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On a Possible Fractal Boundary Dimension for Mammalian Geographical Ranges at Regional Scales: A Case Study in Texas

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At regional or continental scales maps of the geographical ranges of mammalian species appear as a set of planar figures with widely varying shapes and sizes. Each range is different from every other, in ways that do not permit one to relate them to each other, within the framework of Euclidean geometry. This makes quantitative comparisons of range size and shape difficult. Fractals provide a solution to this problem, by permitting one to parameterize the area-perimeter relationship, of a suite of ranges, with a fractal dimension. This dimension may be used to characterize the complexity of range boundaries and their included areas (Milne, 1991).

Area and perimeter have been used in studies at geographical scales ranging from worldwide rain and cloud patterns (Lovejoy, 1982) to deciduous forest boundaries in Mississippi (Krummel et al., 1987). A fractal relationship between area and perimeter is appropriate when range shape varies with range size (Krummel et al., 1987). This requirement would seem to be met for mammalian geographical ranges at regional scales. The purpose of this study is to estimate the boundary dimension, of the geographical ranges of the native mammalian fauna within Texas.

Materials and Methods

Texas occupies 69.2×10^4 km^2 in the south-central region of the U.S.A. Since the states' size, shape, and orientation were determined by political considerations, it may be considered to be an arbitrary (but not random) sample for the study of mammalian macroecology. Shape, size, and orientation should not prejudice some species over others. Combination dot and outline maps were prepared for the geographical distributions of 141 species of mammals native to the state. All known records of marginal specimens were plotted as dots and used as a guide to map preparation. Each map was drawn at the same level of resolution. Nevertheless, the level of resolution depended, in large measure, upon the number and scatter of available collection localities and the number of localities varied from species to species.

The outlines of species' geographical ranges were made by using a series of steps, Δs, marked off with a divider scaled to 16 km per step. Thus, each species' range was determined using the same fixed scale Δs. The lengths of range boundaries were determined as $n\Delta s$ km, where n is the number of steps in a range perimeter. The area of each range was measured by carefully tracing along each step in the range perimeter, using a digital planimeter. These estimates were considered to be the best available, for a data set that includes the distributions of all of the native species of Texas mammals.

Because of difficulties in representing small ranges at a degree of resolution commensurate with those of large ranges, all species whose ranges in Texas were less than 5% of the state, were omitted from the analysis. Likewise ranges greater than 95% were omitted because their shape, within the state, is influenced strongly by the shape of the state itself. The decision to use these particular percentage points, as cut off points, was somewhat arbitrary and was taken *a priori* to examining patterns in the data. The final number of species included in the analysis was 104.

RESULTS AND DISCUSSION

In a scale-invariant pattern, large geographical ranges are statistically similar to magnified small ranges. At the same fixed scale, the area and perimeter of a set of ranges are related by the formula $P = KA^E$ (Hastings and Sugihara, 1993; Sugihara and May, 1990; Mandelbrot, 1982). When log transformed this equation becomes $\log P = \log K + E \log A$, where $\log K$ is the y-intercept and E is the area-perimeter exponent. The statistical relationship, between area and perimeter, is evaluated by regressing $\log P$, the dependent variable, against $\log A$, the independent variable. The boundary dimension D, of the set of ranges is expressed as $D = 2E$ (Hastings and Sugihara, 1993). The mammalian data for Texas were fitted to the equation $\log P = 0.69 + 0.57 \log A$, yielding a boundary dimension of $D = 2(0.57) = 1.14$, ($R^2 = 0.91$, $P < 0.001$). This statewide pattern holds across a scaling domain spanning more than two orders of magnitude in area (Fig. 1).

The boundary dimension for Texas mammals is $D = 1.14$. This value is higher than $D = 1$ for regular geometric figures but is low relative to its interval of possible values $1 \leq D \leq 2$. This low value indicates that the geographical ranges of Texas mammals are rather obtuse in outline, their winding contours on maps notwithstanding. Their two-dimensional spatial pattern does not incorporate a high degree of peninsula-like protrusions, when calculated using data at the resolution currently available.

This boundary dimension for mammalian ranges is not far from the dimension of continents and large rivers, both estimated at $D = 1.20$ (Mandelbrot, 1982). This seems reasonable, since the borders of continents and large rivers may form barriers to mammalian dispersion and hence lend their own shape to the shape of ranges. A low boundary dimension means that the rate of change of range perimeter, as a function of area, is low. Ranges so characterized acquire more area without concomitantly acquiring correspondingly long perimeters.

More area is beneficial in that it should, on average, contain more resources and permit the maintenance of larger populations. Such populations are proportionally less subject to the effects of random events (Brown, 1995). A short perimeter means that the range, as a whole, is less exposed to influences from outside. Conditions outside a species' range are inimical, al-

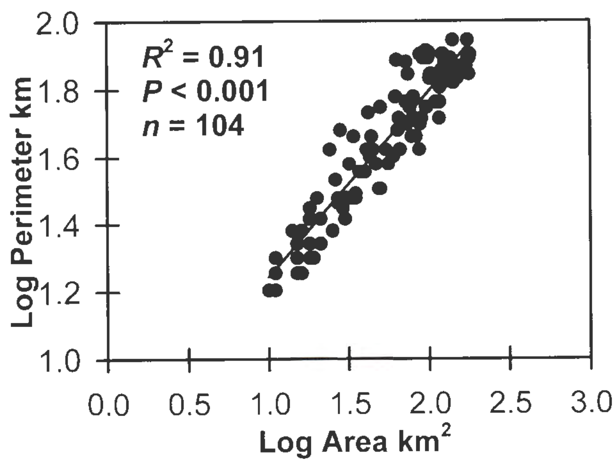

Figure 1.—Double logarithmic regression of range perimeter, as a function of area, for the geographical distributions, within Texas, of native Texas mammals. The boundary dimension, of the ensemble of geographical ranges, is $D = 1.14$.

most by definition, to continued occurrence and reproduction. For example, a shorter-range boundary could restrict the inward flux of deleterious biological agents, such as disease vectors or competitors. In sum, the combination of a larger range area with a shorter boundary could be of value for long-term species survival.

If further work, at different scales, confirms the fractal nature of boundary dimensions, then it may be possible to extrapolate patterns from state or regional studies to continent wide studies. This would mean, among other things, that the many geopolitical and regional studies of mammalian distribution, in the literature, might have significant generality.

A CRITIQUE

The Study Area.—Many species of Texas mammals have range boundaries in Texas, which exactly match all or portions of the state. So the question becomes, how much of the calculated fractal dimension is determined by the shape of Texas and how much by "true" range boundaries? This potential problem was reduced by omitting species whose ranges in Texas cover greater than 95% of the state. This question was examined empirically by calculating the dimension using only species whose boundaries coincide with the state's boundary, by less than or equal to a small proportion, in this case arbitrarily set at 0.25. Eleven points met this criterion, with a mean proportion of 0.20. These test data had $R^2 = 0.89$ and $D = 1.13$, which is close to 1.14. This result suggests that the state-boundary effect induced little bias into the estimated fractal dimension.

Bias due to the use of a study area that is defined by geopolitical criteria should be influenced by the length and nature of that part of a species' range boundary that lies within the geopolitical unit, relative to the length of the boundary of the unit itself. Areas with proportionally long boundaries, defined by important natural features that are barriers to dispersal, should be less affected. This is the case for Texas because a significant part of the states' boundary, the Gulf Coast, coincides with the continent of North America and is an absolute barrier for land mammals.

Scale.—The fractal value herein reported should be considered correct for the degree of resolution, currently available to macrogeographers, for mammals in Texas. This resolution is similar to that observed in standard range maps of mammalian species (as well as many other taxa), at state or regional levels (Anderson, 1972; Armstrong, 1972; Davis and Schmidly, 1994). Many biogeographical interpretations are based upon the use of such maps (Udvardy, 1969; Brown, 1984; Ricklefs and Latham, 1993; Brown, et al. 1996, Lyons and Willig, 1999). It is suggested that the fractal dimension may be found to have relevancy to such studies.

This estimate of the fractal dimension should be considered provisional and subject to change when better distributional data become available. As field parties collect more data it may become possible to draw range maps with greater detail. In this case, it would seem reasonable to anticipate that representations of boundaries may become somewhat more complex. Such improved maps would offer the possibility of exploring the behavior of the boundary dimension under a wider range of variation in spatial resolution.

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It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the Journal of Mammalogy, Evolution, The Texas Journal of Science, Occasional Papers of the Museum, and Special Publications of the Museum. It is with special fondness that we remember Dr. J Knox Jones.

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