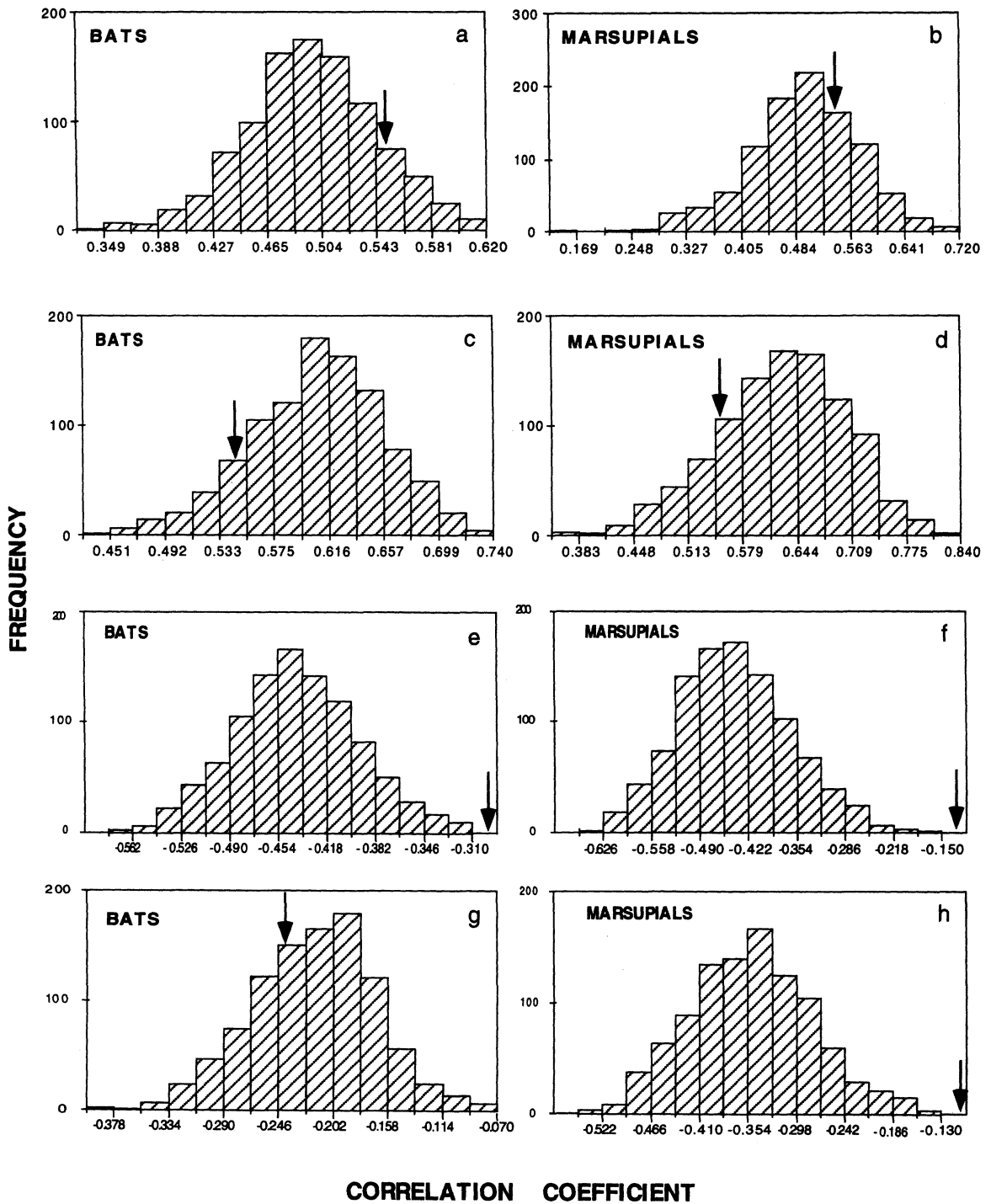


Fig. 7. The probability density function for correlation coefficients generated by simulation analyses of latitudinal range size and most-distal point, as well as for latitudinal range size and mid-latitude, for bats (left column) and marsupials (right column), separately. The vertical arrow indicates the location of the actual correlation coefficient with respect to its corresponding probability density function. a and b) random simulations for most-distal point, for bats ($r = 0.533$, $P > 0.20$, ns) and marsupials ($r = 0.540$, $P > 0.20$, ns), respectively; c and d) pseudo-random simulations for most-distal point, for bats ($r = 0.533$, $P > 0.20$, ns) and marsupials ($r = 0.540$, $P > 0.20$, ns), respectively; e and f) random simulations for mid-latitude, for bats ($r = -0.233$, $P < 0.001$, ***) and marsupials ($r = -0.075$, $P < 0.001$, ***), respectively; g and h) pseudo-random simulations for mid-latitude, for bats ($r = -0.233$, $P < 0.001$, ***) and marsupials ($r = -0.075$, $P > 0.20$, ns), respectively.

Table 1. Summary of simulation results for regression parameters from the relationship between latitudinal range size and mid-latitude for New World bats and marsupials. Note: random refers to a completely random generation of ranges, whereas Pseudo refers to a generation of ranges based on the actual mid-latitudes. Symbols for regression parameters are: r , Pearson product moment correlations; S_y , Standard deviation of the dependent variable (latitudinal range); S_x , Standard deviation of the independent variable (mid-latitude); and m , slope. NA indicates that no comparison was made between actual and simulated S_x because they must be the same in the pseudo-random model. Positive and negative signs indicate the direction of the actual correlation, whereas those in parentheses indicate the position (right- or left-hand tail) of the actual correlation in the probability distribution function created by the null hypotheses.

Method	Bats				Marsupials			
	r	S_y	S_x	m	r	S_y	S_x	m
Random	-0.233*** (+)	19.584*** (-)	11.269*** (-)	-0.405*** (+)	-0.075*** (+)	14.169*** (-)	9.910*** (-)	-0.107*** (+)
Pseudo	ns	19.584*** (-)	NA	ns	-0.075*** (+)	14.169*** (-)	NA	-0.107*** (+)

ns $P > 0.05$; * $0.05 \geq P > 0.01$; ** $-0.01 \geq P > 0.001$; *** $P \leq 0.001$.

variability in affecting the size or distribution of ranges for New World bats or marsupials.

In contrast, latitudinal patterns in range size differed from those expected by chance alone when species are classified by the mid-latitude in their distributions. For both bats and marsupials, the variation in range size (S_y) was statistically smaller than expected by chance and the rate at which range size decreased with increasing latitude was not as precipitous as predicted by the null model (Table 1, Fig. 8). Although the empirical observation that range size increases toward the tropics superficially fails to support Rapoport's Rule, the simulation results suggest that tropical ranges are smaller than expected by chance while temperate ranges are larger than expected by chance (Fig. 2). Shaded regions indicate all possible relationships between latitude and range size. Locations of obvious lacunae correspond to conclusions drawn from the simulations. These observed deviations from our null model are in accord with the spirit of Rapoport's Rule. Clearly, the size distribution of species ranges is more homogeneous than expected by chance, and the geographic distribution of these ranges is related to latitude.

The contrasting results obtained for mid-latitude (significant) and most-distal point (non-significant) suggest mechanisms responsible for gradients in range size. The optimal conditions for a species, rather than its ability to tolerate climatic variability or stress, may exert the stronger influence on whether a species exhibits an extended latitudinal range. Alternatively, the geometric differences between mid-latitude and most-distal point may make the detection of a pattern more likely using mid-latitude. Mid-latitude can be non-random with respect to range size in two ways, whereas most-distal point can do so in only one way. If either the northern or southern terminus of a species range is a consequence of deterministic factors, then the mid-latitude of that range will be affected by deterministic processes, as it is mathematically a consequence of both. However, most-distal point is only sensitive to the terminus that is farthest from the equator, and will only be non-random

if that terminus is non-random. Consequently, a greater likelihood exists that deterministic patterns in range size will be detected using mid-latitude as a descriptor.

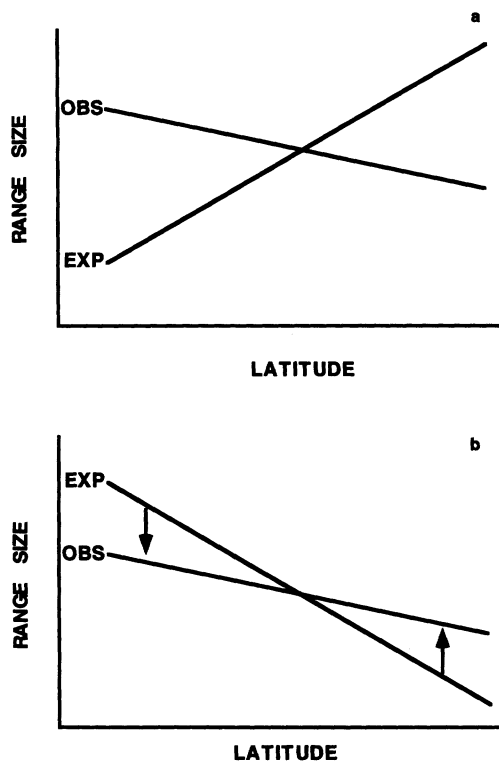


Fig. 8. Illustration of the relationship produced by a straightforward interpretation (EXP) of Rapoport's Rule and the null hypothesis evaluated by simulation models. a) Rapoport's Rule predicts a significant positive relation between latitudinal range size and mid-latitude (EXP); in contrast, empirical patterns for bats and marsupials (OBS) show that range size decreases with increasing latitude. b) Nonetheless, the bounded nature of terrestrial domains geometrically constrains range size to decrease with increasing latitude (EXP). As a consequence, a Rapoport effect (OBS) may be evinced by a less precipitous decline in range size than predicted by chance alone; a pattern exhibited by both bats and marsupials in the New World.

Twin patterns of paired processes

Patterns of latitudinal range size may be confounded by, or be a reflection of, gradients in species richness. To assess this possibility, we conducted pseudo-random simulations in which selected attributes of the observed species richness gradient (locations of midpoints or most-distal points) were retained in the simulated distributions. Regardless of taxon, this had no effect for the analyses based on most-distal point (compare a with c and b with d in Fig. 7). For analyses based on mid-latitude, the effect of the empirical richness gradient was taxon-specific. Marsupials retained a markedly non-random latitudinal gradient in range size after adjusting expectations for the observed latitudinal gradient in richness (compare f with h in Fig. 7). In contrast, much of the non-random pattern in range size for bats was a consequence of their strong latitudinal richness gradient (compare e with g in Fig. 7). When the mid-point of species ranges in the simulations exactly reflected their distribution in the actual fauna, the range sizes of bats were still more homogeneous than expected by chance, but no latitudinal pattern obtained in the distribution of range sizes (Table 1).

If Rapoport's Rule affects a latitudinal gradient in species richness beyond that produced by bounded models (Pielou 1977, Colwell and Hurtt 1994, Willig and Lyons unpubl.), then a weaker pattern should exist when actual species richness gradients are incorporated into the model. Incorporating such a deterministic species richness gradient into the model did weaken the association between range size and latitude. For bats, the association changes from highly significant to non-significant. Although marsupials show a highly significant association regardless of method, it is weaker using the pseudo-random model.

A completely random generation of species ranges results in a parabolic species richness curve with a maximum in the center of the chosen latitudinal endpoints (Colwell and Hurtt 1994, Willig and Lyons unpubl.). Use of continental limits of the New World as endpoints, results in a randomly generated species richness curve that accounts for a significant amount of variation in the New World species richness gradients of both bats and marsupials, but with marked, taxon-dependent deviations (Willig and Lyons unpubl.). Consequently, both the random and pseudo-random methods reflect aspects of a stochastically produced species richness gradient. Moreover, the factors responsible for deviations between the randomly generated richness gradients and the non-random richness gradients must also be responsible for differences in associations derived from the random and pseudo-random models.

The random model predicts that the relation between range size and mid-latitude will be negative as a result of constraints imposed by the bounded nature of the New World. Although the actual correlation between range

size and mid-latitude is negative for bats and marsupials, it is less negative than predicted by the random model (Fig. 8b). Something other than chance and the bounded nature of the New World causes tropical species to have smaller than expected range sizes and temperate species to have larger than expected range sizes.

Historical, ecological, and other geographic factors (e.g., barriers) affect reproductive isolation, adaptive radiation, extinction probabilities, and dispersal routes. The current location of the centers of species ranges may reflect the geographic correlates of these factors to the degree that they are incorporated in the pseudo-random model. For bats, the relationship between range size and latitude does not differ from that produced by the pseudo-random model (Fig. 7g). Consequently, at least part of the Rapoport effect in bats is related to factors associated with the non-random distribution of centers of species ranges (i.e., the latitudinal richness gradient).

The significantly less negative correlation between range size and mid-latitude that occurs when random or pseudo-random models form the bases of statistical inference may be related to a number of factors that affect the small mean range size, regardless of latitude, observed for New World marsupials. Because marsupials cannot or have not had sufficient time to disperse into much of North America, their ranges are not as large as theoretically possible, given the domain of latitudes spanned by the New World. Moreover, many of the larger and more mobile marsupials that occupied diverse trophic roles became extinct after the formation of the Panamanian landbridge, ostensibly as a result of the invasion of South America by northern eutherians (Keast et al. 1972). These large-sized marsupials may have had correspondingly larger latitudinal ranges (Brown and Maurer 1987) compared to the smaller-sized, extant species in the supercohort. The legacy of these extinctions may be reflected in the significantly different correlation observed for modern marsupials compared to that generated by either null model. Finally, the low mobility of marsupials compared to bats, in conjunction with their relatively small size, may result in a finer-scale perception of environmental heterogeneity, wherein populations experience more intensive reproductive isolation by distance or habitat segregation, and are more restricted by aquatic or elevational barriers, than are more mobile taxa such as bats. Hence, even species of marsupial which can disperse to more temperate regions, may be more likely to diverge from their conspecifics and form new taxa with correspondingly restricted ranges. The general failure of marsupials to invade northern North America, the extinction of many larger taxa during the Great American Biotic Interchange, and the different spatial scale at which marsupials perceive environmental heterogeneity, may in concert preclude the group from reflecting the strong geographic bias in range size that a bounded hemisphere imposes on other taxa.

Our observation that high latitude species have larger ranges than expected, given the constraints imposed by the bounded nature of terrestrial environments, is consistent with the local mechanism espoused by Rohde (1996). He suggested that historical patterns of glaciation favored northern species with broad tolerances for climatic fluctuations. This mechanism, if primarily based on the differential extinction of less tolerant species, should also depress the species richness of high latitudes. In work parallel to that reported here, we (Willig and Lyons unpubl.) show that both bats and marsupials have depressed species richness at high latitudes, compared to that produced by a random model. Thus, patterns of range size and species richness for bats and marsupials at high latitudes conform to predictions derived from Rohde's (1996) mechanism.

At low latitudes, a different mechanism may be affecting a reduction in the range size of species. More specifically, Rohde (1992) proposed that enhanced species richness in the tropics is a consequence of greater effective evolutionary time (i.e., shorter generation times, enhanced mutation rates as a consequence of higher temperatures, and extended periods of environmental constancy, together produce higher rates of speciation). If speciation is frequently allopatric, then species ranges become bisected and smaller as a consequence. The enhanced number of species that accumulate from this process may reduce the likelihood or speed with which sister taxa reinvaded each others ranges. Hence, richness will be higher and ranges sizes smaller than predicted by stochastic processes. Our data here support the latter prediction, and elsewhere (Willig and Lyons unpubl.) support the former prediction.

In summary, this study shows that visual inspection of scattergrams of range size and latitudinal descriptors, as well as conventional statistical analyses of their association are biased and unable to distinguish stochastically derived patterns from those affected by deterministic processes. Moreover, the climatic variability hypothesis cannot be invoked for either bats or marsupials. Nonetheless, the Rapoport effect (mid-latitude) detected for bats and marsupials in the New World, is caused by factors other than chance and the geometry of the continents. Latitudinal centers of distribution and their associated ecological characteristics, and evolutionary histories play an important role in determining patterns in range size, at least for bats and marsupials. However, as has been shown with studies of diversity, many environmental factors are correlated with latitude and each may have an effect on diversity gradients. Explanations of latitudinal patterns in range size may be even more complex because of the variety of factors that can affect distributions at the local, regional, or global levels. These factors could act in concert to produce much of the observed gradients in range size, reducing the likelihood that a single factor assumes a dominant role.

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