

Bat species density gradients in the New World: a statistical assessment

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Abstract. Bat species density gradients in North America, South America, and the continental New World were analysed by a variety of multivariable statistical procedures. Multiple regression analyses were performed to identify which of four possible descriptors (latitude, longitude, area, or biome richness) best accounted for variation in bat species density among quadrats. Independent descriptors were considered to be meaningful if they met two criteria: the descriptor must make a significant contribution to the multiple regression and it must augment R^2 by at least 5%. Because different taxa might respond to independent descriptors in different ways, separate analyses were conducted for molossids, vespertilionids, phyllostomids, non-phylostomids, and all bats. Latitude was consistently the most important predictor of bat species densities ($r^2 > 0.72$), except in the case of vespertilionids in the continental New World, in which latitude was unimportant ($r^2 = 0.03$) and the two most important variables (longitude and biome richness) together only accounted for approximately 40% of the variation. Even a control analysis on data for Brazil (for which finer resolution of ecological life zones was available) failed to identify biome richness as an important predictor of species densities but did indicate that latitude was again the most important

predictor. Polynomial regression analyses were used to identify the best relation between bat species density and the most important predictor (latitude) from the multiple regressions. Separate analyses were conducted for all combinations of geographic focus (continental New World, North America, and South America) and taxonomic affinity (all bats, phyllostomids, non-phylostomids, molossids, and vespertilionids). The polynomial of choice must be a statistical improvement over lower degree polynomials, and the next higher polynomial, if significant, must increase r^2 by less than 5%. Although the statistically appropriate relation varied from a first to ninth degree equation, the polynomial of choice for South America, North America, and the continental New World were first, second, and second degree equations, respectively, and each accounted for more than 80% of the variation in species densities. Phyllostomids consistently increased faster with decreasing latitude than did non-phylostomids. The large cosmopolitan insectivorous families did not increase in species richness in the tropics (Vespertilionidae) or showed especially slow rates of increase (Molossidae).

Key words. Mammalia, Chiroptera, species density, areography, latitudinal gradients, multivariate analysis.

INTRODUCTION

Geographic regions differ markedly in the number of species that they contain. Several general global patterns of species density (the number of species that occur within a sampling unit) have been recognized, the most prominent of which is the tendency for numbers of species to increase from high latitudes to low latitudes. Although latitudinal gradients in species density long have been perceived to exist for most terrestrial macroorganisms, empirical studies confirming the manner in which density actually changes from temperate to tropical regions are few. The patterns of density of North and Central American mammals have received much attention. Simpson (1964), for example, used a quadrat method to investigate patterns in North American mammal density. He reported that overall mammalian species density increases from high to low latitudes; however, he also noted differences in the strength of the

trend for different taxa. Wilson (1974), using Simpson's quadrats, found that quadrupedal mammals did not exhibit a latitudinal density gradient, but rather were concentrated at mid-latitudes. Moreover, Wilson (1974) reported that bat density showed a distinctly non-linear increase toward tropical latitudes that accounted for the overall pattern attributed to mammals in general. More recently, McCoy & Connor (1980) used a different method (latitudinal bands) to examine latitudinal trends in mammalian species density. They demonstrated results different from those of Wilson (1974) for quadrupedal mammals. In contrast, McCoy & Connor's technique did not produce results that appreciably differed from those of Wilson (1974) for gradients of bat species density. They concurred that the observed latitudinal trend for overall mammalian density is largely attributable to the increase in bat species density from the North American Temperate Zone to the Central American Tropics.

Each of the previously cited investigations limited its focus to North and Central America, primarily because reliable distribution maps for North American mammals were available in Hall & Kelson (1959). Moreover, the systematics and distributional status of South American mammals were relatively poorly understood or documented at that time. Several interpretive problems result from the use of only North America in a study of latitudinal trends in species density. North America does not include the full range of low latitudes (the southernmost point in Central America extends to about 7° 30' N latitude) and does not include the equator. In addition, conclusions about observed trends must be tempered because of the absence of corroborative evidence from southern latitudes. Without data from South America, it is possible that the observed 'latitudinal trends' in North America are primarily affected by the shape of the continent or some other unique aspect of either its geography or evolutionary history, rather than the result of latitude.

Herein, we describe large-scale patterns of bat species density of the continental New World as a whole, including North America, Central America, and South America. Our study is limited to bats for two reasons: (1) previous studies attributed most of the increase in mammalian diversity in tropical North America to the contribution of the Chiroptera, and (2) bats are the only group for which reliable distribution maps are available for South America (Koopman, 1982). Moreover, the New World Tropics contains the richest microchiropteran fauna in the world (approximately 75% of living genera) with more than twice as many genera as are known from either the Oriental region or Africa (Patterson & Pascual, 1972).

MATERIALS AND METHODS

An equal area projection map for North and South America was superimposed with a grid system of 500×500 km (250,000 km²) quadrats (Fig. 1). A total of

232 quadrats contained at least some portion of the continental land masses; however, some quadrats contained land areas too small to measure with precision and were excluded from further consideration (the smallest measured area used in subsequent analyses was 1825 km²). Four independent descriptors (area, latitude, longitude, and biome richness) were used to characterize each quadrat. The area of the continental land mass within each quadrat was estimated using a compensating polar planimeter. Latitude and longitude values to the nearest degree were obtained directly from the equal area projection maps for the geometric centre of each quadrat. The number of biomes within each quadrat was obtained from the world vegetation map in *The Times Atlas of the World* (1983) for New World analyses. A finer and more detailed delineation of biomes for Brazil was obtained from the Provisional Ecological Map of the Republic of Brazil (Tosi & Velez-Rodriguez, 1983) in consultation with the Provisional Life Zone Map of Brazil at 1:5,000,000 Scale (Tosi, 1983); these data were used only in the analysis for Brazil alone. The number of bat species per quadrat was obtained from species distribution maps in Hall (1981) for North and Central America and in Koopman (1982) for South America.

Multiple regression analyses (step-up algorithms) were performed using SPSS program REGRESSION (Nie *et al.*, 1975) in order to identify the independent quadrat descriptors that best account for variation in bat species densities. Independent descriptors were considered to be meaningful (significant and appreciable) if they met two criteria: (1) the descriptor had to be significant ($P < 0.05$) in the multiple regression, and (2) the descriptor had to produce a ΔR^2 of at least 0.05, where ΔR^2 represents the change in the per cent variation in bat species density accounted for by the descriptor added to the multiple regression equation. Multiple regressions were conducted for the New World, as well as for Brazil only. Because different taxa might relate to independent descriptors in different ways, separate

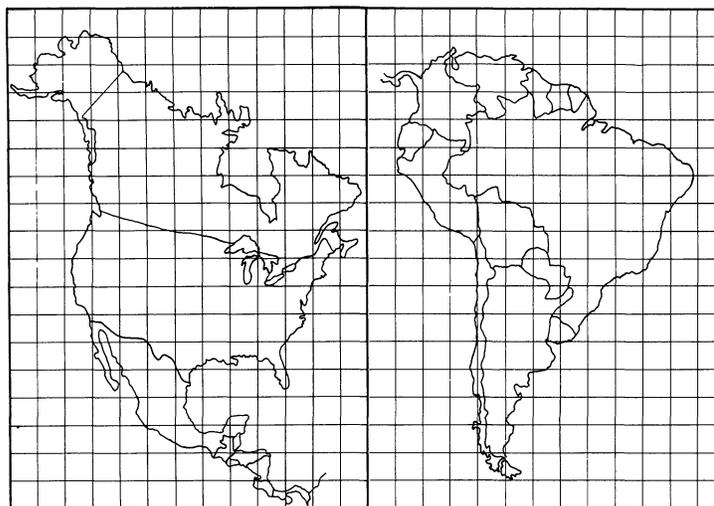


FIG. 1. Equal area projection map of North and South America from *Goode's Atlas of the World* superimposed with a grid system in which each quadrat (scale=500 km on a side) represents sampling units (250,000 km²) for which bat species density, mid-latitude, mid-longitude, land area, and biome richness were determined.

analyses were performed on five groups: all bats, phyllostomids, non-phyllostomids, vespertilionids, and molossids. Only quadrats with non-zero species densities for the taxon under consideration were used in analyses.

Polynomial regression analyses were performed using BMDP program P5R (Dixon & Brown, 1979) in order to identify the best relation between bat species density and the most important independent descriptor (latitude) from the multiple regressions. Again, two criteria were evaluated in determining the polynomial of choice. The chosen polynomial must be a statistical improvement over lower degree polynomials, and the next higher polynomial, if significant, must increase r^2 by less than 0.05. These criteria designate the simple polynomial that accounts for significant and appreciable variation in species density. Fifteen different analyses were conducted for all combinations of geographic focus (New World, North America including Central America, and South America) and taxonomic affinity (all bats, phyllostomids, non-phyllostomids, vespertilionids, and molossids). Again, only quadrats with non-zero species densities for the group of concern were included in the analyses.

RESULTS

Multiple regression analyses

Latitude is the most important of the four independent descriptors examined for predicting species densities except in the case of New World vespertilionids (Table 1). The

simple r^2 for latitude is 0.72 or greater for all taxa except vespertilionids, which have a simple r^2 of 0.03. Again, with the exception of vespertilionids, only latitude meets the statistical and appreciable criteria for acceptance as an important factor in accounting for species densities. Moreover, in the case of vespertilionids, two descriptors (in decreasing order, longitude and biome richness) are required to meet the above criteria, and even then, R^2 is only 0.41.

Because of the finer detail present in the ecological map of Brazil, the analyses restricted to bat distributions within that country should be more sensitive to detecting an effect of biome on species density, if one exists. Multiple regression results (Table 1) did not fulfil that expectation. As for the entire New World, latitude accounted for most of the variation in species densities for all groups of bats in Brazil, except for molossids, in which area, biome richness, and longitude together represent the significant independent descriptors, but account for only 32% of the variation. In fact, biome richness never exhibited a ΔR^2 of more than 6%.

Polynomial regression analyses

Based upon the results of the multiple regression analyses, latitude was used as the independent variable in all subsequent polynomial analyses. Although the statistically appropriate polynomial relation varied from a first (North American phyllostomids) to ninth (North American non-phyllostomids and all North American

TABLE 1. Multiple regression analyses for bat species richness as a function of LAT (latitude), LONG (longitude), AREA, and BIOME. Results are reported for all combinations of geography (New World and Brazil) and taxonomy (all bats, phyllostomids, non-phyllostomids, vespertilionids, and molossids).

New World					Brazil				
Source	Partial β	ΔR^2	Simple β	r^2	Source	Partial β	ΔR^2	Simple β	r^2
All bats									
LAT	-0.98	0.81	-0.90	0.81	LAT	-0.79	0.76	-0.87	0.76
LONG	0.12	0.01	-0.51	0.26	LONG	0.30	0.07	0.44	0.19
AREA	0.04	0.00	0.03	0.00	BIOME	0.09	0.01	0.17	0.03
BIOME	0.02	0.00	0.10	0.01	AREA	0.09	0.01	0.15	0.02
Phyllostomid bats									
LAT	-0.93	0.74	-0.86	0.74	LAT	-0.75	0.72	-0.85	0.72
LONG	0.10	0.01	-0.49	0.24	LONG	0.37	0.11	0.50	0.25
AREA	0.02	0.00	0.01	0.00	BIOME	0.12	0.02	0.18	0.03
BIOME	-0.02	0.00	0.06	0.00	AREA	0.05	0.00	0.11	0.01
Non-phyllostomid bats									
LAT	-0.99	0.85	-0.92	0.85	LAT	-0.77	0.65	-0.81	0.65
LONG	0.14	0.01	-0.51	0.26	AREA	0.19	0.03	0.26	0.07
AREA	0.08	0.01	0.07	0.00	LONG	0.08	0.01	0.21	0.04
BIOME	0.08	0.01	0.16	0.03	BIOME	-0.02	0.00	0.12	0.01
Vespertilionid bats									
LONG	0.73	0.35	0.59	0.35	LAT	0.63	0.46	0.68	0.46
BIOME	0.27	0.06	0.24	0.06	BIOME	-0.22	0.03	-0.26	0.07
LAT	-0.25	0.04	0.16	0.03	LONG	-0.15	0.03	-0.28	0.08
AREA	0.17	0.03	0.08	0.01	AREA	0.09	0.01	-0.02	0.00
Molossid bats									
LAT	-0.81	0.72	-0.85	0.72	AREA	0.36	0.17	0.41	0.17
BIOME	0.18	0.04	0.05	0.00	BIOME	0.26	0.06	0.35	0.12
LONG	-0.13	0.02	-0.55	0.31	LONG	0.22	0.06	0.14	0.02
AREA	0.11	0.01	0.12	0.02	LAT	-0.13	0.01	-0.26	0.07

Microchiroptera) degree equation, the simple polynomial (based upon the statistical and appreciable criteria) only varied from a first to second degree equation (Table 2; Figs. 2–4). Interestingly, the simple polynomials for South America, North America, and the New World are first, second, and second degree equations, respectively, and each accounts for more than 80% of the variation in species densities.

DISCUSSION

Quadrats versus latitudinal bands

Two methods of assessing latitudinal gradients have appeared in the literature. Quadrat methodologies similar to that of Simpson (1964) have been applied to a variety of taxa in a number of different geographic settings (North American amphibians and reptiles: Kiester, 1971; North American birds: Cook, 1969; North American mammals: Wilson, 1974; Argentine birds: Rabinovich & Rapoport, 1975; American (U.S.) and Australian reptiles: Schall & Pianka, 1978; South American hystricognath rodents: Mares & Ojeda, 1982). This approach has been criticized by McCoy & Connor (1980), who used the same mammalian distribution data (Hall & Kelson, 1959) as that used by Simpson (1964) and Wilson (1974), but subjected it to an analysis based upon latitudinal bands. McCoy & Connor (1980) purported that latitudinal distributions are not independent of longitude, and demonstrated the effect by comparing plots of species richness versus latitude produced by

TABLE 2. Polynomial regression analyses for bat species richness as a function of latitude for the New World, North America and South America. Characteristics defined in text.

Characteristics	New World	North America	South America
All New World microchiroptera			
Degree of statistical polynomial	4	9	3
r^2 of statistical polynomial	0.898	0.935	0.840
Degree of simple polynomial	2	2	1
r^2 of simple polynomial	0.868	0.872	0.803
Phyllostomid bats			
Degree of statistical polynomial	3	1	3
r^2 of statistical polynomial	0.774	0.879	0.768
Degree of simple polynomial	1	1	1
r^2 of simple polynomial	0.726	0.879	0.704
Non-phylostomid bats			
Degree of statistical polynomial	3	9	3
r^2 of statistical polynomial	0.867	0.864	0.862
Degree of simple polynomial	1	1	1
r^2 of simple polynomial	0.852	0.789	0.835
Vespertilionid bats			
Degree of statistical polynomial	2	3	8
r^2 of statistical polynomial	0.483	0.680	0.588
Degree of simple polynomial	2	2	2
r^2 of simple polynomial	0.483	0.650	0.518
Molossid bats			
Degree of statistical polynomial	3	6	3
r^2 of statistical polynomial	0.779	0.878	0.738
Degree of simple polynomial	1	1	2
r^2 of simple polynomial	0.716	0.746	0.728

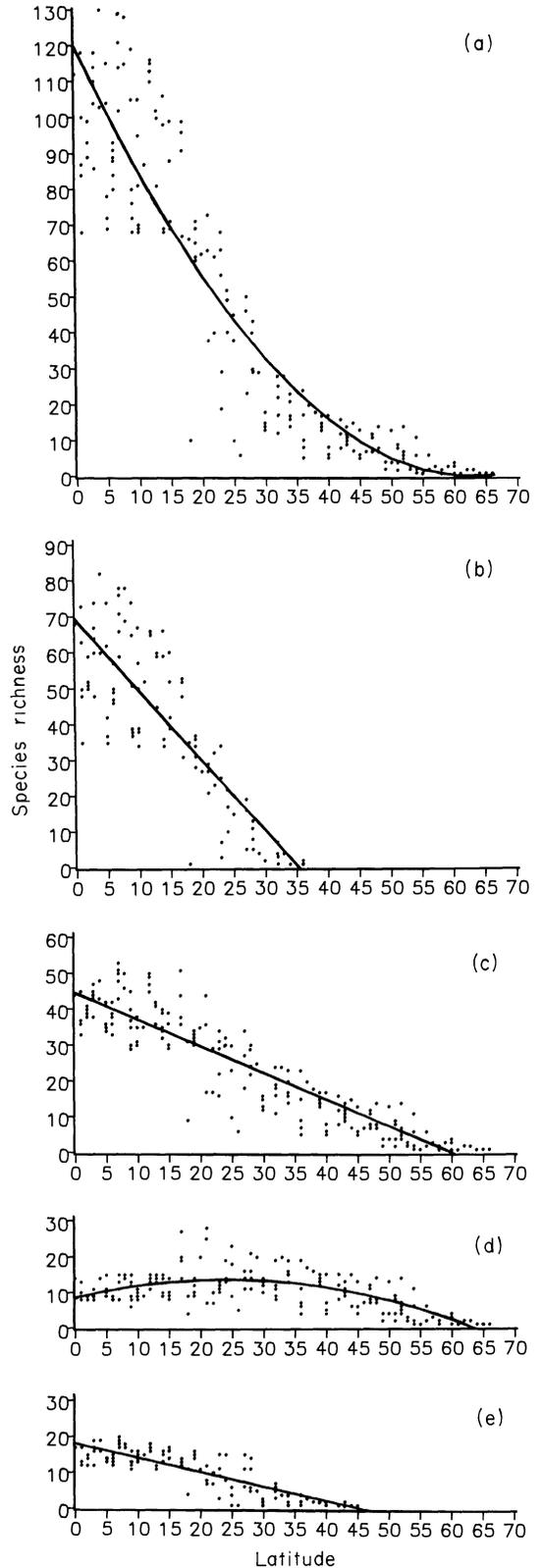


FIG. 2. Bat species density as a function of latitude for combined data from North and South America (a, all bats; b, phyllostomids; c, non-phylostomids; d, vespertilionids; e, molossids). The bold line in each graph represents the simple polynomial (see text for criteria) that best accounts for the variation in species densities (see Table 2).

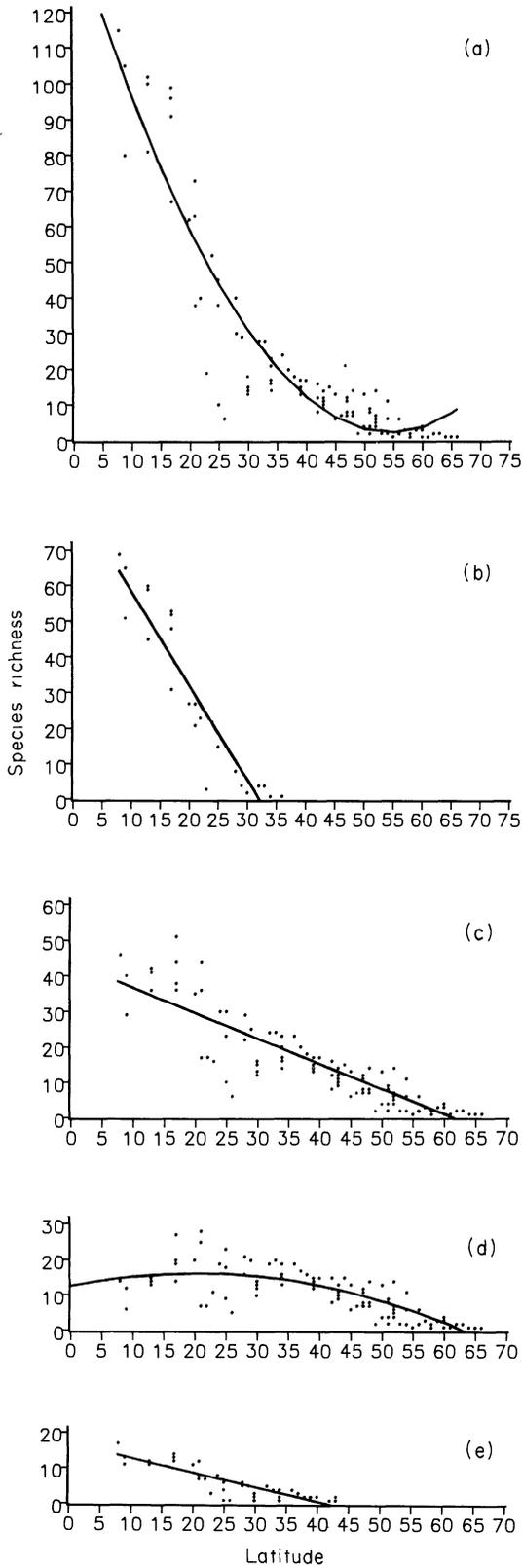


FIG. 3. Bat species density as a function of latitude for data from North America (a, all bats; b, phyllostomids; c, non-phylostomids; d, vespertilionids; e, molossids). The bold line in each graph represents the simple polynomial (see text for criteria) that best accounts for the variation in species densities (see Table 2).

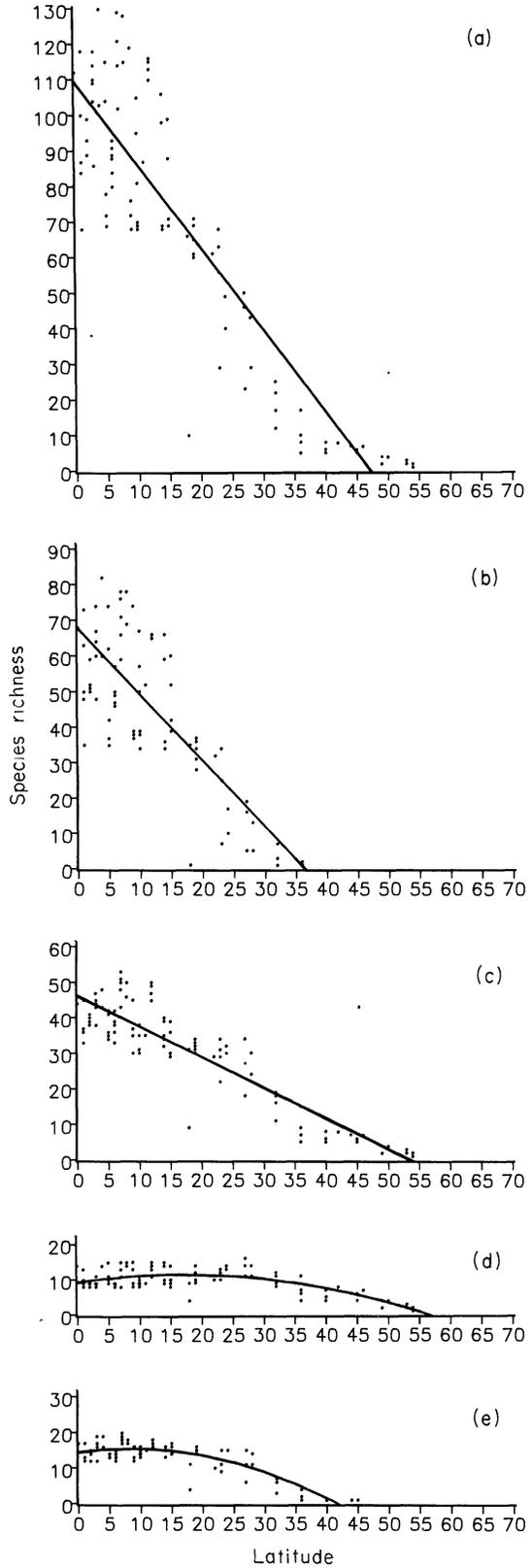


FIG. 4. Bat species density as a function of latitude for data from South America (a, all bats; b, phyllostomids; c, non-phylostomids; d, vespertilionids; e, molossids). The bold line in each graph represents the simple polynomial (see text for criteria) that best accounts for the variation in species densities (see Table 2).

		LONGITUDE			QUADRAT BAND		
		1	2	3	\bar{Y}	S TOTAL	
LATITUDE	1	ABCDE	ABCDE	ABCDE	5	00	5
	2	ABCDE FGHIJ KLMNO			5	71	5
	3	ABCDE	FGHIJ	KLMNO	5	00	15

FIG. 5. The effect of inter-quadrat variation in species identity and density on 'quadrat' and 'band' methodologies (see text for a complete explanation).

the two methods. The difference between results for band and quadrat methods was apparent for quadrupedal mammals, but not for bats. Although longitudinal variation in species composition can influence latitudinal patterns of species densities, it does not do so to an appreciable extent for North American bats (i.e. bat species composition does not vary much among quadrats within a latitudinal band).

We believe that quadrat and band methods each reveal unique information concerning latitudinal gradients and extend an example of McCoy & Connor (1980) to illustrate our contention (for the discussion that follows see Fig. 5). In part, both methods fail to incorporate aspects of the spatial variation in species density. As McCoy & Connor (1980) correctly demonstrated, a consideration of quadrat diversity alone would fail to detect that latitude 3 had 3 times the total species richness as latitude 1 (Fig. 5) because interquadrat variation in taxonomic composition is not integral to quadrat methodologies. On the other hand, a consideration of band totals alone (the method of McCoy & Connor, 1980) would fail to distinguish between latitudinal bands 2 and 3 because intra-band or longitudinal variation in species densities are not incorporated into band analysis. Neither method considers all of the information present in the data. We restrict our attention in this paper to quadrat methodologies, in part because McCoy & Connor (1980) previously demonstrated qualitative convergence between band and quadrat methods, and because we wished to assess characteristics of bat density gradients that band methodologies cannot reveal. In another paper, Willig & Sandlin (1989) extend this analysis to include band techniques and compare such results to those obtained here.

Species density trends

Compared to latitude, it is clear that longitude, biome richness, and area do not account for much of the variation among quadrats in bat species density (based upon multiple regression analyses). Our analyses show that latitude is an excellent predictor of total bat species density in the New World, accounting for approximately 81% of the variation among quadrats. Even vespertilionids, which exhibited a simple r^2 for latitude of 0.03, showed a marked increase in r^2 equal to 0.48 when a second degree polynomial was utilized.

Simpson (1964), Wilson (1974) and McCoy & Connor (1980) also found that latitude was the best predictor of bat species richness from among the variables that they tested. However, their studies included only North and Central America. Conclusions from these studies must be tempered because the observed trends may be the result of the particular geography or biogeographic histories of North and Central America, rather than the result of latitude and its correlates (e.g. incident solar energy, precipitation, periods of exposure to light). Our results demonstrate that despite the distinct biological and geological histories of North and South America, the pattern of increasing bat species density with decreasing latitude is present in both hemispheres of the New World. Similar analyses to those presented here for Eurasia and Africa, or Australia would provide further evidence concerning the factors affecting bat species density.

Our data indicate not only that latitude is the best predictor of bat species density, but also that biome richness, longitude, and area (as measured here) are poor in comparison. The low simple β and simple r^2 of each independent descriptor except latitude (Table 2) suggests that longitude, biome, and area were not excluded because of high communality or correlation with latitude. Even when we restrict our attention to Brazil, for which we have more finely resolved information on biome distribution, latitude is the primary descriptor of species density, except in the case of molossids. This suggests that habitat diversity may not be the critical characteristic of tropical zones that contributes to high bat diversity, or that the spatial heterogeneity measured by biome richness is too crude, even at the level used in the analysis for Brazil, to produce detectable results. In support of the former notion, Willig & Mares (1989) failed to identify biome-specific bat assemblages in Venezuela. Rather, bat species were highly eurytopic and usually occurred in two or more biomes. The exclusion of longitude from all of the multiple regression analyses for the New World further supports the notion of McCoy & Connor (1980) that potential longitudinal differences within latitudinal bands do not have an appreciable or consistent effect on bat diversity. This is in contrast to the results obtained for quadrupeds where longitudinal effects were pronounced. Moreover, Mares & Ojeda (1982) analysed distributional data on hystricognath rodents in South America, and concluded that neither latitude nor longitude was an important predictor of species densities. Instead, they concluded that the area within latitudinal bands (comparable to 'available space' of Anderson & Koopman, 1981) alone accounts for 'apparent' latitudinal trends in diversity. For all taxonomic groups of bats that we analysed, area exhibited quite low simple r^2 and at most contributed 3% to the variation in species density revealed by multiple regression analyses.

Organisms of lower vagility (e.g. many rodent species) would be expected to be more habitat-restricted, and consequently should exhibit species density patterns different to those elucidated for bats. In particular, area or biome richness ought to account for more of the variation in rodent species density than we found for bats. Birds, like bats, are vagile, and might be expected to respond similarly

to latitude, longitude, area, and biome richness. None the less, extensive migratory abilities characterize many bird species; and may strongly influence density patterns, resulting in low r^2 for any independent descriptor.

Many hypotheses (e.g. history, refugia, time, stability, habitat diversity), not all of which are mutually exclusive, have been developed to account for observed latitudinal trends in species density of various organisms (for reviews see Pianka, 1966; Osman & Whitlatch, 1978; McCoy & Connor, 1980). The data and analyses in our study, and in most previous studies as well, were designed to determine which of several general factors are good predictors of species density; as a result, they provide only limited information on the evolutionary development of species or their distributions. We feel that the strength of the latitudinal species density gradient in bats warrants careful consideration of factors directly associated with latitude (e.g. temperature) in any model attempting to account for bat distributional patterns (see McNab, 1969, 1983).

Our taxon-specific analyses provide information on the form and degree of response of particular bat taxa to latitude and suggest more specific factors that may affect diversity. Regardless of geographic focus, different bat taxa do not respond to latitude in the same manner (compare lettered graphs within Figs. 2–4). Although phyllostomids and non-phyllostomids both increase in a linear fashion with decreases in latitude, the rate of increase is consistently faster for phyllostomids than non-phyllostomids (compare graphs B and C within Figs. 2–4). Unlike other bat groups, vespertilionids do not achieve highest species densities at the equator, rather they are most speciose at mid-latitudes from approximately 15° to 30°. Of all bat groups responding linearly to latitude, molossids increase most slowly, and in South America, fail to increase beyond 15°. The large cosmopolitan insectivorous families do not increase in species richness in the tropics (Vespertilionidae, Fig. 2E), or conversely show especially slow rates of species increase with decreasing latitude (Molossidae, Fig. 2D) compared to New World fruit-eating bats (Phyllostomidae, Fig. 2A). Perhaps the combined effects of the foliage-gleaning insectivores (Phyllostominae) and other New World aerial insectivorous families (Mormoopidae, Emballonuridae, Furipteridae, Natalidae, Thyropteridae) have precluded the diversification of the more broadly distributed molossids and vespertilionids. Physiological constraints, on the other hand, seem to limit the range expansion by phyllostomids into temperate regions of North and South America (McNab, 1969, 1983).

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