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SYDNEY ANDERSON¹

ABSTRACT

Existing theory on the geographic ranges occupied by species focuses on individual species, the density of species at different places, and not on the question as to what the size-distribution of the ranges of species in a larger fauna is or how this distribution may be explained. The ranges of North American terrestrial mammals

are examined and a regular decline in the number of species having ranges in successively larger size-classes of ranges is found. The frequency distribution does not fit the lognormal or any of several other familiar distributions and further work is needed to develop a model that does fit. Other taxa and faunas should be examined also.

INTRODUCTION

One major parameter in the data or phenomenon of interest to biogeographers is the size of the geographic range occupied by a species. The pattern or frequency distribution based on sizes of such ranges of the different species in a fauna is also of interest. The former is commonly considered; the latter rarely. The present paper considers the latter.

First the scientific history (not faunal history) and existing theory that bear on the question are outlined. Then, because concepts of space used by organisms are varied and sometimes confusing, the question of such concepts at different organizational levels is examined in order to relate these concepts. Upper and lower boundaries for them in the Mammalia are presented as examples. Then, using North American terrestrial mammals as an example of a fauna, I consider

the methods and basic data available for examining the frequency distribution of sizes of geographic ranges and go on to examine that distribution. To put the continental pattern in perspective, the faunas of several progressively smaller areas within North America are also examined. History ends with the present. To illustrate the state of knowledge now, the opinions of several mammalogists (as to the frequency distribution being studied here) are related to the actual distribution. Logically, this might have been included at the end of the historical discussion, but the actual presentation will be more comprehensible where it is included (on page 8).

Some of the details of the actual frequency data for sizes of species ranges are outlined. Latitudes and major systematic groups are compared to range sizes. Finally, some hypotheses are dis-

¹Curator, Department of Mammalogy, the American Museum of Natural History.

cussed, predictions made, and future work suggested. Before I began the study I had the idea that some simple and regular pattern might emerge. That idea could be regarded as a hypothesis. I do not think it is important whether hypotheses are formulated before, during, or after data are gathered and analyzed, or even whether the questions and ideas of interest are formulated linguistically as hypotheses. Often, however, such formulations clarify thought, expedite the gathering of the most relevant data, and thus focus the study.

ACKNOWLEDGMENTS

Dr. Karl F. Koopman contributed by allowing me to use his notes on the current status of North American mammals, by arguing various points with me, and by reviewing the manuscript. Other colleagues in the department and elsewhere also contributed ideas. Drs. Richard G. Van Gelder and Guy G. Musser, and my volunteer research assistant Ms. Mary Evensen, reviewed the manuscript and made helpful suggestions. I am grateful to all of these persons and to others who have helped; especially my secretary, Ms. Margaret Canning, whose usual diligence expedited this paper.

HISTORY AND EXISTING THEORY

There are few comprehensive and quantitative summaries on the sizes of geographic areas or ranges occupied by the species of any major taxa in areas of any size, let alone continental regions. Two principal reasons for this are (1) that in few cases are there adequate data on ranges for entire groups over sizable areas, and (2) that few persons have been interested in examining the data available. The latter may relate to a dearth of theory that would lead one to examine the data. As background for the present study of ranges of terrestrial mammals in North America, prior work and relevant theory are here reviewed.

Many data on ranges of taxa of plants were compiled by Willis (1949, and earlier works cited therein). He advanced the hypothesis that the area occupied by a taxon is related to its age more than to anything else, and he established that the frequency distribution of areas occupied by different species form what he called a

"hollow curve." I explored the prevalence of such curves in a variety of taxonomic distributions but did not consider the sizes of areas occupied by species (Anderson, 1974). Some of the ideas developed there led to the present study.

The influence of size of an island area on the probability of survival of a newly arrived species and on the probability of extinction was treated by MacArthur and Wilson (1967) along with distances from the mainland and between islands, and other factors, but they did not deal with the question of why species occupy areas of different sizes in the absence of conspicuous discontinuities of habitat. Their theory of island biogeography has been applied in contexts other than islands of land surrounded by water. For example, Dritschilo et al. (1975) considered the ranges of host species of mice as islands occupied by species of parasitic mites.

Some ecological relationships of the theory of island biogeography have been discussed by Simberloff (1974). The mathematical relationships of species abundance distributions, principally in an ecological context, were lucidly summarized by May (1975). He compared the lognormal, broken stick, simple geometric series, and logseries distributions. When a pattern of relative abundance arises from the interplay of many independent factors, a lognormal distribution is predicted by theory and usually is found in nature. This distribution reflects the statistical Central Limit Theorem.

The lognormal distribution may be viewed as uninteresting since it does not suggest any special biological properties of the population under consideration except that many independent factors are involved. It seems to me that the presence of many such distributions in our science is interesting if for no other reason than to demonstrate how ignorant we are, how poor our predictions are liable to be, and how much work remains to be done.

In addition to the paper by May noted above, other papers in a symposium volume edited by Cody and Diamond, 1975, deal with many aspects of the relationships of such ecological and community concepts as stability or steadiness, resilience, population size, probabilities of extinction, niche formation, diversity in biotas,

patchy vs. continuous distributions, effects of disturbance, species-packing level or α -diversity, productivity in ecosystems, and competitive exclusion.

In only one of the papers did an author tie any of these related phenomena and theories to the question of the sizes of ranges of species. Rosenzweig (1975) presented data on the average size of the total ranges of the species of bats found at each of some 39 different places in the United States and Canada. He demonstrated a negative correlation between average size of range and faunal diversity (number of species of bats) and suggested that this may be the result of more intense habitat selection in more diverse faunas. I offer a different explanation below.

The thesis that distribution and abundance are different aspects of the same problem was exhaustively and convincingly explored by Andrewartha and Birch (1954). Their recommended approach (p. 10) to explaining distribution and abundance included the following steps: (1) study the physiology and behavior of the species, (2) study the physiography, climate, soil, and vegetation of the area occupied, (3) experiment or observe further in the field or in the laboratory, and (4) measure the numbers of the animal as accurately as possible over a long period of time. Their approach was to consider factors affecting each species separately. The fact that other species are among these factors is acknowledged, but the emphasis is on the species separately. The question of how these separate species ranges might be distributed among all possible sizes of areas was not really addressed by these authors.

The question of influences on the extent of geographic ranges of species was addressed by Hesse, Allee, and Schmidt (1937, chapt. 8). Their definition of range was the area inhabited by a species as delimited by lines connecting the outermost known localities, even though within this range only certain habitats are occupied. This is acceptable as a working concept although problems arise in special cases, as is true with most concepts. They wrote that range depends on (1) geologic age of the taxon, for a younger taxon may have had access to fewer routes of dispersal, (2) the vagility or capacity for active dispersal or passive transport of the species, (3) the ecological

valence or amplitude of the range of the conditions of life, within which an animal is able to exist, and (4) existing barriers. The dynamic nature of a range was clearly stated, ranges may expand or contract, or move from one area to another. The extent of range for a species has some minimum value below which the probability of accidental extinction, reduction in variability, and inbreeding may jeopardize its survival. The size of this range may differ with the species, but would be roughly equal to the area needed to survive by one pair multiplied by the number of pairs needed to maintain variability at some [undefined, but presumably important] level. The approach of these authors is like that of Andrewartha and Birch in focusing on the factors affecting the range of a single species. Again the question of whether this can lead to any generalization about the various ranges within a fauna is not addressed.

One of the few authors who have considered species areas in larger faunas and how these relate to other large-scale processes such as evolution and phylogeny is Boucot (1975, and earlier papers). He observed that taxa with larger geographic ranges have longer stratigraphic records in some groups of fossil invertebrates and discussed related theory on how this affects our interpretation of rates of morphological change and of taxonomic diversity.

Mammalogists have scarcely considered ranges in terms of size-frequency distributions in a continental fauna, or in any other smaller area. They have considered the numbers of species at different places (species density) and the degree of coincidence of boundaries (the delimitation of faunal areas). The question of limits to a given species has been much considered also. The relationships of the numbers of species in areas (or samples) of different sizes has been considered to some degree in the literature.

Suppose that a given number of species is postulated in the fauna of a certain space, e.g., the mammalian fauna of North America. Has any generalization been formulated that describes the frequency distribution of areas occupied by the species? Is there any theory that would explain or predict the distribution?

No one has summarized existing knowledge of areas for North American mammals nor

explained in theory any pattern that may exist. Nor am I aware of any such treatment of any other group of animals. The question has been considered by botanists to some degree.

The compilation by Hall and Kelson (1959) of distributional data for mammals of North America, in the form of range maps for virtually all species, provides a valuable source of information. This source has been used in an analysis of species density, that is the numbers of species present in different parts of the continent, by Simpson (1964). The density of borders of species ranges has also been analyzed in order to better define faunal areas within the continent by Hagmeier (1966). I have commented in greater detail on these analyses elsewhere (Anderson, 1972).

The expansions of the ranges of seven species of terrestrial mammals in Europe were examined by Nowak (1975). Actual ranges are expressed in square kilometers and changes in the historically documented record are described. These seven species are only about 4 percent of the 185 in the fauna. Nowak noted (p. 112) that according to "a rough analysis the decrease of ranges of mammals and birds, in the last few hundreds of years, was not greater (both as regards the number of species and the surface area lost) than the expansion." This implies an equilibrium of sorts; however, Nowak also indicated that in his judgment the fauna has not overcome its reduction during the last glaciation, and that there are still unoccupied niches available. These views seem to imply that an equilibrium has not been reached. The main points to me are that the dynamic nature of an approximate equilibrium is suggested and that data on seven specific mammals and 21 species of other taxa are used to examine some of the processes and patterns that are involved.

THE QUESTION OF SPACE OCCUPIED AT DIFFERENT LEVELS

We have been considering the geographic areas occupied by species or their "ranges" (sometimes termed distributions). The vertical component of space occupied is negligible on the geographic scale, hence, it is meaningful to express range in square miles or square kilometers. Area or space occupied may also be examined at other levels.

The smallest biologically meaningful area occupied by a species is the area physically occupied by one individual at one time. I will call this an α -area. An aggregate of α -areas is clearly shown on an aerial photograph of a herd of wildebeest or nesting colony of flamingos, for example. Among mammals, α -areas range from about 4 cm² for a small shrew to 200 m² for a blue whale.

An individual moves in time and the area traversed defines a home range or β -area. A β -area may be measured or calculated in various ways depending on the species involved, and it may be defined in detail in somewhat different ways. The known marginal sites of occurrence may be connected by lines and all of the area enclosed measured, for example; or if a large enough number of data points in space and time for an individual are known, some density or probability function may be derived and used. Among North American mammals, β -areas range from less than .1 ha for some small rodents (Stickel, 1968) to 100 km² for a cougar, and many more species have ranges near the lower end of the range than near the upper end. This excludes from consideration a few migratory bats, caribou, and some widely ranging marine mammals.

The next larger meaningful area would be a composite of the β -areas of all the individuals in a contiguous population, whatever the size of this γ -area might be. This concept might also be expressed in terms of a unit of suitable habitat, which in most cases would be more or less continuously inhabited by individuals. There are degrees of contiguity and continuity, as is usual in biological phenomena, but the general concept of a γ -area is useful. The concept of a deme in population genetics is equivalent. Among mammals, γ -areas range from about 1 km² for the entire range of an insular species like *Microtus breweri* (confined to Muskeget Island off the Massachusetts mainland) to 10⁷ km² for the original range of the lynx, subspecies *Felis lynx canadensis*.

The largest biologically meaningful unit of area for a species is the total species range. This area I term a δ -area, and these are the areas with which this paper chiefly deals. Knowing that the δ -area expands, contracts, and moves from one place to another during the species lifetime, we might define a larger area to encompass the total

lifetime range of a taxon, but in most cases virtually nothing is known about this. Among mammals, δ -areas range from 1 km² for *Microtus breweri* again to 5.1×10^8 km² for *Homo sapiens*, assuming that this species occupies the entire surface of Earth.

Biogeographic areas larger than those of individual species are commonly used. These are composites of different species and are usually recognized, if not always defined, on the basis of congruence of species boundaries, faunal communality, and related terms. These are biomes, life-zones, and other faunal areas, and may be termed ϵ -areas. In order to depict areas at the different levels from α to ϵ it is necessary to use

maps of different scales, and in order to obtain useful data it is necessary to use sampling and measurement techniques of different orders of magnitude. In figure 1, for example, as sample areas become progressively smaller relative to species ranges or δ -areas, the frequency distribution of occupied parts of the sample area changes. Finally it becomes impossible to say anything meaningful about these areas, except that they are all larger than the sample area. Conversely, in order to say anything meaningful about γ -areas one must use smaller sample areas and more refined data (i.e., measurements at a greater level of precision). Data on the γ -area or habitat level are used along with data on the

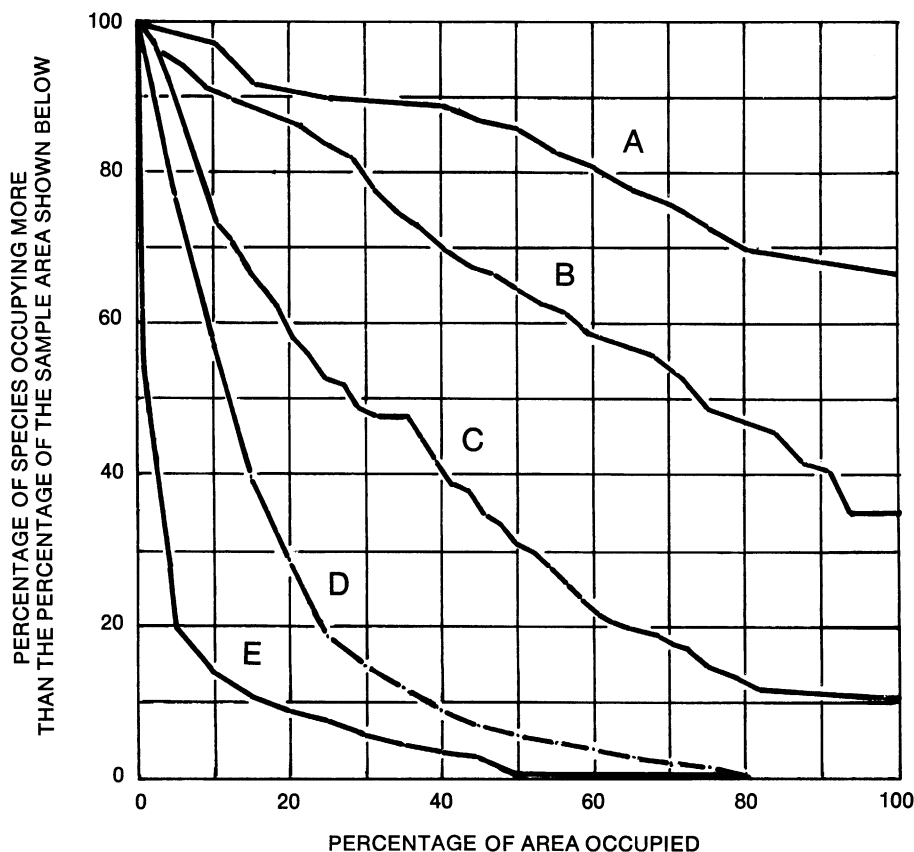


FIG. 1. The relationship of percentages of species occupying different percentages of the total area in areas of four different sizes and a comparative curve to show the average mammalogist's impression of the relationship for one of the four areas. The curves are: A. 63 species in about 12 counties in central Kansas, B. 79 species in Kansas, C. 120 species in Colorado, D. the average of the estimates of six mammalogists for all species of terrestrial mammals in North America, and E. the actual values for 714 species in North America.

α -level (localities of individual specimens) in order to decide what ranges are on the δ -level. Where there are many α -points (dots on the range map) and where there are good data on habitat requirements together with clear boundaries of habitats (γ -areas) in the area being studied, as is true for some species in many parts of Colorado, then δ -area boundaries can be drawn with a precision on the order of a few kilometers.

A point that is sometimes overlooked and is usually, of necessity, smoothed over, even by knowledgeable zoogeographers, is that the boundaries (of δ -areas) mapped for different species, even when drawn by one author and in one region, are not equivalent in accuracy. In fact, the boundary of a single species represented by a single continuous line on the map varies in its reliability from place to place. For example, on a range map for *Dipodomys merriami* published in 1959 (Hall and Kelson, p. 531) the line in Nevada distinguishes with delicacy certain tongues of unoccupied area of less than 100 km. width (even less than 10 km. in one case) and in Chihuahua the line sweeps boldly and encompasses an area of more than 200 km. in width which was later (Anderson, 1972, p. 311) shown probably to be unoccupied by the species. The scales used in mapping vary with the ranges of species also, so an error of $9 \times 10^4 \text{ km}^2$ for *D. merriami* in Chihuahua is not so great relative to the total range of the species, about $2 \times 10^6 \text{ km}^2$; however, some 30 percent of North American species have ranges smaller than $9 \times 10^4 \text{ km}^2$ (as shown in figure 2).

METHODS AND BASIC DATA

The geographic ranges of North American mammals were measured on maps published by Hall and Kelson (1959) except that newer information on the ranges and taxonomy was included. The maps of Hall and Kelson are roughly equal-area projections, departures therefrom seemed less than 5 percent. Errors in the scales of miles drawn were probably greater than 5 percent in some cases. An error of linear scale of 10 percent would cause an error in the measurement of area of about 20 percent.

A square ruled grid was prepared on a trans-

parent acetate film. The grid unit was read from the scale of miles on each map. The number of squares of the grid occupied by the mapped range was counted. Any square more than half occupied was counted. The unit distance was then squared and multiplied by the number of squares occupied. This gave the number of square miles, which was converted to square kilometers. The measurements finally were rounded to the nearest value of one significant figure, for example 1650 became 2000 and 64,500 became 60,000.

The ranges vary over more than six orders of magnitude, from those species known from a single locality, in which case the range was assumed to be 10 km^2 , up to $2 \times 10^7 \text{ km}^2$ in the case of *Lutra canadensis*, *Canis lupus*, and *Castor fiber*. The North American part of the range only was measured for species that occur also in one or more other continents. North America includes Middle America south through Panama and the Caribbean Islands south through Grenada in the Lesser Antilles. It also includes Greenland.

Historical ranges were used rather than present ranges. The ranges of some species have been much reduced by man since Europeans arrived. These species are chiefly large carnivores and artiodactyls: *Canis lupus*, *C. rufus*, *Ursus americanus*, *U. arctos*, *Gulo gulo*, *Lutra canadensis*, *Felis onca*, *F. concolor*, *F. pardalis*, *F. lynx*, *Cervus elaphus*, *Alces alces*, *Rangifer tarandus*, *Antilocapra americana*, *Bison bison*, *Oreamnos americanus*, and *Ovis canadensis*. Not only have ranges been reduced to various degrees, but populations have been reduced in areas still occupied.

The population levels of many other species have increased as a result of human activity and some species have expanded their ranges, probably in response to climatic changes as well as human activity. Among these are *Didelphis virginiana*, *Dasypus novemcinctus*, *Spilogale putorius*, *Baiomys taylori*, and *Sigmodon hispidus*.

For most species, information is either not adequate to reveal significant changes in ranges or changes have not occurred in the last hundred years or whatever other time is well enough known to judge.

The species with most drastic reductions of

ranges all had ranges of at least $1 \times 10^6 \text{ km}^2$ and hence appear at the extreme right end of the curves in figures 1 and 2. The effect of human activity on geographic ranges has been to reduce those of a few (less than 5%) of the species. This would tend to move the right-hand tail of the curve slightly to the left. If the changes were made on the graph, the difference in the curve would be scarcely detectable.

Homo sapiens, the species that comes closest to occupying all of North America and is the only non-introduced species occurring also in Eurasia, North America, and South America, was omitted from my analysis. I omitted also nine introduced species with established ranges in North America, namely *Rattus norvegicus*, *Rattus rattus*, *Mus musculus*, *Dasyprocta aguti* (on St. Thomas prior to 1852), *Myocastor coypus*, *Herpestes auropunctatus*, *Cercopithecus aethiops*, *Cercopithecus mona*, and *Lepus europaeus*. I omitted also those species (69) occurring in South America and not ranging into North America north of Nicaragua. I omitted the marine species, namely those of the Cetacea, Sirenia, the pinniped Carnivora, and the genus *Enhydra*. Two species of highly dubious status (*Oryzomys fulgens*, taxonomy dubious; *Coendou prehensilis pallidus*, West Indian records dubious) were omitted.

The ranges of the remaining species of native North American terrestrial mammals were measured. The latitude of the "center of gravity" (or point at which a piece of cardboard the shape of the range would balance) for each species was estimated.

Taxonomic work from 1924 (Miller) to 1955 (Miller and Kellogg) had reduced the number of recognized species from 1399 to 1065. By 1959 Hall and Kelson recognized 1003. The actual dates would have been about two years earlier in each case because of the production time for volumes of this type. Most of these reductions in numbers of species are the result of the discovery of intergrades between previously recognized species that are thereafter recognized as one species or as subspecies thereof. A few new species, or species new to North America are still being discovered from time to time. Both of these events increase the number of recognized species. Hall and Kelson (1959, p. vi) made the above

comparison and estimated that of their 995 species (eight introductions omitted), perhaps 125 will eventually be found to intergrade and hence be regarded as subspecies only. This would reduce the total to 870. Of these, they noted that approximately 170 are confined to an island or some isolated mountain mass. In each such case, the most closely related species is on the mainland or with a range separated by some barrier. If these isolated species are all to be synonymized, the total would become 700. Revisions have proceeded since 1959 and my figures for 1975 compare as follows.

Taking the 1959 figure of 1003 and subtracting nine introductions, 49 cetacea, 14 pinnipeds, one sirenian, and the sea otter, yields 929 species. My count for 1975, omitting these same groups (and three other special cases mentioned above) is 911, a net reduction of 18 recognized species. Excluding the 69 species not reaching north of Nicaragua (and occurring in South America as well as North America) leaves the 842 used in my analysis of ranges. Of these, 100 are insular. This does not include species with isolated ranges on islands or on mountaintops on the mainland, such as Hall and Kelson included in their figure of 170.

Of the 100 insular species, 26 are now extinct. These are *Geomys cumberlandius*, *Oryzomys victus*, *Elasmodontomys obliquus*, *Quemisia gravis*, *Hexolobodon phenax*, *Plagiodontia spelaeum*, *Isolobodon portoricensis*, *Aphaetretus montanus*, *Heteropsomys insularis*, *Homopsomys antillensis*, *Brotomys voratus*, *B. contractus*, *Boromys offella*, *B. torrei*, six species of *Nesophontes*, three species of ground sloths, and three species of *Megalomys*. All of these except *Geomys cumberlandius* were confined to one or more Caribbean islands, and most are known only from sub-Recent remnants found in caves. No species on the mainland has become extinct in historic times.

Most of the 15 species that occur both in North America and in Eurasia were, in 1959, regarded as specifically distinct on these two continents. The 15 species (and the names used for North American representatives in 1959) are: *Lemmus sibiricus* (*nigripes* and *trimucronatus*), *Dicrostonyx torquatus* (*groenlandicus*), *Canis lupus*, *Vulpes vulpes* (*fulva*), *Ursus arctos* (a

plethora of names), *Ursus maritimus*, *Mustela nivalis* (*rixosa*), *Felis lynx* (*canadensis*), *Cervus elaphus* (*canadensis*, *merriami*, and *nannodes*), *Alces alces*, *Rangifer tarandus*, *Gulo gulo* (*luscus*), *Castor fiber* (*canadensis*), *Microtus gregalis*, and *Microtus oeconomus*.

Increasing taxonomic knowledge also can increase the number of recognized species by showing that a formerly recognized species actually consists of two or more distinct species. Recent examples are seen in Gardner (1973) who re-separated *Didelphis virginiana* from *D. marsupialis*; Thaler (1972, and other works) who has divided several species of *Thomomys*; Schmidly (1973) who has divided *Peromyscus boylii*; and Zimmerman (1970) who has divided *Sigmodon hispidus*.

COMPARISON OF SIZES OF SPECIES RANGES IN SMALLER AREAS WITH THE CONTINENTAL PATTERN

The ranges of species in Colorado (Armstrong, 1972) and Kansas (Hall, 1955) were ascertained. The cumulative percentages of species occupying different percentages of the total area of each state are compared (curves B and C in figure 1) with two curves (D and E) for all terrestrial mammals of North America and one curve (A) for a smaller area in central Kansas. The sample area there was roughly square and included about 12 counties or 2.6×10^4 km² which compares with 1.8×10^5 km² for all of Kansas, 2.3×10^5 km² for all of Colorado, and 2×10^7 km² for all of North America. The numbers of species in these four sample areas are 63, 79, 120, and 714, respectively. Colorado is not only larger than Kansas but is much more diverse in topography and habitat than is Kansas.

I asked six mammalogists who have considerable familiarity with North American terrestrial mammals and who are interested in biogeography to draw simple frequency diagrams of their estimates of the sizes of ranges of these mammals. An average (and rounded) cumulative frequency plot of their quick and unstudied estimates is shown as curve D in figure 1 for the comparison with the actual distribution (curve E) based on my measurements. Two of the six persons estimated the frequency in the first class to be

greater than in any other class, but neither of them went so far as the actual distribution. The extent of the "hollow curve" distribution is not widely known.

If the reduction in sample area is taken an order of magnitude smaller, we find that in Douglas County, in eastern Kansas, an area of about 1.2×10^3 km², there are 52 species of mammals and all but *Geomys bursarius* occupy the entire area, so that the curve if drawn on figure 1 would nearly coincide with the upper border of the graph.

The estimates of the six mammalogists for all North American mammals erred in the direction of the frequency distribution found in smaller areas within the continent. The bias is quite understandable. Each of these persons has worked more closely with some smaller area within a continent than with the entire continent, and might be expected to extrapolate from the local familiarity.

WHAT IS THE SIZE DISTRIBUTION OF RANGES?

In figure 2 are graphed the ranges for insular and non-insular species separately as cumulative percentages of species. The abscissa is on a log scale. The names of some familiar islands and areas on the mainland are given to aid the reader in visualizing the scale used.

For species with small ranges (up to 10^3 km² and including many known from only one locality), the estimates are in most cases in error (on the low side) by a greater percentage than for species with larger ranges. It is unlikely that a species known from only one location lives only at that location. It is more likely that some significant area is occupied and that this area is somewhere among the smaller ranges of species, so that inadequate sampling accounts for the relatively poor estimate. In figure 2, a broken line is drawn to show my hypothesis as to the distribution of the species with small ranges that will be approached as better data become available.

I plotted the centers of ranges of species against latitudes with different symbols for different orders, but the resulting graph is too complex for convenient reproduction here. Some dif-

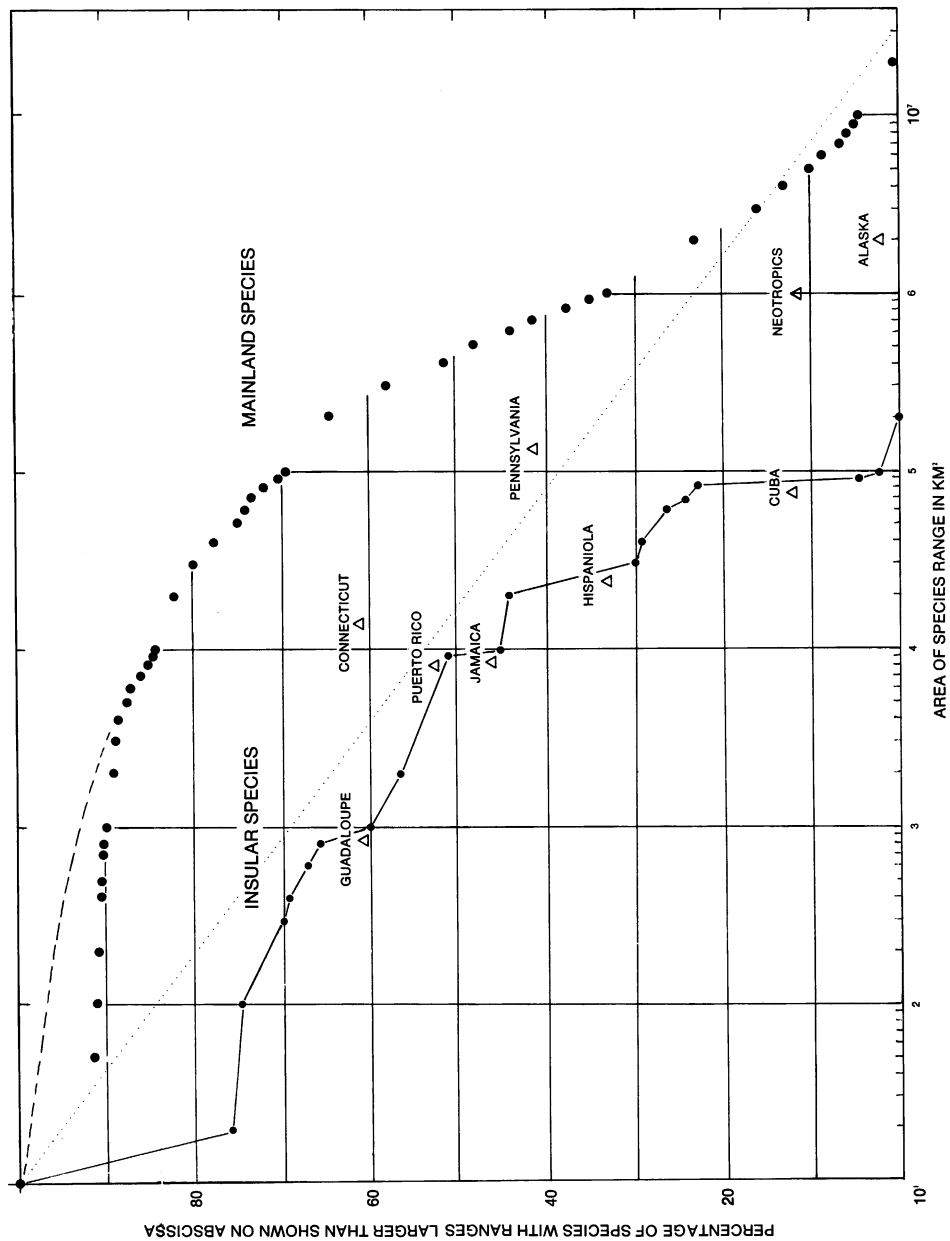


FIG. 2. Cumulative plots of ranges of North American terrestrial mammals, insular and non-insular species separately. Same data are plotted in a different way in figure 1.

ferences in both sizes of geographic ranges and latitudes of the centers of ranges for the species of the major orders are shown in figure 3. The abscissa is logarithmic for ranges. Insular species occupy smaller ranges, as would be ex-

pected, and artiodactyles and carnivores occupy larger ranges than average. Chiroptera are noticeably more southern, as are insular species. This tendency of insular species results from the presence of a more diverse fauna *and* more is-

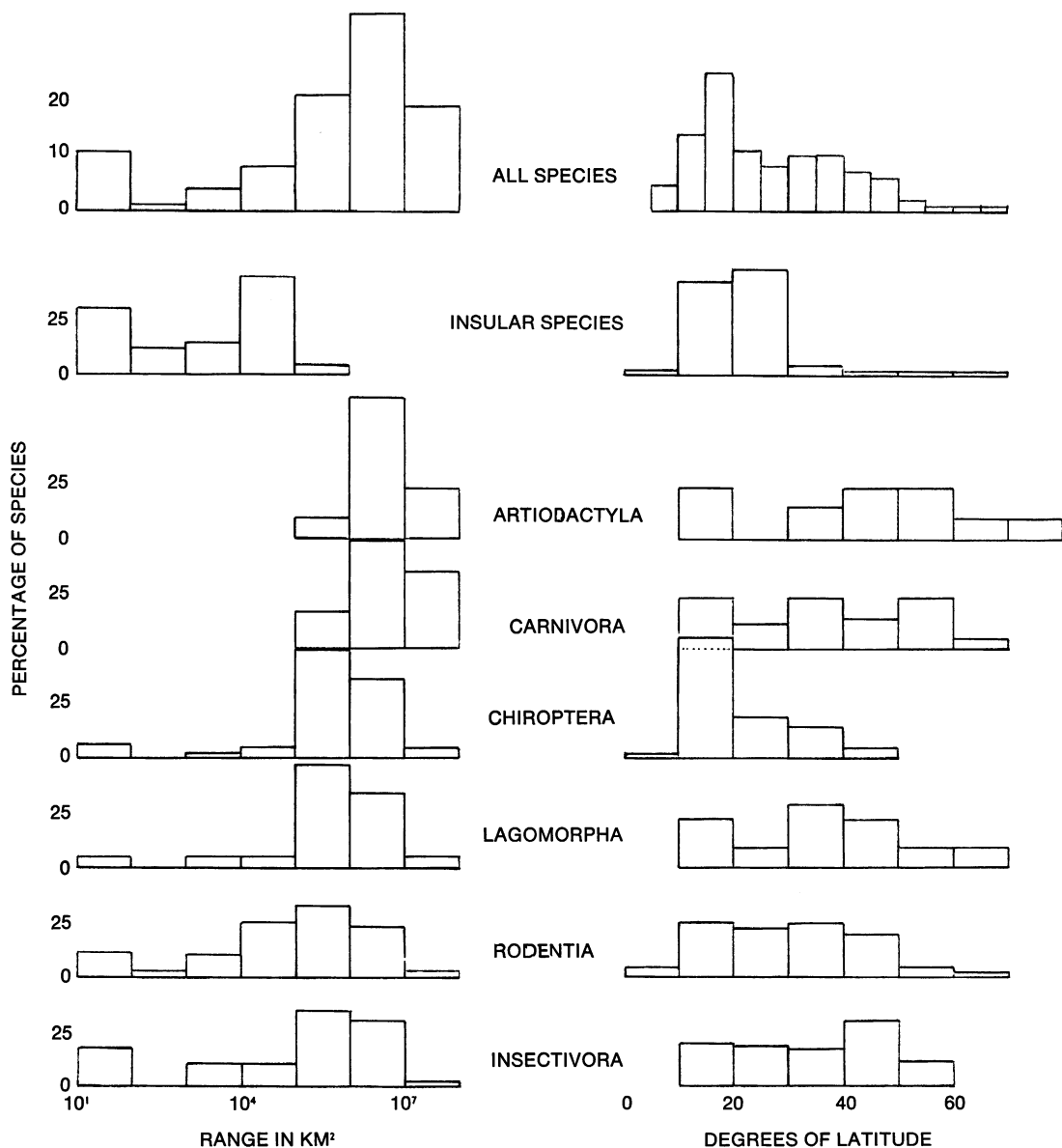


FIG. 3. Graph showing the percentage of the species of each of eight groupings whose geographic ranges fall in each of seven orders of magnitude (at left) and the centers of whose ranges fall in each of seven 10-degree ranges of latitude (at right). The top right plot is divided into 5-degree ranges.

lands in the tropical part of the continent. There are many islands in northern Canada but not much diversity.

Several observations based on the complex graph from which data for figure 3 were extracted are as follows. From 10^3 to 10^6 km² in range size, bimodality as to latitude is evident. There tend to be tropical and temperate species with the centers of their ranges averaging (for ranges of different sizes) from 15 to 20 degrees of latitude for the tropical species and near 35 degrees for temperate species. At ranges larger than 10^6 the tropical-temperate distinction does not exist and the average range is centered at progressively more northern latitudes as ranges become larger. The species with the largest ranges (about 2×10^7 km²) are centered at about 49 degrees. The bimodality reflects a major faunal distinction. The other observations largely result because North America is shaped the way it is, large at the north and narrow at the south. If South America were analyzed in the same way, I suppose that the bimodality would be evident but that the species with larger ranges would predominate near the equator rather than farther away from the equator. I postulate that ranges of species in a more diverse fauna do not necessarily have smaller average ranges (contrary to the hypothesis of Rosenzweig, 1975), even though this happens to be true for North American bats. An examination of the facts for other groups, such as rodents, and for other faunas, such as South America, would be interesting.

DISCUSSION

Are the species spread evenly throughout the possible ranges? The use of a logarithmic scale for ranges makes it difficult to answer this question from graphs such as figures 1, 2, and 3. In figure 4 are plotted the numbers of species present in each 100 km² size class, averaged over each order of magnitude. It is clear that the species are not spread evenly, but that they are about an order of magnitude (10 times) less "concentrated" in each successively larger order of magnitude of range.

I predicted in reference to figure 2 that when better data are available there will be fewer species in the area of 10^1 km² range and more in

ranges from 10^2 to about 3×10^3 km². Taking this into account, I suggest that the best estimate of the actual distribution in figure 4 would be curvilinear, more or less as shown by the broken line.

The hypothesis of equal probability of occurrence of species in all possible sizes of ranges having been examined and rejected, let us consider several other hypotheses or "distributions" developed and explicated chiefly by ecological theorists. Some of these distributions have been posited to imply or suggest possible community relationships or interactions among the components.

The Central Limit Theorem of statistics states that the means of samples drawn from a population of any distribution will approach the normal distribution as sample size increases (Sokol and Rohlf, 1969, p. 130). May (1975, p. 89) stated it in more general terms, "essentially all additive statistical distributions are asymptotically gaussian, or 'normal.'" He suggested that the lognormal reflects the Central Limit Theorem and that broken-stick, geometric, and logseries distributions may reflect features of community biology. It is my view that these three distributions may or may not reflect features of community biology, depending on a variety of circumstances in each model examined. The Central Limit Theorem may also be significantly involved.

The way in which the lognormal may reflect the Central Limit Theorem in the case of ranges of species (assuming that they had a lognormal distribution, even though they do not exactly have that distribution) is to interpret the range of a species as the result of the interaction of a variety of relatively independent environmental and internal factors or as a representation or "mean" of a sample of all these factors. Independence is relative. A deterministic philosophical view would hold that nothing is really independent and that things that seem independent are merely so poorly known or so complex in interaction that we do not perceive of or have any way of dealing with the interaction. Pragmatically we have to act as though they were independent until we figure out connections.

Do the areas for North American mammals conform to any of the four principal distribu-

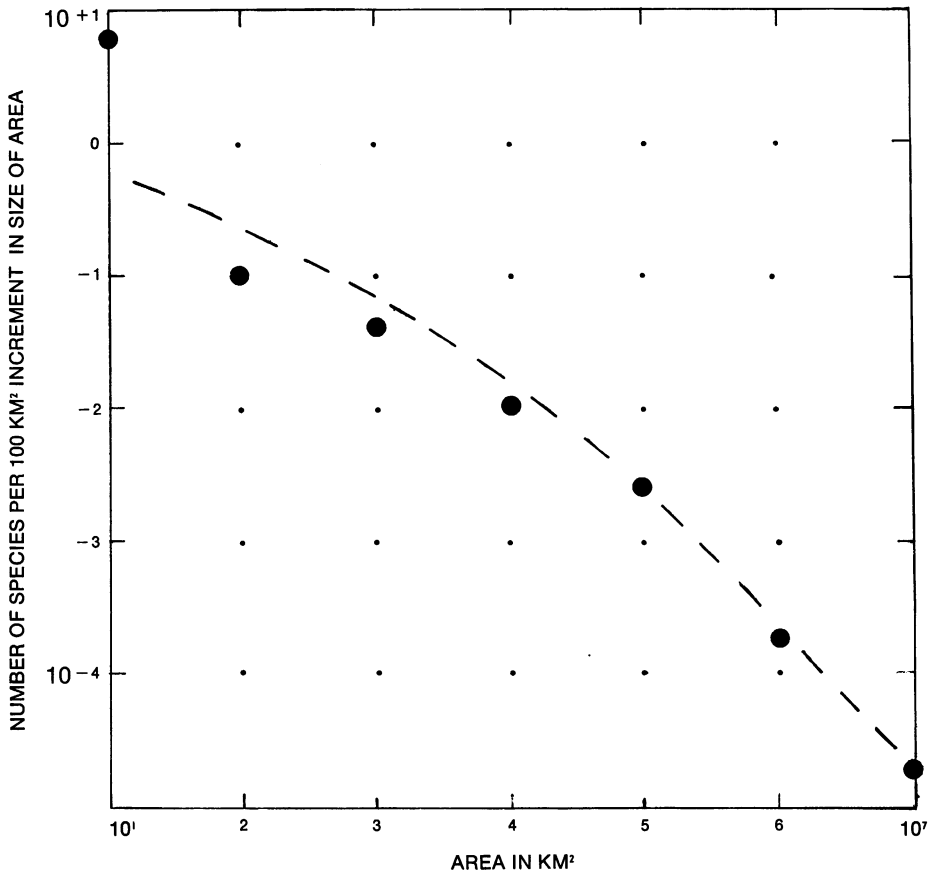


FIG. 4. Graph for North American terrestrial mammals showing the number of species (averaged for each succeeding order of magnitude) having ranges of any given size. Counts are grouped in 100 km² increments. The negative values on the ordinate are powers of 10, thus 10⁻⁴ or .0001 species per 100 km² increment for a range of 10⁶ (1,000,000) km² means that there are so few species with ranges of this size that most increments or size-classes of 100 km² are unoccupied and, on the average, there is about one species for each 10,000 size-classes.

tions summarized by May (1975), namely the lognormal, broken stick, simple geometric, or logseries? Each of these can be examined by graphic means more easily than by computation, although some simple computation is needed to work out the graphs.

I computed a broken stick distribution for comparison. The largest ranges for the North American mammals are larger than in the "broken stick" model and the smaller ranges are smaller. This model (MacArthur, 1957, discussed by Anderson, 1975) assumes that some finite resource is divided randomly into discrete seg-

ments. Species ranges are not discrete; they overlap. Species "niches" in a more abstract sense may be discrete, however. There seems to be no theoretical reason to expect the distribution to fit this model.

In figure 5, percentages of species on a probability scale are plotted against cumulative log (X10) classes to test for conformity with a lognormal distribution. Conformity, which would be shown by a linear relationship, does not exist over all, although the upper three or four points approach linearity.

Plotting the areas occupied by the species on

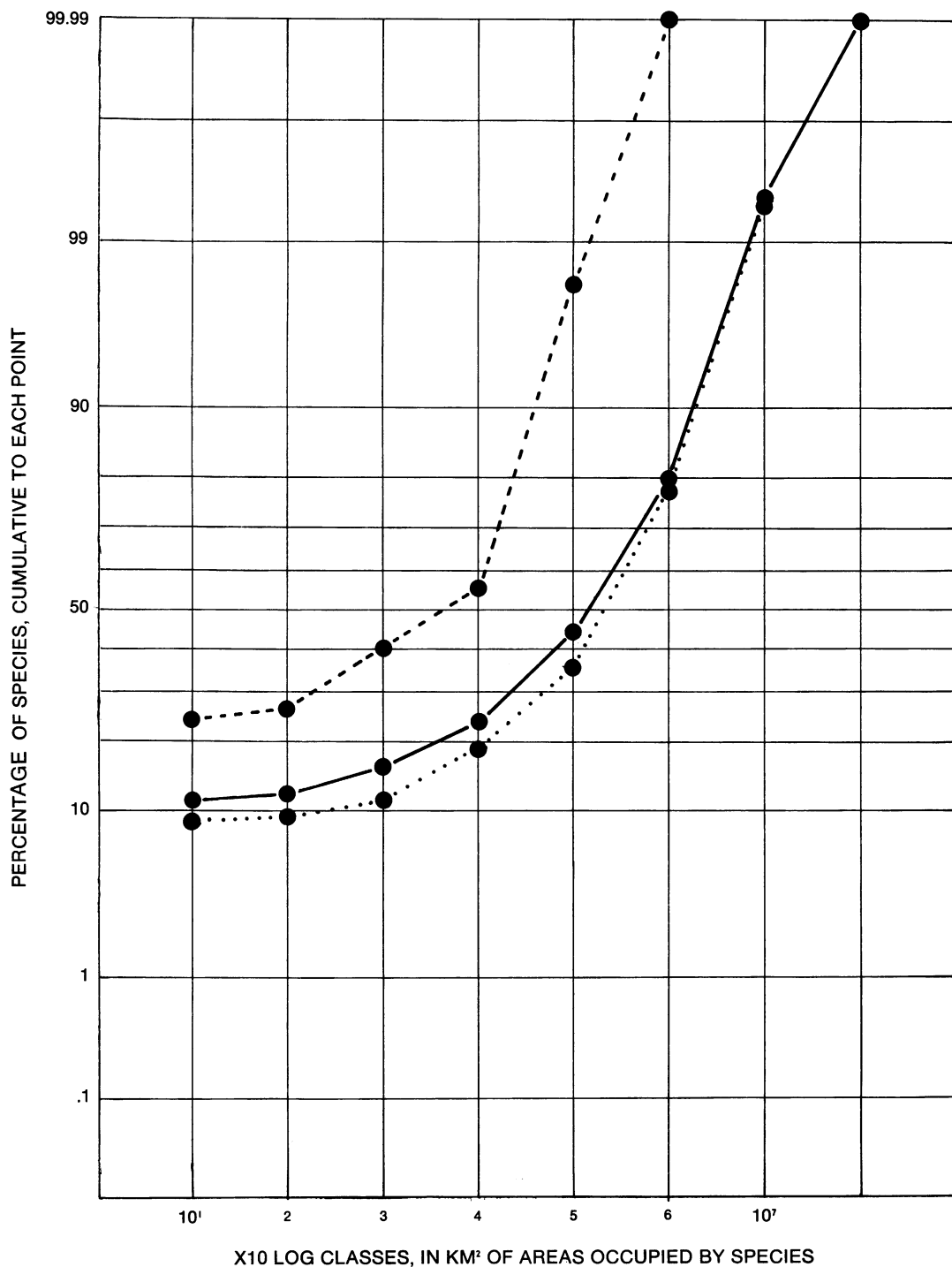


FIG. 5. Cumulative percentages of species in X10 (1-10, 11-100, 101-1000, etc.) log classes (abscissa) plotted on probability scale (ordinate) to see whether distributions are lognormal. Since the points are not on straight lines, the distributions are not lognormal. The three curves are (top to bottom), 100 insular species, 714 insular and mainland species, and 614 mainland species. Some "mainland" species also occur on islands, but the island range is usually a negligible part of the total range.

a log scale against their rank order on an arithmetic scale should give a straight line if a geometric or logseries exists. This was done and the fit was not close.

The actual distribution is not as I had suspected it might be (lognormal), nor does it fit well with any one of several distributions familiar to ecologists. It is, however, a very regular distribution and this suggests the need for further testable hypotheses or models to help explain this regularity. The study of such models will be the subject of a later paper. The examination of other groups of organisms to see whether the distributions of sizes of geographic ranges resemble that found for North American terrestrial mammals would also be interesting.

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