

GRADIENTS OF SPECIES DENSITY AND TURNOVER IN MARSUPIALS: A HEMISPHERIC PERSPECTIVE

MICHAEL R. WILLIG AND MICHAEL R. GANNON

*Ecology Program, Department of Biological Sciences and the Museum,
Texas Tech University, Lubbock, TX 79409-3131 (MRW)
Department of Biology, The Pennsylvania State University,
3000 Ivyside Park, Altoona, PA 16601-3760 (MRG)*

Although marsupials represent a taxonomically and ecologically diverse group of mammals (Infraclass Metatheria), little is known concerning their large-scale areographic patterns. Distributional data for North and South America were analyzed by statistical techniques to ascertain the degree to which latitude, biome richness, and area account for patterns of species density. In general, mid-latitude accounted for more variation among bands than did other descriptors, but the form of the relation between species density and latitude differed between North and South America. Marsupials in North America exhibited more simple relations (quadratic) between species density and latitude than did their South American counterparts (cubic). Nonetheless, both models are consistent with a subtropical maximum. Turnover of species between quadrats within a band did not contribute to latitudinal gradients in species density in a significant fashion in either continent. Such complex results may reflect the dynamic interaction of contemporary ecological forces (habitat selection, competition, physiological constraints) superimposed on a pervasive historical legacy (i.e., extensive radiation in South America, subsequent reduction in diversity after placental invasion during the late Pliocene, re-invasion of Central America from the south).

Key words: marsupials, species richness, beta diversity, New World, areography, macroecology

Systematists, biogeographers, and ecologists long have been intrigued by distributional patterns of species (Brown and Gibson, 1983; Brown and Maurer, 1989; MacArthur, 1972; Rapoport, 1983; Rhode, 1992; Stevens, 1989) because they reveal important attributes of evolutionary processes (Brown, 1995; Rosenzweig, 1995). Mammals, like other taxa (Cook, 1969; Kiestler, 1971; Rabinovich and Rapoport, 1975; Schall and Pianka, 1978), show increasing species density (number of species per sampling unit) as one proceeds from high to low latitudes in North America (Simpson, 1964), yet this pattern may primarily be attributable to the Chiroptera rather than to quadrupedal terrestrial mammals (Wilson, 1974). McCoy and Connor (1980) also evaluated patterns of mammalian species density in North America; they

detected marked differences between volant and non-volant mammals in the form of the latitudinal gradient based on band analyses. These results should be interpreted with caution because latitudinal trends in North America could be affected strongly by the shape of the continent or by other unique aspects of geography or evolutionary history, rather than by latitude per se (Willig and Sandlin, 1991; Willig and Selcer, 1989). Moreover, most previous analyses, with the exception of Ruggiero (1994), have failed to include the equator and much of tropical America, although the impetus for investigating trends in mammalian species density stems, at least in part, from a fascination with the high diversity supported in tropical areas.

More recently, Willig and Selcer (1989) and Willig and Sandlin (1991) demonstrat-

ed the utility of methodological approaches based on quadrats and bands, quantified the strong relation between species density of bats and latitude in both North and South America, and concluded that longitude, area, and biome richness account for little of the variation in species density among sampling units. In addition, they found that different taxa of bats respond to latitude in different ways, and that the increase in species density of bats in tropical areas occurs despite increased faunal turnover between quadrats in more temperate regions. Comparable studies of latitudinal trends in other speciose mammalian taxa are lacking; however, Mares and Ojeda (1982) did evaluate patterns of species density of hystricognath rodents in South America, and found latitude and longitude to have less predictive power than area. Following the general approach of those who came before her, Kaufman (1995) documented that both bats and non-volant mammals contributed in a significant fashion to the mammalian diversity gradient in the New World. More specifically, she showed that gradients of species richness are linear and indistinguishable in North and South America after the effects of area are removed via covariance analyses. Nonetheless, non-volant mammals represent a diverse and taxonomically heterogeneous group. It is unclear if the generalities for the group apply to constituent taxa (e.g., marsupials, rodents, carnivores) in a consistent or comparable fashion. Indeed, Ruggiero (1994) clearly has documented that peaks in species density in South America differ for subsets of the mammalian fauna (i.e., bats, marsupials, carnivores, edentates, artiodactyls, primates, and hystricognath rodents).

The New World marsupials compose an old lineage (Infraclass Metatheria) that currently exhibits moderate diversity, nonetheless its areographic patterns remain quantified poorly at present. The oldest records of New World marsupials (*Kokopellia juddi*) occur in the late early Cretaceous of North America (Cifelli, 1993a, 1993b). Their

original diversification there approximately corresponds to the Albian (Woodburne and Case, 1996), and is consistent with their absence from the Campanian and Hauterivian deposits from the southern cone of South America (Bonaparte, 1990). Nonetheless, marsupials were already diverse in their earliest records (Tiupampa Fauna) from early Paleocene deposits of South America, including representatives of all three cohorts of Metatheria (Alphadelphia, Ameridelphia, and Australidelphia, sensu Marshall et al., 1990). Subsequent expansion into Australia was achieved via an Antarctic route (Woodburne and Case, 1996; Woodburne and Zinmeister, 1982). South American marsupials successfully radiated into insectivore, frugivore, granivore, omnivore, and carnivore adaptive zones during the Tertiary (Marshall, 1982; Patterson and Pascual, 1972). Reduction in marsupial diversity in the New World appears to have been affected, at least in part, by invasion of North American placentals into South America via the Pleistocene land bridge. Of the extant families of marsupials, only three (Didelphidae, Caenolestidae, and Microbiotheriidae) occur in the New World; most species are didelphids. Herein, we describe large-scale patterns of species density of marsupials in the continental New World, including North, Central, and South America.

MATERIALS AND METHODS

Because of the biogeographic history and geography of the New World, as well as the radiation of marsupials on southern continents, we analyzed data separately for North and South America before examining general patterns in the New World. Quantitative methods follow those of Willig and Selcer (1989) and Willig and Sandlin (1991).

An equal-area projection map of North and South America was superimposed with a grid system, defined by the intersection of 5° lines of longitude and latitude (Fig. 1). The resultant 28 latitudinal divisions defined 27 bands that each span 5° of latitude. Two bands (7.5°N and 12.5°N) include portions of both North and

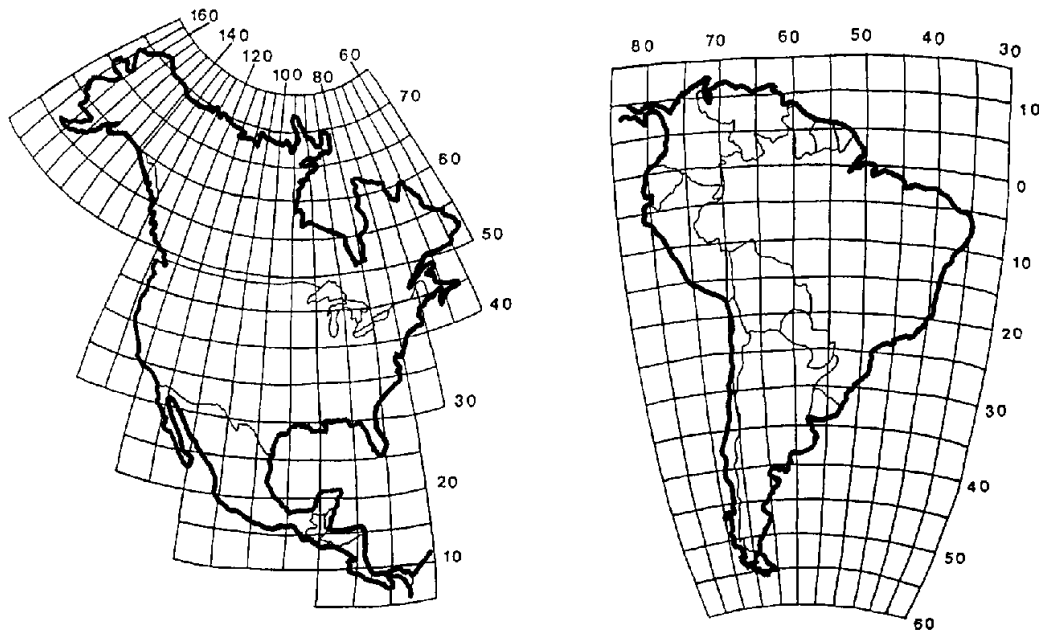


FIG. 1.—Maps of North and South America showing location and size of quadrats and bands that were used in analyses of species density of marsupials.

South America, complicating a straightforward delineation of North and South American bands. We somewhat arbitrarily considered bands south of 10°N latitude to be in South America. As a consequence, most of Panama and a small portion of Costa Rica were included in a South American band, similarly small portions of coastal areas in the Caribbean north of 10°N latitude in Venezuela and Colombia were considered to be a part of a North American band.

Three independent descriptors (land area, mid-latitude, and biome number) characterized each band. The area of the continental land mass within each band was estimated using a compensating polar planimeter. Equal-area projection maps directly provide mid-latitude. The number of biomes within bands was obtained with reference to the world vegetation map in Times Atlas of the World (1983). The number of marsupial species per band (marsupial species density) was obtained by referencing species distribution maps in Hall (1981) for North and Central America and Streilein (1982) for South America. Known collection localities for marsupials reported by Eisenberg (1989) were used to extend distributions of species in northern South America. Although Wilson and Reeder

(1993) contains a list of mammal species of the world, it does not provide a rationale for the inclusion or exclusion of taxa compared to those in Hall (1981) or Streilein (1982). Distributional uncertainty (e.g., two species recognized by Wilson and Reeder, 1993, are known only from their type locality) or systematic problems (e.g., 14 species recognized by Hall, 1981, or Streilein, 1982, were not referenced, even as junior synonyms, by Wilson and Reeder, 1993) argue against reliance on the list of marsupial species in Wilson and Reeder (1993). The recent commentary by Ojeda and Monjeau (1995) highlights a number of problems and presents additional critiques concerning the marsupial section in Wilson and Reeder (1993). Even if the listing in Wilson and Reeder (1993) withstands the test of time, areographic biases that could result from reliance on Hall (1981) or Streilein (1982) are not apparent.

Step-wise multiple regression analyses were performed using SPSS-X program REGRESSION (SPSS, Inc., 1988) to evaluate the contribution of independent descriptors to variation in marsupial species density. First (X^1), second (X^2), and third (X^3) powers of the value of each independent descriptor resulted in each band be-

ing described by nine variables. The importance of a descriptor, X_i (e.g., mid-latitude, area, or biome richness), was assessed as the sum of the ΔR^2 for each of the three powers of the descriptor (i.e., X_i^1 , X_i^2 , X_i^3) that were incorporated into the multiple regression equation. In this fashion, descriptors associated with species density in a non-linear way could be detected by our analyses.

Because latitude and area of bands are correlated with each other, as well as with species density, it is impossible to distinguish between pure areal effects and pure latitudinal effects. To assess latitudinal effects after removing the effect of area, a two-step multiple regression was performed in which all linear, quadratic, and cubic functions of area were forced into a multiple regression equation; all three powers of each of the other independent descriptors, as well as those related to area, subsequently were subject to addition or removal via step-wise algorithms (SPSS-X Program REGRESSION; SPSS, Inc., 1988).

Polynomial regression analysis was performed to identify the best relation (up to a quartic equation) between marsupial species density and latitude using BMDP program P5R (Dixon and Brown, 1979). Two a priori criteria were used to identify the polynomial of choice (Willig and Selcer, 1989); the chosen polynomial must be a statistical improvement over lower polynomials, and the next higher-order equation, even if significant, may not increase R^2 by ≥ 0.05 . In this fashion, we identify the most simple and significant relation between species density and latitude.

The extent of species replacement between quadrats along a gradient within a band, or beta diversity (Whittaker, 1972), was estimated by the turnover index (B_i) of Wilson and Shmida (1984). Cody (1975) and Routledge (1977) have shown this measure to be superior to other indices. It is additive, as well as independent of sample size and alpha diversity; it thereby can be used to compare species-rich and depauperate systems. The calculation of B_i is given by

$$B_i = [|G(H)| + |L(H)|]/2A$$

where $G(H)$ represents the cumulative gain in species along the band, $L(H)$ is the cumulative loss of species along the band, and A is the average species density of quadrats within the band. Both $G(H)$ and $L(H)$ are based on com-

TABLE 1.—A correlation matrix for independent descriptors as well as for species densities in North America (upper right triangle, $n = 8$) and South America (lower left triangle, $n = 12$) based upon band methods. For each cell in the matrix, the correlation coefficient (r , above) and significance level (P , below) are given.

Attribute	Latitude	Area	Biome number	Marsupial richness
Latitude		0.941 <0.001	0.808 0.015	-0.802 0.017
Area	-0.852 <0.001		0.848 0.008	-0.717 0.045
Biome number	-0.023 0.943	0.178 0.581		-0.618 0.103
Marsupial richness	-0.827 0.001	0.853 <0.001	0.367 0.240	

parison of all $n-1$ pairs of adjacent quadrats (defined by the intersection of 5° meridia) within a band containing n quadrats. If B_i is independent of latitude, the regression between B_i and mid-latitude should be nonsignificant. Conversely, a significant regression with a negative slope indicates that increased diversity in tropical areas (if detected by band methods) is, at least in part, a product of greater species turnover between quadrats in tropical bands.

RESULTS

General areographic patterns.—The descriptors used to characterize bands were correlated, but the associations depended upon continent (Table 1). Although, the correlation between area and latitude was highly significant ($P < 0.001$) regardless of continent, the association was positive in North America and negative in South America. The association between biome number and latitude was positive in North America and nonsignificant in South America.

The highest species density of marsupials occurred at subtropical latitudes of South America, with latitudes in North America harboring few species (Fig. 2). Nonetheless, continent-specific differences characterized the relationships between species density and the various descriptors (latitude, area,

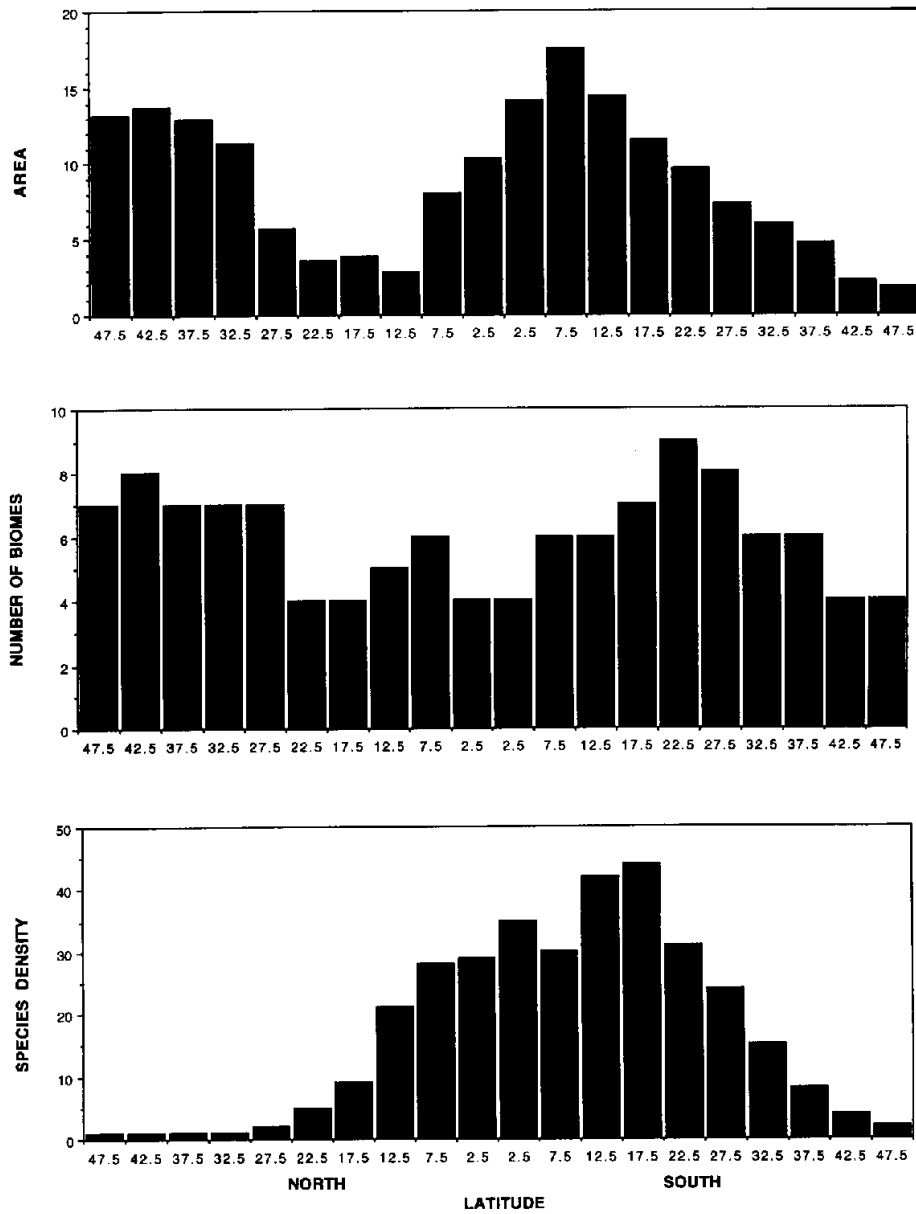


FIG. 2.—Patterns of change in area, number of biomes, and species density with mid-latitude throughout the New World for bands spanning 5° of latitude (see Fig. 1).

and biome number). The species density of North American marsupials was negatively correlated with all three descriptors, whereas the species density of South American marsupials was negatively correlated with

latitude, but positively correlated with area and biome number (Table 1).

Multiple regression analyses.—Mid-latitude accounted for much of the variation in species density of marsupials in both North

TABLE 2.—Results of multiple-regression analyses of species density of marsupials as a function of latitude, area, and biome richness. Separate analyses were conducted for North and South America. Cumulative contributions of each descriptor to R^2 , based on linear, quadratic, and cubic relations, indicate the importance of a variable in accounting for variation in richness of marsupial species; ns indicates that none of the three powers of a descriptor accounted for a statistically significant increase in R^2 .

Continent	Cumulative ΔR^2 of descriptor		
	Latitude	Area	Biome
North America	0.991	ns	ns
South America	0.804	ns	ns

America and South America (Table 1), and was the only descriptor to be selected in multiple regression analyses for the continents separately (Table 2). The two-step multiple regression for the New World accounted for 19% of the variation in species density of marsupials after forced entry of linear, quadratic, and cubic powers of area; however, the model was not significant ($F = 1.258$; $d.f. = 3, 16$; $P = 0.322$). Subsequent step-wise adjustments removed cubic and quadratic powers of area before including the linear power of mid-latitude. Once mid-latitude was entered in the equation, the linear power of area was removed, and the final regression equation significantly accounted for 60% of variation in species density based on latitude alone ($F = 27.534$; $d.f. = 1, 18$; $P \ll 0.001$).

Polynomial regression analyses.—Be-

cause latitude historically is considered to be an important factor affecting species densities from the perspective of geographical ecology (Stevens, 1989), we chose to evaluate the form of the relation (Table 3). In general, the gradient (Fig. 3a) in North America (quadratic) was both qualitatively and quantitatively different from that in South America (cubic). Species density in South America consistently was greatest at subtropical latitudes, whereas the gradient in North America was consistently one in which richness decreases with increasing latitude.

Within-latitude diversity trends.—Turn-over of species between quadrats within latitudinal bands was independent of latitude (Fig. 3b) for both North America (regression analysis: $F = 0.83$; $R^2 = 0.12$; $d.f. = 1, 6$; $P = 0.398$) and South America (regression analysis: $F = 2.82$; $R^2 = 0.22$; $d.f. = 1, 10$; $P = 0.124$). As a consequence, any latitudinal patterns in species density based upon analyses of bands was not affected by gradients in beta diversity.

DISCUSSION

Unlike most hemispheric patterns of species density, that of marsupials contains a distinctly non-tropical maximum. The Mollossidae is the only other broad-ranging mammalian taxon in the New World to exhibit a subtropical maximum based on equivalent types of analyses (Willig and Selcer, 1989). Nonetheless, areographic patterns of species density for marsupials are similar to those obtained for bats in a number of ways. Species density of bats in the

TABLE 3.—Results of polynomial regression analyses of species densities of marsupials as a function of mid-latitude using band methods. Separate analyses were conducted for North and South America. An asterisk (*) indicates the polynomial degree that satisfies a priori acceptance criteria.

Continent	Polynomial degree							
	1		2		3		4	
	R^2	ΔR^2	R^2	ΔR^2	R^2	ΔR^2	R^2	ΔR^2
North America	0.643	0.643	0.832*	0.189	0.898	0.066	0.921	0.023
South America	0.684	0.684	0.832	0.148	0.898*	0.066	0.921	0.023

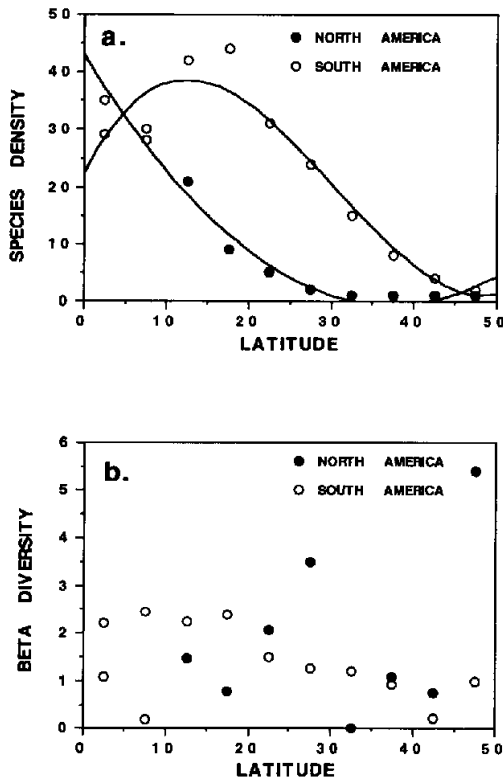


FIG. 3.—Relationship between: a, species density of marsupials and latitude for North and South America (North America, $Y = 37.037 - 1.886X + 0.024X^2$, $R^2 = 0.957$; South America, $Y = 24.484 + 2.987X - 0.158X^2 + 0.002X^3$, $R^2 = 0.937$) based on band analyses and b, turnover of marsupial species (B) and latitude for North and South America (a significant association between turnover and latitude was not detected for either continent).

New World primarily is related to latitude for all bats, as well as for each of the chiropteran families or subfamilies (Willig and Sandlin, 1991; Willig and Selcer, 1989). Our results for marsupials (Fig. 3) indicate an important role for latitude-related factors in affecting species density by accounting for 95.7 and 93.7% of the variation among bands in North America and South America, respectively. Even in the hybrid multiple regression for the New World, latitude accounted for 60.4% of the variation in species richness of marsupials. The non-signif-

icant role of area is a consequence of opposite trends in North and South America; species density increases with area in South America, but decreases with area in North America (Table 1), and even this is likely a consequence of confounding interactions with latitude. The lack of replication for bands at particular latitudes prevents the demarcation of unique effects that can be attributed to latitude or area in a fashion that is not confounded by continental shape. A quadrat approach that decouples latitude and area, while simultaneously assessing their unique effects, offers much promise in future areographic studies (Lyons, 1995; S. K. Lyons and M. R. Willig, in litt.).

Northern versus southern gradients.—The different gradients of species density in North and South America (Table 3 and Fig. 3) are likely a consequence of their different latitudinal extents (e.g., North America does not have an extensive tropical component) as well as a result of interacting historical and geographic factors. In South America, increasing area toward the tropics magnifies the negative gradient in species density, whereas in North America, decreasing land area toward the tropics could diminish such a gradient (Fig. 2). Nonetheless, both northern and southern patterns are consistent with a New World gradient that attains a maximum in subtropical South America (Figs. 2 and 3a). The less complex relations in North America compared to South America (quadratic versus cubic relation) reflect processes in the northern portion of the hemisphere, likely related to physiological stress on particular species, a relatively recent invasion into North America during the Great American Interchange across the Pleistocene land-bridge in Central America, and competitive disadvantages with resident eutherian species. In contrast, the subtropical maximum of marsupials in general, may reflect the adaptive radiation of the group in South America, before northern and southern continents were connected. In addition, subtropical latitudes in South America experience higher

richness of biomes than do their tropical counterparts (Fig. 2). This, along with the low mobility of marsupials, may have resulted during evolutionary time, in the production of a number of endemic or quasi-endemic forms that have distributions corresponding to particular subsets of biomes (e.g., all three extant species of caenolestids in the Andes Mountains).

Implications for conservation of biodiversity.—Recent commentaries have questioned the dogma that the tropics contribute most to New World biodiversity and have criticized the almost exclusive focus of international conservation efforts in tropical regions (Mares, 1992; Redford et al., 1990). Our results for marsupials strengthen the contention that global efforts to maximize biodiversity must consider taxonomic hierarchy. Clearly, for marsupials, subtropical latitudes, as well as latitudes at the interface between subtropical and temperate regions, harbor the highest species richness of marsupials in the New World. Ruggiero's (1994) analysis of latitudinal gradients of species richness in South America lends further support to the contention that the subtropics harbors a fauna of special concern for conservation. She has documented that in addition to marsupials, edentates, carnivores, artiodactyls, and hystricognath rodents attain highest richness at subtropical latitudes. In fact, after adjusting for the width of 2° latitudinal bands, species density of bats, marsupials, carnivores, edentates, artiodactyls, and hystricognath rodents decrease from 10° N to ca. 10° S latitude.

If conservation efforts are to preserve subtropical diversity, additional investigation of marsupial richness at the level of local communities should focus on areas between 5 and 25° S latitude. Indeed, relatively little work has been conducted on any aspect of mammalian biology in vast regions of the pantanal of Brazil, Bolivia, and Paraguay, or in the wet and dry chaco of Paraguay and Argentina (Redford and Eisenberg, 1992; Redford et al., 1990). The

general correspondence of subtropical maxima for many mammalian taxa in South America demands re-evaluation of hemispheric conservation strategies. Indeed, evaluation of the second derivative for the nonlinear model in South America (Fig. 3) suggests that the most rapid increase in marsupial species density occurs in the subtropics, in the vicinity of 26° S latitude. This subtropical area comprises a nexus of phytogeographic regions, including wet chaco, dry chaco, pantanal, cerrado, and interior Atlantic rainforest, and may represent the southernmost extension of tropical influence in South America.

Scale.—Spatial scale is an important consideration in comparisons of the response of different mammalian taxa to environmental gradients. Although heuristically pleasing to assume that regional effects are a consequence of local interactions, broad-scale approaches such as those presented here may not reflect processes that occur at the level of populations or communities. In fact, Wiens (1984) contended that results based upon regional-scale approaches may be mathematical artifacts rather than reflections of local processes. In contrast, Allen and Starr (1982) purported that no single metric or scale has hegemony over another in the detection of biologically meaningful structure. Although resolution of this controversy is beyond the scope of our data, it is important to keep these considerations in mind when interpreting the patterns detected at the scale of our analyses. In fact, our analyses and those of most other evaluations of species density cannot resolve which combination of the 10 classical (Pianka, 1983) and 4 recently proposed (Huston, 1979; Rhode, 1992; Stevens, 1989; Terborgh, 1985) mechanisms accounts for increases in species richness with decreasing latitude in particular. Thus, our selection of band width may bias subsequent analyses in a particular scale-dependent fashion. However, we have restricted our taxonomic comparisons to marsupials and bats in situations in which bands

were of the same size. Also, size of home ranges of either bats or marsupials is so much smaller than the size of our sampling units that we consider any biases to be consistent for the mammalian taxa we compare. Moreover, analyses at a smaller scale (2°), although restricted to South America, resulted in the same general conclusions as those we present concerning latitudinal gradients of species density for bats and marsupials (Ruggiero, 1994).

The areographic effect of current habitat selection and dispersal barriers upon present distributional limits of marsupials are difficult to separate from the consequences of early marsupial radiation and subsequent interaction with eutherians after establishment of the Panama land bridge. The melange of factors that impinge on current and past distributions of marsupials clearly diminish the preeminence of any single factor (e.g., productivity, heterogeneity) in accounting for present areographic patterns. Nonetheless, our results reflect strong historical factors that result in marsupials exhibiting non-tropical maxima.

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