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Areography of North American Fishes, Amphibians, and Reptiles

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ABSTRACT

Sizes of geographic ranges of species of freshwater fishes (635), amphibians (141), and reptiles (199) occurring north of Mexico in North America were measured and compared with each other and with ranges of birds and mammals. All groups have "hollow curve" frequency distributions in which most species have small ranges; and all groups have latitudinal gradients in which more species occur at lower latitudes. For fishes and amphibians the greatest density is in the southeastern United States and not the southwest. The frequency distributions of range sizes for amphibians and reptiles are approximately lognormal. The geometric means (in 10^5 km^2 units) for ranges of species in these groups are: fishes 0.82, salamanders (Caudata) 0.86, lizards (Lacertilia) 2.8, turtles (Chelonia) 4.1, frogs and toads (Anura) 4.6, snakes (Serpentes) 6.2, and the alligator (Crocodilia) 8. Comparable means for mammals and birds are 5.8 and 16, respectively. At most local areas in North America, the percentage of the continental fauna present for each of these groups is correlated with the mean size of the geographic ranges in the groups. Exceptions for certain localities or subgroups are of interest. Species of amphibians and reptiles occurring in places of higher diversity have smaller geographic ranges. Available space (probably chiefly related to climatic conditions) and analytical artifacts provide a better explanation than competition for this correlation. Fishes were not examined in this regard; adequate data have not been assembled. Amphibians and reptiles have a higher percentage of species that are North American endemics than do mammals and birds, which are groups with generally larger species ranges. On the average, fishes have smaller ranges than amphibians and reptiles but have a higher percentage of intercontinental cosmopolitan species (or a smaller percentage of North American endemics) than do amphibians and reptiles. This is because fishes have Arctic and coastal proclivities not present in the other groups.

INTRODUCTION

Areography is the study of geographic areas occupied by different species of animals and plants: Sizes and shapes of ranges, placement of ranges relative to each other and relative to latitudes, habitats, and other factors, and changes that occur in ranges with time are

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considered. The similarities and differences among different groups of organisms and how these may be related to the histories and attributes of the groups are of ecological and evolutionary interest.

In a study of birds (Anderson, 1984) hypotheses relating sizes of geographic ranges to competition, diversity, age of taxa, eurytopy, niche width, vagility, latitude, abundance, sizes of individuals, and trophic levels were briefly noted. All of these hypotheses, and others, need to be more explicitly formulated and tested with additional data in order to develop a more comprehensive and more unified theory. This report examines the North American ranges of fishes, Amphibia, and Reptilia and contrasts their areographic patterns with those reported earlier for mammals and birds (Anderson, 1977, 1984). The present analyses are limited to faunas north of Mexico and excluding islands south of Florida. The previous analyses of the "higher" vertebrates used data for North America south through Panama and Grenada. Comparisons between classes would have been easier if comparable geographic areas had been used, but the task of assembling comparable data (from widely scattered sources) for the "lower" vertebrates in the southern part of North America was formidable.

Data on freshwater fishes of the Greater Antilles have been summarized recently by Lee, Platania, and Burgess (1983). This ichthyofauna includes 59 native secondary freshwater species, 24 introduced primary and secondary freshwater species, and 50 marine intruders; 57 of the native species are Antillean endemics, the other two occur also on the mainland. However, omitted from the 59 native species and classified as marine intruders were about 20 species which were included in the "Atlas" (Lee et al., 1980). Only five species of freshwater fishes are known from the Lesser Antilles. Revision of this account to include Antillean data would further accentuate the preponderance of small geographic ranges among freshwater fishes.

I did review the Mexican checklists of Smith and Taylor (1945, 1948, 1950). The distributional data there are quite limited and are now out of date. The taxonomy is also dated and perhaps overly "split." However, a number of new species have been named from Mexico since then. Inclusion of Smith and Taylor's nominal species and a currently revised estimate would have approximately tripled the numbers in my analysis. Data on the Antillean herpetofauna are available (MacLean, Kellner, and Dennis, 1977; Schwartz and Thomas, 1975) and could be used in areographic analyses. Some accounts for states in Mexico (for example, Hardy and McDiarmid, 1969, for Sinaloa; and Duellman, 1965, for Michoacán) exist also. However, no comprehensive list for the entire area south of the United States has been published.

The first concern in this analysis is description; the data are being examined for patterns. Patterns that exist in the data may suggest hypotheses about causes and correlations which can then be tested, either with data now available or in later studies.

ACKNOWLEDGMENTS

I am grateful to Mr. David S. Lee, Drs. Charles S. Anderson, Don E. McAllister, C. L. Smith, and Richard G. Zweifel for advice and information. I also thank the student volunteers who helped in compiling data and in computations, especially Ms. Mary Evensen, Ms. Nancy Olds, and Mr. Russel D. Robbins. Dr. James N. Layne made available the fine ecological library at the Archbold Biological Station near Lake Placid in Florida, on my visit there in 1984.

Some of these ideas were presented in a symposium at the Field Museum of Natural History in 1978, and comments by Dr. David G. Raup and others there stimulated my work in this area.

METHODS

I used the "Atlas of North American freshwater fishes" (Lee et al., 1980) as my primary source of information for data on fishes. The following rules were applied in measuring the ranges:

1. The entire range (not just the part of the range within the continental area defined above) was included for each species used.

2. Areas from which a species has been extirpated in historic times were included.

3. Areas into which a species has been introduced by man were excluded.

4. Species introduced into North America from other continents were excluded.

5. Species with inadequate data for total ranges were excluded. The inadequacy was with the parts of ranges beyond the maps of the "Atlas," whether in Eurasia, south of the United States, or at sea.

6. Any species with more than half of its range outside the continental area as defined, whether this involved oceanic areas or freshwater areas in Mexico or Eurasia, was excluded.

7. The published maps have different scales and the scales are not shown on the maps. Therefore, some known dimension (such as the length of the northern border of a given state) was selected for each printed map and then measured on the map. A border was then drawn around each species range (most maps for fishes show dots but not borders). A grid of squares on transparent film was placed over each map and the squares that were more than half occupied by the range of the fish were counted. Given these values, a simple computer program was written to calculate the range for each species and then round the value to one significant figure in units of square kilometers.

On the basis of the above rules, 132 species were excluded, and 635 species of fishes were selected for analysis; 613 of these were teleosts. The exclusion of the 22 nonteleosts would have made the group taxonomically neater (less polyphyletic), but would not have altered the areographic results appreciably.

The numbers of species of fishes excluded from the analysis for the above reasons are roughly as follows:

25 with more than half of their ranges in Eurasia
43 with more than half of their ranges south of the United States
9 anadromous species with large and poorly known oceanic parts of their ranges
20 principally oceanic in distribution
32 introduced from outside the area of study (five of these were introduced from Central America and are therefore North American endemics in a broader sense).

TABLE 1

Ranges of Groups of Vertebrates in North America North of Mexico. Means Are in Units of 10^5 km^2

Group	n	Geometric Mean	Arithmetic Mean
Cypriniformes	261	1.1	—
Perciformes	196	0.76	—
Other fishes	178	0.58	—
All fishes	635	0.82	7.3
Amphibia			
Caudata	86	0.86	4.9
Anura	55	4.6	11
Reptilia			
Lacertilia	78	2.8	6.9
Chelonia	38	4.1	11
Crocodilia	1	8	8
Serpentes	82	6.2	13
Mammalia	315	5.8	—
Aves	609	16	—

These exclusions total 129. A few other species were excluded because their ranges were uncertain. The total fish fauna (including both those excluded and the 635 species used) is about 777. The "Atlas" did not include strictly marine species along the coasts of North America. If these were included the North American ichthyofauna would be much larger. The list of the American Fisheries Society (1980) included 2268 species of fishes from the United States and Canada (both freshwater and marine fishes of the continental shelf).

In some respects, fishes are a more diverse lot than amphibians or reptiles. There are three classes and more than 20 orders in North America. The data were tallied order by order. Most orders are represented by relatively few species (as is generally true for the taxa within higher taxonomic groups, Anderson, 1974). Geometric means were computed (table 1) for the two largest orders, the Cypriniformes and the Perciformes, which together include 72 percent of the 635 species analyzed.

The principal sources for data on amphibians and reptiles were the field guides of Conant (1958) and Stebbins (1966), supplemented by the more precise maps in the "Catalogue of American amphibians and reptiles" for species with published accounts.

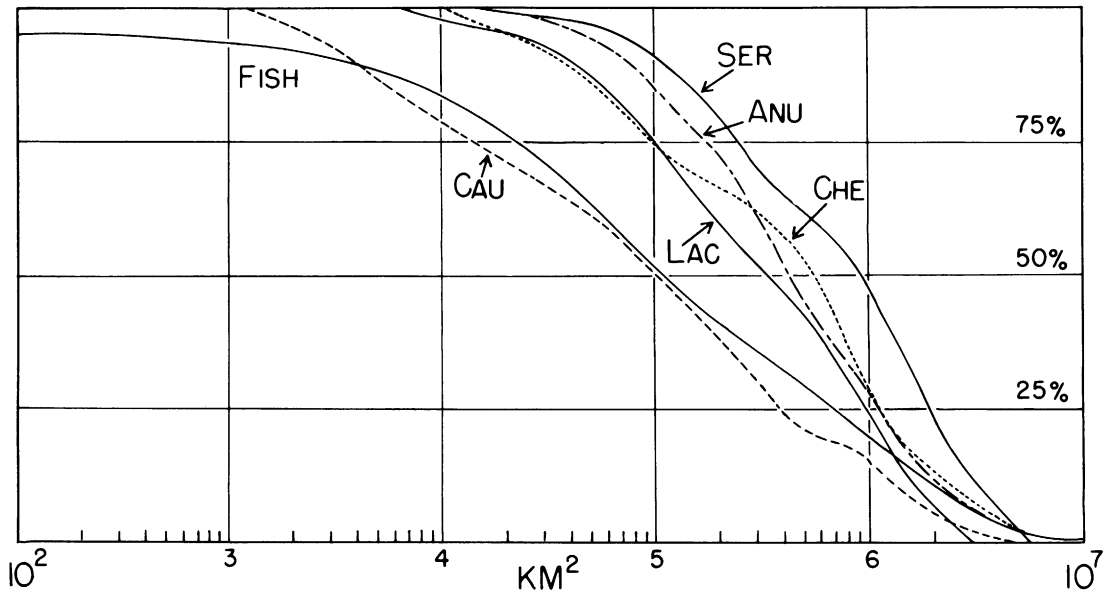

FIG. 1. Cumulative plots of ranges of species of North American "lower" vertebrates of several groups. Abscissa shows sizes of geographic ranges of species on a logarithmic scale. Ordinate shows percentages of species with ranges larger than values shown on abscissa. Groups of species are: fishes, Caudata, Anura, Lacertilia, Chelonia, and Serpentes. Original data were grouped as explained in text and would lie as a series of irregular steps if plotted. With six taxonomic groups on one graph, the stepped plots would be difficult to disentangle visually. Curves therefore were drawn by hand to make visual comparison of the groups easier.

The species selected were 141 amphibians and 200 reptiles. The same rules outlined above were applied in this selection, except that boundaries were already present and did not need to be drawn by me on the herpetological maps.

Since it was apparent that the Caudata differ noticeably from the Anura and there were less differences between orders of reptiles, data were analyzed separately for each of five orders of amphibians and reptiles.

RESULTS

The results are presented as answers to a series of questions.

How do the groups of "lower" vertebrates compare in sizes of geographic ranges of their species? A cumulative plot on a percentage scale shows the relative sizes of ranges in different groups (fig. 1). The geometric and arithmetic means and numbers of species included in the samples of groups are given in table 1. Figure 2 illustrates the relative sizes of the different orders of magnitude in km^2 for comparison with the values in figure 1 and elsewhere.

Geometric means for Cypriniformes and Perciformes are close to that for all fishes. Differences between orders of fishes were not apparent in scanning the raw tally sheets. This situation contrasts with the condition among amphibians, reptiles (to a lesser degree), mammals, and birds (Anderson, 1984) in which the species of some orders have appreciably larger ranges than those of other orders.

The difference between the Caudata and the fishes is negligible. The Anura and the three orders of Reptilia graphed have noticeably larger ranges than fishes and salamanders. Among these groups, the Serpentes have the largest ranges.

Geometric means for mammals and birds were recomputed using only species occurring north of Mexico so results would be comparable with those for the "lower" vertebrates (table 1). Mammals have smaller ranges

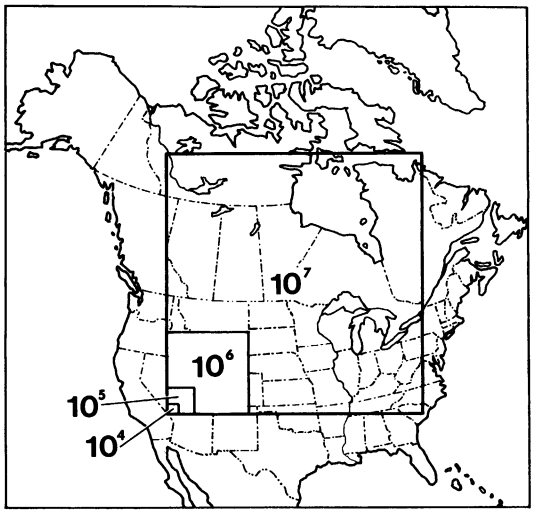

FIG. 2. Map showing relative sizes of four successive areas an order of magnitude apart (in km^2) for comparison with values given on logarithmic scales used in figure 4 and elsewhere. For example, figure 4 shows that half the species of both fishes and salamanders have ranges smaller than 10^5 km^2 and figure 3 shows the size of such a range relative to the size of the continent. The square for 10^6 is 1000 km on each side.

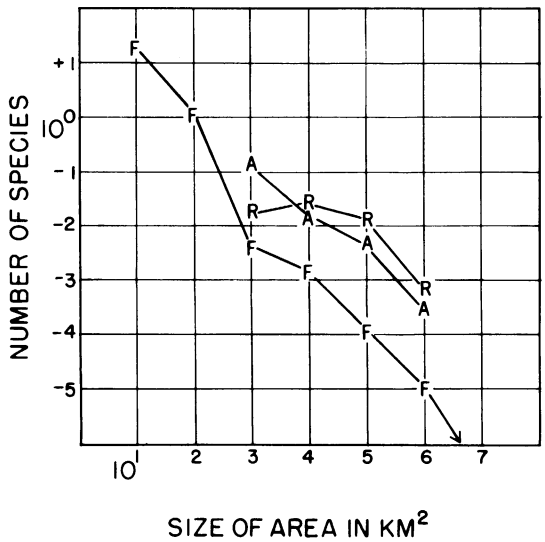

FIG. 3. Area–rarity correlation. Graph for North American fishes, amphibians, and reptiles showing numbers of species (averaged for each succeeding order of magnitude) having ranges of any given size. Counts of species are expressed in terms of the number per 100 km^2 increment. There is a distinct negative correlation between size of range and number of species having ranges of that size in each of the three groups.

than snakes; birds have ranges more than twice as large as snakes.

A noncumulative frequency plot on a log scale (fig. 3) illustrates the degree of increasing rarity of species having larger ranges. In all of these groups there are more species that have smaller ranges than have larger ones. As a rough approximation, the number of species occupying geographic ranges of a certain size tends to decrease by an order of magnitude with each increase of range size by an order of magnitude. This occurs also among North American mammals and birds. Among the groups compared in this way, the reptiles are least typical.

If a distribution of this sort is plotted with horizontal and vertical arithmetic scales, a classic "hollow curve" results and most of the relevant pattern shown in figure 3 is not apparent. This is the reason for plotting results on a log scale.

Is the distribution lognormal? A cumulative plot of percentages on a probability scale indicates whether a distribution is lognormal (fig. 4). Since the points for reptiles on this graph fall close to a straight line, the distribution is approximately lognormal. A lognormal distribution occurs in North American birds, but not in mammals. There are differences of opinion about the significance of a lognormal distribution. It has been argued in an ecological context that a lognormal distribution reflects an equilibrium and that departures therefrom indicate disturbance (Ugland and Gray, 1982), but this may not be relevant in the present context. See also Discussion.

Is the "area–percentage hypothesis" supported? I observed earlier (Anderson, 1984, fig. 7) that the percentages of continental species of different groups (such as birds or mammals) present in different local areas are positively correlated with sizes of geographic ranges in each group. For example, if 9 percent of North American birds and 6 percent of the mammals are present in a given place and if a comparable ratio of these percentages

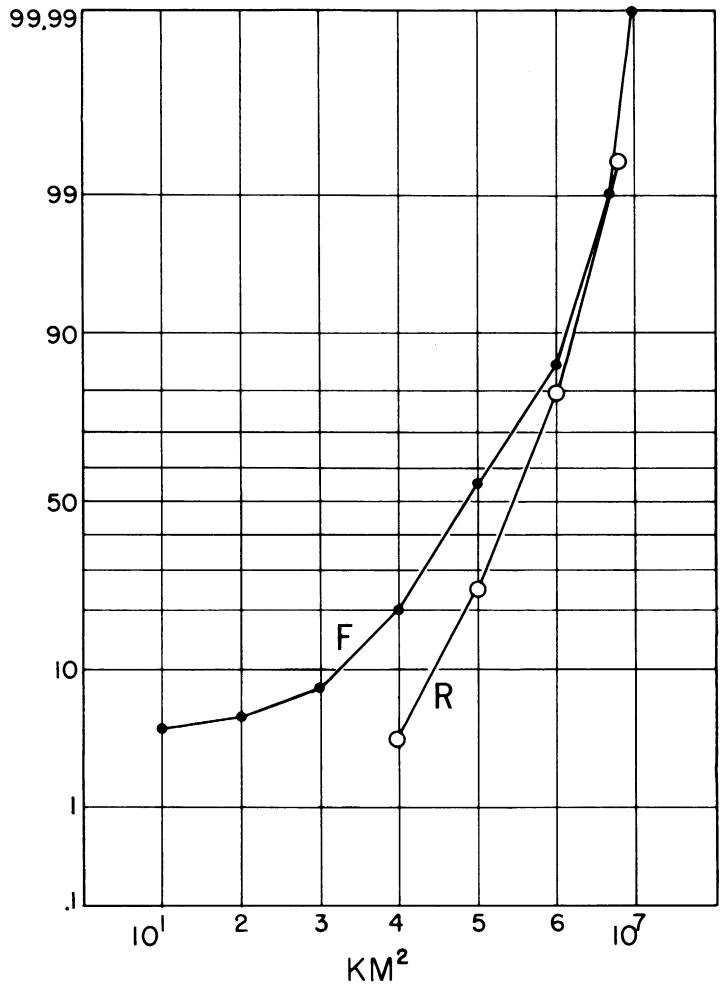

FIG. 4. Cumulative percentages of species in ×10 (1–10, 11–100, 101–1000, etc.) log classes of geographic ranges in km² (abscissa) are plotted (percentages on a probability scale on the ordinate, cumulative to each point) to see whether distributions are lognormal. This would be the case if points fell on a straight line. Fishes (F) and reptiles (R) are plotted. Neither is precisely lognormal although reptiles approach that condition. Amphibians, if plotted, would lie between the curves shown.

occurs at other sample sites, then birds probably have larger geographic ranges than mammals. I hypothesized, therefore, that these percentages would be useful (in the absence of more direct measurements of ranges) in predicting the sizes of ranges in different groups. The correlation needs to be quantified and tested with larger sets of data, the relationship is not absolutely linear and exceptions in certain localities or subgroups are of interest in themselves, as will be noted below. This correlation also suggests the following reciprocal prediction: if the species of one group have larger ranges than those of another group, assuming generally similar patterns of distribution in the two groups (for example, as regards hollow curve frequencies and latitudinal gradients), then a larger percentage of fauna of the continent of the first group will be present in most local areas examined. If the positive area–percentage correlation is not present in comparisons among groups or if certain data points deviate from the relationship (as in fig. 5), this suggests a

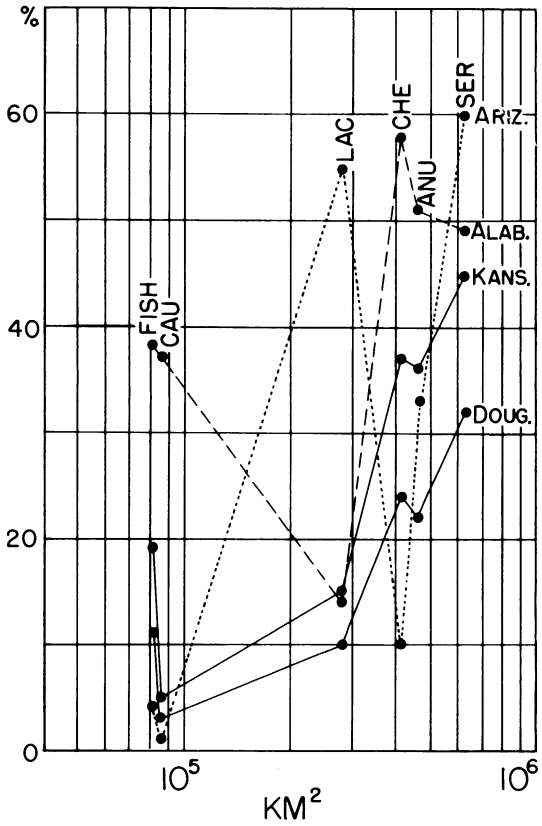

FIG. 5. Area–percentage correlation. Groups that include species with larger geographic ranges tend to be represented in local areas by larger percentages of the continental fauna. Geographic ranges are expressed as geometric means of the sizes of geographic ranges of all North American species of each group and are plotted in km^2 on the abscissa. Percentages of the continental fauna for each group are shown on the ordinate. Four sample areas are labeled at the right and the points for each area are connected by lines; areas are Arizona, Alabama, Kansas, and Douglas County, Kansas. The following groups are shown: fishes, Caudata (CAU), Lacertilia (LAC), Anura (ANU), and Serpentes (SER).

difference between the groups in the pattern of placement of the species ranges within the continent.

The area–percentage hypothesis is here tested with herpetological data by plotting the species densities of amphibians (fig. 6) and reptiles (fig. 7) in North America. These are adapted from the detailed maps of Kiester (1971). A comparable map has been prepared

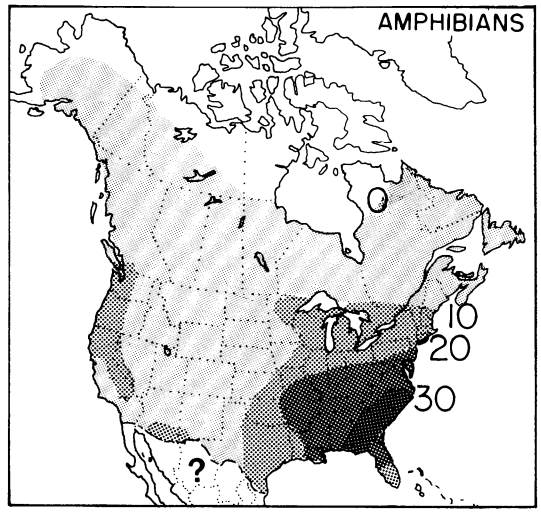

FIG. 6. Map showing species density of North American Amphibia. Percentages of species of the entire continental fauna that are present in different areas are shown. Percentage figures shown are equivalent to counts of 0, 14, 28, and 42 species, respectively (adapted from Kiester, 1971).

by McAllister et al. (in press), and the pattern resembles that for amphibians in having highest densities in the southeastern states, although in the fishes the area of greatest den-

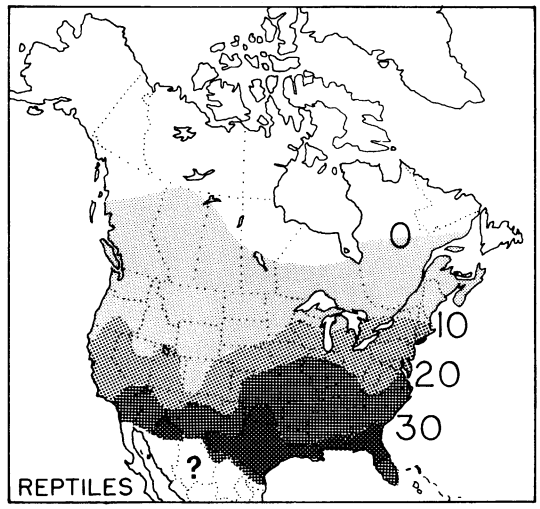

FIG. 7. Map showing species density of North American Reptilia. Percentages are used, as in figure 1, for comparison. Values shown are equivalent to counts of 0, 20, 40, and 60 species, respectively (adapted from Kiester, 1971).

TABLE 2
Percentages of the Continental Fauna Occurring in Selected Areas for Groups of "Lower" Vertebrates[a]

Area/Group	Source	No. of Species	Percentage
Douglas Co., KS			
Fishes	Cross, 1967	71	11
Amphibians			
Caudata	Collins, 1982	3	3
Anura	Collins, 1982	12	22
Reptiles			
Chelonia	Collins, 1982	9	24
Lacertilia	Collins, 1982	8	10
Serpentes	Collins, 1982	26	32
Kansas			
Fishes	Cross and Collins, 1975	123	19
Amphibians			
Caudata	Collins, 1982	8	9
Anura	Collins, 1982	20	36
Reptiles			
Chelonia	Collins, 1982	14	37
Lacertilia	Collins, 1982	12	15
Serpentes	Collins, 1982	37	45
Alabama			
Fishes	Lee, Platania, and Burgess, 1980	241	38
Amphibians			
Caudata	Mount, 1975	32	37
Anura	Mount, 1975	28	51
Reptiles			
Chelonia	Mount, 1975	22	58
Lacertilia	Mount, 1975	11	14
Serpentes	Mount, 1975	40	49
Arizona			
Fishes	Lee, Platania, and Burgess, 1980	26	4
Amphibians			
Caudata	Mount, 1975	1	1
Anura	Mount, 1975	18	33
Reptilia			
Chelonia	Mount, 1975	4	10
Lacertilia	Mount, 1975	43	55
Serpentes	Mount, 1975	49	60
Lauderdale Co., AL			
Fishes	Lee, Platania, and Burgess, 1980	133	21

[a] These data plotted in figure 5.

sity lies between the Appalachians and the Mississippi River instead of eastward from the Appalachians as in the amphibians. Other data are in table 2 and figure 5.

At most places in the United States and southern Canada the percentage of reptiles present is greater than that of amphibians. In parts of northern Canada and Alaska one or more amphibian species occur where no reptile occurs, thus reversing the percentages. The generality of the area–percentage hypothesis is supported, and the exceptional areas in Canada and Alaska suggest a difference from the general pattern within the continent, namely that two or three anurans live much farther north than any reptile. Why they do this is another interesting question.

The species of amphibians that occur north of the range of reptiles (and their ranges in millions of km^2) are *Bufo americanus* (4), *B. boreas* (3), *Rana pipiens* (10), *R. sylvatica* (7), *Pseudacris triseriata* (8), and *Taricha granulosa* (0.4; this, the only salamander, reaches southern Alaska along the west coast only). The four anurans are not only the northernmost species but the species with the largest ranges among amphibians. "*Rana pipiens*" is actually a complex of species, which I have not attempted to sort out here.

In figure 5 the groups with larger average ranges (to the right in the graph) are represented by higher percentage values, but there are conspicuous exceptions. In Arizona, lizards are unusually well represented and turtles are relatively few. In both of the samples from Kansas (one for the entire state and one for Douglas County only) fishes are well represented in comparison to salamanders and lizards. In Alabama, the pattern seen in Arizona is reversed; there are relatively many turtles and few lizards. Fishes and salamanders are also well represented in Alabama.

Is the "area–diversity hypothesis" supported? Rosenzweig (1975) hypothesized that the species occurring in places of higher diversity have smaller geographic ranges. Competition, available space, methodology, and possibly other factors, may influence such a negative correlation. The roles of competition and available space in causing such a correlation were discussed at length earlier (Anderson and Koopman, 1981). The problem of methodology was mentioned only briefly and warrants more discussion.

Under certain conditions, the method used

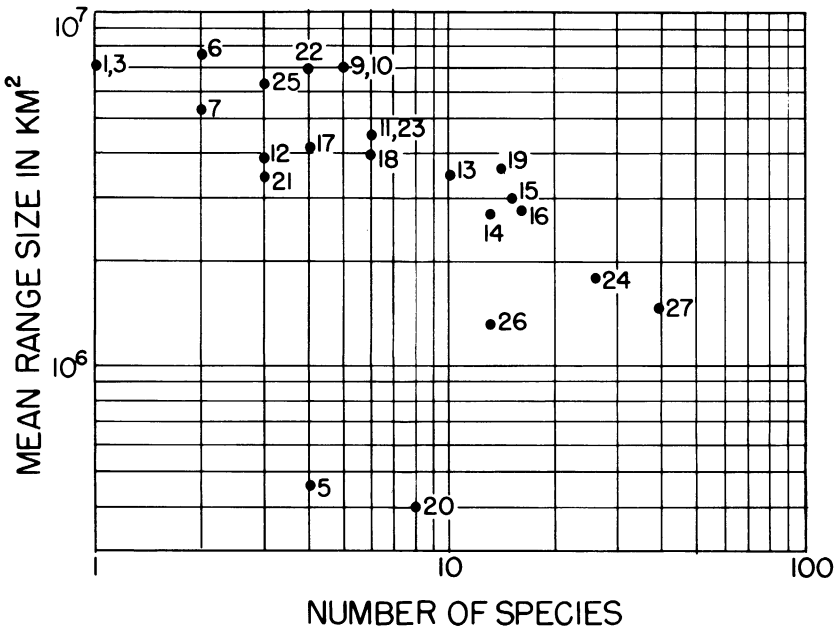

FIG. 8. Area–diversity correlation. Diversity of North American Amphibia (numbers of species shown on abscissa) at different sample sites. The numbers refer to sites shown on a previously published map (Anderson and Koopman, 1981). Missing numbers are for sample sites with no amphibians. Diversity is plotted against the average range size (geometric mean of sizes of ranges of all species present for each site, on the ordinate in km^2).

here would tend to create a negative correlation. Since a given widely ranging species will occur at more sample points than a species with a smaller range and since many of the species in the faunas analyzed here do occur at more than one sample point, the measurements (geometric means) for range sizes of the different points are not entirely independent.

A sampling problem of the same general nature was noted by Connor and McCoy (1979, p. 816) when they reported that "an inverse relationship between the linear correlation coefficient [comparing numbers of species in a sample and the size of the sample area] and latitude may be due to high latitude species possessing greater geographic ranges; hence few new species are encountered when we examine large versus small areas." This particular "species–area" relationship has long been a problem in ecology.

If ranges of species were randomly placed on the continent, a negative correlation of diversity and range size would not be expected (a correlation near zero would result). No major group of North American vertebrates, however, is distributed randomly. All show a general pattern (with local exceptions) of increased diversity farther south, and in all groups the frequency of occurrence of species with smaller ranges is generally greater than those with larger ranges. These two major areological patterns influence the correlation of diversity and range size. Since there are relatively few species with large ranges and since these few tend to occur at more sample points, increased diversity is achieved by the addition of species having smaller ranges. Also, the mean of the ranges for all species in the sample will decrease as the number of species increases.

The area–diversity correlation is examined in figures 8 and 9 for amphibians and reptiles, respectively. The numbered sample points are the same ones used in earlier studies of mammals (Anderson and Koopman, 1981, fig. 1) and birds (Anderson, 1984). The correlation is negative in both cases, and is higher for the

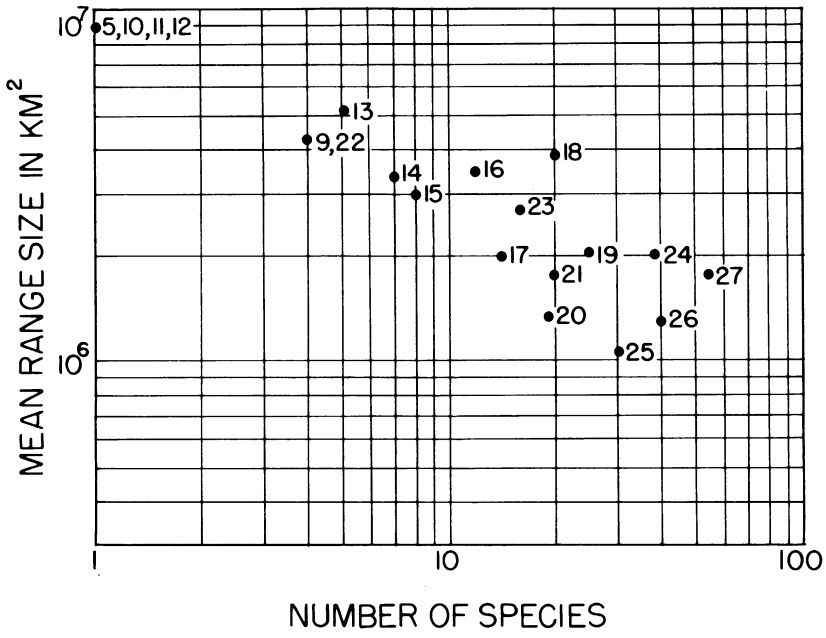

FIG. 9. Area–diversity correlation for North American Reptilia (same conditions as those in fig. 8).

reptiles than for the amphibians. Correlation coefficients, calculated using log values, are −.925 for reptiles and −.497 for amphibians. I have not prepared a similar analysis for the fishes. In general, species ranges are smaller for species from more diverse faunal samples. Whether this generality applies to species of these groups in other continents or to species of other groups anywhere can be answered only by studying those situations.

The relationship of diversity and range size has been critically examined in North American mammals and birds and in South American bats (Anderson, 1977, 1984; Anderson and Koopman, 1981). Why does this pattern occur in North American vertebrates? Plausible factors that have been hypothesized include competition (examined and largely rejected by Anderson and Koopman, 1981), available space (seemingly important, at least for North and South American mammals), and the method of grouping data (i.e., an artifact of analysis). To the extent that the observed negative correlation of diversity and range size results from the areological patterns, the problem becomes how to explain the patterns (for example, the latitudinal gradient in diversity and the hollow curve distribution of range sizes) rather than how to explain the negative correlation of diversity and range sizes seen in figures 8, and 9.

The data support the "diversity–area hypothesis" in a descriptive sense but do not provide evidence for possible causes thereof.

How do groups compare in regard to degrees of North American endemism? At least 26 of the species of fishes in North America north of Mexico are known to occur also in Eurasia and at least 27 occur also in South America. These 53 species comprise 7 percent of the total of 764. Two amphibians and about seven reptiles native to the United States also range into South America and no species ranges into Eurasia. These nine species comprise about 3 percent of the total of 340.

Taxonomic revision might combine nominal species of snapping turtles of the genus *Chelydra* or make similar changes in other cases. These changes probably would not raise the percentage much above 3 percent of the herpetofauna. The 7 percent for fishes and 3 percent for amphibians and reptiles are not exactly comparable to the figures of 13 percent and 50 percent derived earlier (Ander-

son, 1984) for mammals and birds, respectively, because all of North America was analyzed for these groups. If data were available for the "lower" vertebrates, using the larger area would increase both the number of species in the fauna and the number that occur in both North and South America. Whether use of the entire continent for the "lower" vertebrates would have increased the percentages of species co-occurring in North and South America (and, if so, by how much) is not known. Zweifel (personal commun.) has estimated that it probably would not, because of the large number of Central American endemics. It is clear that birds are notably more cosmopolitan than the "lower" vertebrates and perhaps the mammals also are.

The reason that fishes, despite their small average ranges, have larger percentage of cosmopolitan species (intercontinental in this case) than do amphibians and reptiles is that some fishes have Arctic or coastal proclivities. This ability to occupy more northern habitats has produced Holarctic distributions for certain fishes and the ability to use estuarine as well as freshwater habitats has produced transamerican (North and South) distributions for certain other species of fishes. The analysis of freshwater fish provides a somewhat comparable fauna for comparison with the mostly terrestrial groups of vertebrates but it provides a distinctly narrower viewpoint of fishes as a whole. The strictly marine fishes that border on both North and South America are about two to three times as numerous as the freshwater species. For example, Villa (1984) reported 196 freshwater fishes in Nicaragua and about 500 marine species nearby; and the American Fisheries Society (1980) reported 2268 species for Canada and the United States, and about one-third of these were freshwater fishes.

How do the latitudinal gradients compare in different groups? The latitudinal gradient in species density of North American freshwater fishes has been shaped by geographic, geological, and climatic factors (as recently documented by McAllister et al., in press). Data in table 2 (71 species in Douglas County in eastern Kansas, and 133 in Lauderdale County in northern Alabama) suggest that there is a north to south gradient of increasing species density. However, Arizona had only 26 native species (some of these may be extinct now). Arizona has had about three times as many species introduced as were originally native (Minckley, 1973). Introductions have changed the ichthyofauna drastically in areas like Arizona and have increased the ranges of species that have been widely introduced. (As noted earlier, areas of introductions were not included in the measured geographic ranges of species.) A detailed map and ample discussion of species density for much of the continent are available in McAllister et al. (in press).

The gradients for amphibians and reptiles are shown in figures 6 and 7. Amphibians, like the fishes and unlike the reptiles, are less diverse in the arid southwestern states than a strict latitudinal gradient would predict. Species density presumably increases southward into Mexico. Hardy and McDiarmid (1969) studied the herpetofauna of Sinaloa on the west coast of Mexico and recorded 121 species (if introduced species and marine species are omitted), which is slightly more than the 115 species recorded for Arizona and less than the 163 species reported (Duellman, 1965) for Michoacán in southern Mexico. Of the 163 species in Michoacán, only 23 occur in the United States.

Latitude affects animal distributions only through various environmental factors such as temperature and light, and the importance of latitude may have been overemphasized in the literature. It is desirable to compare carefully such influences with various attributes of the animals and with other environmental factors.

DISCUSSION

Some discussion on possible meanings or causes of the patterns described is in order, although a more detailed analysis is being postponed to a later paper on the theory of range size (RS) distributions.

A host of questions (and few satisfying answers) comes to mind.

Why are there different numbers of species in different groups?

Why does each group have the numbers of species it has rather than a larger or smaller number?

Why are species densities different in different areas?

Why is the percentage of the continental fauna that is present in a given local area different for different groups?

Why are there more species with smaller ranges than with larger ranges?

How useful are particular explanations of particular cases?

What more general models can be formulated?

The phenomena addressed by these questions have both short-term and long-term aspects. The short-term tends to be of ecological interest and the long-term of evolutionary interest. Evolution has an important "historical" or time component that is less important in an ecological context. It is easier to focus on one aspect and to ignore the other, than to integrate the two, although integration should be our eventual goal.

Smaller ranges have been associated (in one context or another) with the following (see Anderson, 1984, for a brief commentary and selected references): (1) more competition; (2) more diversity; (3) younger taxa (geologically or phylogenetically); (4) stenotopy (for example, narrower physiological tolerances); (5) narrower ecological niches; (6) less vagility (mobility in terms of both behavior and functional morphology); (7) lesser latitudes (because of warmer climates, less extreme seasonal variation, or other factors); (8) lower population density; (9) smaller individuals (see also McAllister et al., in press, for data on fishes); (10) lower trophic levels; (11) less available space; and (12) patchier distributions.

There are other factors that may be important in certain groups or in general; this list is not exhaustive.

The author of a textbook may easily select examples to illustrate all of these relationships. It is nearly impossible, however, to find well-documented studies of appropriate sets of data that will test how general such correlations are.

Multivariate methods help in sorting out effects, however it is difficult to get a good set of data together on even one factor (for example, on range sizes of an order of reptiles) and the difficulty is multiplied if one also needs independent measurements of competition, geological age, stenotopy, vagility, or whatever. Most of the work lies ahead of us. The complexity of the task is illustrated by Pianka's (1977) correlation of species densities of reptiles (1), birds (2), and mammals (3), average annual sunfall (4), average annual precipitation (5), and average annual actual evapotranspiration (6) in North America. He found significance in his data for all paired correlations except 1 versus 3, 2 versus 4, and 4 versus 6. Kiester (1971) correlated 1 and 3 and showed that reptiles become more diverse from west to east, whereas mammals become more diverse from east to west across the central United States. McAllister et al. (in press) used multivariate methods to correlate species density of fishes with geographic and climatic variables and found that density increases with temperature, precipitation, and the humidity of the summer season and decreases with latitude, longitude, and fogginess.

Even a casual review of the hypotheses suggested above reveals that they may lead to contrary predictions. The hypotheses need to be tested with new data and to be reconciled with each other. The process of developing hypotheses from observed correlations should go beyond asserting that what has been observed in one set of data is to be expected in another set. Causes should also be considered, although this is not always easy to do. Values of A and B may be highly correlated in a set of data because A causes B, because B causes A, because A and B are caused by C, or fortuitously. The scientific process, as I perceive it, is hypothetico-deductive as well as inductive; hypotheses originate in theory as well as observation.

A hypothesis will be more useful in advancing knowledge if it is formulated as a prediction that can be tested with data from other groups. For example, if we are to explain the small ranges of fishes in comparison to those of reptiles in terms of the relative isolation of watery habitats, then we should first predict that other aquatic organisms will also have small ranges and, second, suggest groups for further study. We return to this below.

From these and earlier studies it is clear that all classes of vertebrates in North America have gradients in latitudinal species di-

versity; there are more species in warmer and more southern areas. It is also clear that each of the classes has a hollow curve frequency distribution; there are more species with smaller ranges than with larger ranges.

Other continents also exhibit greater diversity in more tropical parts, however the situation is less clear for Australia. Recher (1969) noted a latitudinal gradient in density of bird species there, however Shall and Pianka (1978) reported that latitudinal species density gradients generally do not increase toward lower latitudes for Australian terrestrial vertebrates.

The basic latitudinal gradient in reptiles in North America is clear (fig. 7, adapted from Kiester, 1971). The gradients in amphibians and fishes exist in a general way, but the southern part of the United States has a much higher density in the southeast than in the southwest (fig. 6, adapted from Kiester, 1971; McAllister et al., in press). Latitudinal gradients are known in many groups of organisms other than vertebrates. Possible causes have been discussed by various authors, but no clear consensus as to causes has emerged. Probably, it is different factors that are of major importance in different groups. Both Kiester (1971) and McAllister et al. (in press) have correlated various environmental factors with species density.

It may be postulated that freshwater fishes as a group have generally smaller geographic ranges than any other class of vertebrates in North America because water is less continuously distributed than land. This relative discontinuity may operate to isolate local populations (short-term) or to accelerate evolution of new species having relatively smaller ranges (long-term). In spite of this, some species of freshwater fishes have large ranges. If the factor postulated here limits the range sizes of fishes, we might predict that the more aquatic members of other groups will have smaller ranges than their less aquatic "peers." I tested this prediction with data for Chelonia and Caudata.

Since most turtles are more or less aquatic, I computed the geometric mean of the ranges of the most terrestrial North American turtles (five species of *Terrapene* and *Gopherus*). This mean is 6.8×10^5 km^2, which is slightly larger than the mean of 4.1×10^5 for turtle species ($n = 38$) in general. The geometric mean of the ranges of the 12 most aquatic species of salamanders is 5.3×10^5 km^2, which is actually larger than the mean of 8.3×10^4 of salamanders (86) in general. All of these values are greater than the geometric mean for fishes (table 1) of 8.2×10^4 km^2. There are only a few aquatic lizards in the world, and none in North America, and it may also be noted that the (terrestrial) lizards of North America have smaller ranges than the mostly aquatic turtles. Whatever confidence we may have had in the hypothesis that an aquatic habitat (or its discontinuity) tends to cause smaller ranges is reduced by these data. Other data and other hypotheses may well be brought to bear on this question later.

Perhaps both fishes and salamanders have small ranges because they occupy relatively restricted habitats in which the limiting factors are different. Before this hypothesis can be tested the terms must be defined and quantitative measurements devised. What is a "relatively restricted habitat" and how can it be measured? What is a "limiting factor" and how can it be measured? Unless evidence beyond the small size of ranges being considered can be found, the explanation (or hypothesis) contributes little beyond some additional terms and a small circular argument.

The mere occurrence of hollow curve distributions does not help in comparing ranges of different groups because hollow curve distributions occur in all groups and also in a great variety of other situations, including the numbers of individuals of different species in ecological samples, numbers of species belonging to more inclusive taxa (such as genera) in taxonomic classifications, atoms of different elements in the solar system, and names in telephone books (Anderson, 1974).

Various unrelated mechanisms and chance can generate hollow curve distributions including lognormal distributions. These processes were discussed in theoretical and mathematical terms by Boswell and Patil (1971, see also references cited therein and papers by other authors in the same volume). I will attempt in a later paper to formulate a more general model for such distributions in data on geographic ranges of species.

Nevertheless, there are differences in de-

tails of the distributions in different groups, which may provide clues or suggest hypotheses for testing.

The fish fauna includes an unusually large number of species with extremely small geographic ranges (46 species, or 7.2% of 635 species, have ranges of less than 1×10^3 km^2). In comparison, among the amphibians and reptiles only a few species of salamanders have ranges smaller than that value. Some of these were distinguished taxonomically since the summaries of Conant and Stebbins were published and were not included in my original analysis.

McAllister et al. (in press) have used the data from the "Atlas of North American freshwater fishes" for a broader analysis of faunal patterns than I have done here. They included an examination of range sizes and stressed the hollow curve range-size distributions discovered (independently of my work). Some comparisons of their results and mine are interesting because the sampling and measuring procedures were somewhat different. They measured ranges of 144 species (randomly selected from a larger sample of 501 species of fishes) by estimating the proportion of each state or province it occupies, multiplying this by the known range of the political unit, and then summing the values. They also estimated ranges of 501 species by counting the occupied one degree quadrats and multiplying by an average quadrat size (at 36°N lat.). Their larger sample of 501 species was somewhat biased against large ranges by the omission of some widely ranging species (for various reasons, as they pointed out) and by the truncation of the analysis at about 48°N lat. My sample included 635 fishes and their entire ranges, so my estimates should be larger than theirs. Considering these variations, our independent measurements are reasonably consistent. Comparative values (all in units of 10^5 km^2) are:

	Arithmetic mean	Geometric mean	Median
Sample of 144	9.3	not given	1.4
Sample of 501	2.2	not given	0.8
Sample of 635	7.3	0.82	0.9

To assess the effect of the geometric mean of the fishes with extremely small or extremely large ranges, the geometric mean was recomputed after omitting the smallest ranges, the largest ranges, and both, with the following results (in 10^4 km^2):

	Geometric mean
With bottom 5% (32 species) omitted	13
With top 5% omitted	6.6
With bottom and top 5% omitted	10
With none omitted (635 species)	8.2

The low geometric mean for salamanders is partly due to 14 species (16.3% of 86) that have ranges smaller than the smallest range of any other amphibian or reptile. When the geometric mean is recomputed with these 14 omitted, the value for salamanders increases from 8.6 to 17 ($\times 10^4$ km^2). (Revision of these data to include the recent work on salamanders mentioned above would decrease the mean by increasing the number of salamanders with smaller ranges.)

The differences between groups in figure 1 can not be attributed to a few extremely small or large ranges. The mean range size of fishes and salamanders changes only slightly when either extreme is excluded. None of the other orders seems to have disproportionate numbers of either very large or very small ranges. The question still remains as to what is there in the history of the groups, in their habitat requirements, or in their other attributes that causes differences in sizes of ranges.

Recent books with titles such as *Ecological Diversity, Evolutionary Ecology, Ecology, Zoogeography, Principles of Biogeography, Systematics and Biogeography, Marine Biogeography,* and *Biogeography* rarely mention the sizes of areas of geographic ranges of species. Müller (1981) devoted more emphasis than most authors to the distribution of organisms in space (Die Arealsysteme) but did not deal quantitatively with the distribution of sizes of geographic ranges. One of these works (Pielou, 1979, p. 96) stated, perhaps prophetically:

> If "overlap patterns" can be characterized quantitatively, and if comparisons can be made among empirical frequency distributions of the measurements obtained from different regions and from different taxonomic groups, the results may well prove illuminating in ways that cannot yet be foreseen.

The recent book on areography by Rapoport (1982) should stimulate such efforts.

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