CHAPTER 6

Fractal-Based Spatial Analysis of Radiotelemetry Data

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The inherent complexity of ecosystems presents formidable challenges to biologists interested in describing, modeling, and managing animal populations (Milne 1997). Researchers now recognize that a multiscale approach is required to elucidate the spatio-temporal components of ecosystem complexity and to understand animal movement patterns in natural landscapes

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(Ritchie 1998, With et al. 1999). Because ecological complexity varies with scale, observations at multiple scales and multiscale approaches to data analysis are required (Johnson 1980, Milne 1997).

Although animal movements are known to be spatially and temporally complex, few studies have examined the multiscale features of movement patterns. Analytical tools traditionally used by wildlife biologists, while useful in summarizing and modeling space use, generally fail to explicitly consider scaling issues (Gautestad and Mysterud 1993). Thus, new approaches are required to characterize the scaling properties of animal distributions. Fractal geometry is particularly suited to this task, as it explicitly takes a multiscale approach (Mandelbrot 1983, Milne 1997).

While fractal geometry has not been widely used to analyze radiotelemetry data, a number of recent studies have used fractals to characterize and model animal movement paths (e.g., With et al. 1999). Movement paths have traditionally been modeled using random walks (Kareiva and Shigesada 1983), with the aim of translating movement data into simple measures of displacement and habitat residency (Turchin 1998). Random walk models assume that movement positions are not spatially autocorrelated. A continuous path must therefore be represented as a simplified, discrete set of uncorrelated moves prior to analysis. An alternative view recognizes that the line segments connecting adjacent steps will continue to reveal a complex, erratic path as observation frequency increases (Gautestad and Mysterud 1993). This is the essence of the fractal approach. Instead of simplifying an inherently complex path as a discrete set of moves, one recognizes the underlying complexity and characterizes its scaling properties using the power law distribution (Viswanathan et al. 1996, Turcotte 1997).

Generally, it is difficult to obtain continuous movement-path data for a variety of reasons. Individuals may be logistically difficult to follow, or the act of following them may alter their behavioral pattern. In addition, movement paths are generally only available for short time intervals and may not include key movements, such as dispersal (Turchin 1998). An alternative approach is to obtain periodic fixes on animal positions using radiotelemetry. The result is a set of points that defines a utilization distribution (Worton 1989; see also Chapter 5). Radiotelemetry data are used in wildlife biology and natural resource management to determine home ranges (White and Garrott 1990), to summarize and model dispersal (Turchin 1998), or to quantify habitat selection (Manly et al. 1993). However, most of the currently available analytical approaches are not spatially explicit, and fewer still consider the multiscale features of animal movement patterns (Gautestad and Mysterud 1993, Viswanathan et al. 1996).

Data from radiotelemetry fixes often reveal that individuals have indistinct home range boundaries and show local variations in their intensity of space use (Worton 1989, Gautestad and Mysterud 1995). Standard techniques, such as home range analysis, cannot fully characterize these complex dispersion patterns (Loehle 1990). As an alternative strategy, Gautestad and Mysterud (1993) suggest a multiscale approach to the analysis of radiotelemetry data. They hypothesize that animal movements result from complex interactions between coarse and fine-grained responses, so that individuals relate to their environment in a multiscale, hierarchical manner. The result is a complex utilization distribution with fractal properties (i.e., scale-free and characterized by clumps within clumps within clumps; Gautestad and Mysterud 1993).

In this chapter, we propose a method for the multiscale analysis of spatial radiotelemetry data based on fractal geometry and the generalized entropy. In addition, we outline a fractal-based dispersal model known as the Lévy flight. We illustrate the method using radiotelemetry data from a disjunct population of sage grouse (*Centrocercus urophasianus*) in northwest Colorado.

MULTISCALE ANALYSIS OF RADIOTELEMETRY DATA

Radiotelemetry data are often used to obtain new insights into how a landscape is used by an individual or population. A set of radiotelemetry fixes is a sample from an underlying spatio-temporal distribution and, thus represents an empirical estimate of the utilization distribution of an individual or population. Utilization distributions are typically underdispersed (contagious), indicating that some regions are used disproportionately relative to others (Turchin 1998; see also Chapter 5). The degree of contagion is thought to reflect both the scale-invariant spatial complexity of available habitat (Etzenhouser et al. 1998) and the intrinsic behavioral dynamics of animal movements (Gautestad and Mysterud 1993).

A number of statistical methods are available to test the null hypothesis of spatial randomness in dispersion data (Upton and Fingleton 1985). The simplest tests consider only nearest neighbors and, thus, assess pattern only at fine spatial scales. More rigorous second-order approaches produce a profile of how spatial pattern changes with scale (Ripley 1977, Kenkel 1993). These methods, while useful in evaluating deviations from spatial randomness, do not explicitly characterize important features of the utilization distribution, such as the degree of contagion. Alternative methods are therefore required to fully explore the scaling features of animal location data.

Fractal geometry (Mandelbrot 1983) provides the tools necessary to characterize and model multiscale contagion in radiotelemetry data. Spatial data are said to display fractal properties if the same underlying pattern of contagion is resolved on an ever-diminishing scale. The degree of scale-invariant contagion is quantified using a scaling parameter, *D*, known as the fractal dimension (Schroeder 1991, Kenkel and Walker 1996). A multiscale, fractal-based approach to the analysis of radiotelemetry data is useful in addressing the following questions:

ARE ANIMAL MOVEMENTS STATISTICALLY SELF-SIMILAR?

Self-similarity is defined as invariance against changes in scale. Scale invariance is an attribute of numerous natural phenomena and laws, and is the unifying concept underlying fractal geometry (Schroeder 1991, Kenkel and Walker 1996). As an example, consider a map of the spatial dispersion of radiotelemetry fixes. If a map scale is not indicated, it may be difficult if not impossible to determine whether the map covers 10 m or 10 km, particularly if the same general pattern manifests itself across scales. This intuitive notion of scale invariance provides the rationale for applying the fractal power law distribution to spatio-temporal radiotelemetry data. In practice, statistical self-similarity is demonstrated if the fractal dimension is found to be independent of scale (Turchin 1996, Milne 1997).

Self-similarity represents a fundamental departure from the scale-specific paradigm that pervades much of wildlife biology and theoretical ecology (Gautestad and Mysterud 1993, 1995). The demonstration of fractal scaling in animal movements therefore has far-reaching consequences for the analysis of radiotelemetry data and for modeling movement patterns in natural landscapes (Viswanathan et al. 1996).

IF MOVEMENT PATTERNS ARE SELF-SIMILAR, WHAT IS THE DEGREE OF SPATIAL CONTAGION?

Unlike other statistical distributions, the power law does not include a characteristic length scale and can therefore be applied to scale-invariant phenomena (Turcotte 1997). The fractal dimension *D*, derived from the power law distribution, is used to quantify the degree of scale invariance. A smaller *D* value indicates greater contagion (Schroeder 1991).

As a scale-invariant measure of spatial contagion, the fractal dimension provides valuable insight into how an individual or population uses the landscape (With et al. 1999). While home range analysis gives important information on the spatial *extent* of animal movements, it generally provides limited insight into the spatial *dispersion* of those movements. At one extreme, an individual may simply move through the area randomly, eventually visiting all regions of its home range ($D = 2$, which is implicitly assumed in most home range models; see Gautestad and Mysterud 1995). Alternatively, an individual may visit some regions of its home range more frequently than others, and some areas may not be visited at all. This results in a contagious pattern ($D < 2$), suggesting a preference for some areas and underutilization of others. Because individual locations indicate areas where conditions satisfy the requirements of a species (Milne 1997), the degree of spatial contagion may be indicative of underlying physical and biological processes. An individual with a movement pattern of $D = 2$ uses its home range markedly different from one with a movement pattern of $D = 1$.

WHAT FACTORS MIGHT CONTRIBUTE TO THE DEGREE OF CONTAGION OBSERVED?

The fractal dimension can be used as a comparative index of self-similarity to test specific hypotheses related to how individuals and populations perceive landscapes (Crist et al. 1992). For example, it is known that animal movement patterns are often affected by natural and human-induced habitat fragmentation (Storch 1997, Wiens 1997), but to what degree? One could compare the fractal scaling of animal movements in two populations, one occupying a fragmented landscape and the other an unfragmented one. Comparisons could also be made within the same population over time (e.g., comparing movement patterns in harsh vs. mild winters), between sexes or age-classes, or across species (e.g., Etzenhouser et al. 1998, With et al. 1999). Comparative approaches can provide valuable insights into the processes determining spatial contagion on the landscape. Standard statistical methods can be used to compare individual D values from two or more populations (Gautestad and Mysterud 1993). Alternatively, Monte Carlo simulation can be used to estimate confidence limits for measured D values (Loehle and Li 1996).

FRACTAL ANALYSIS OF SPATIAL PATTERN

BOX COUNTING

A number of approaches are available to explore fractal phenomena and estimate the fractal dimension (Frontier 1987, Schroeder 1991, Hastings and Sugihara 1993, Kenkel and Walker 1996, Milne 1997). Here, we consider estimation of the fractal dimension for a point pattern (utilization distribution) derived from radiotelemetry fixes. Box counting is the most commonly used approach for estimating D (Hastings and Sugihara 1993, Turcotte 1997).

Formally, box counting obtains a δ covering of a point pattern. A square box of side length δ is centered on each point, and a count is made of the number of boxes N_δ required to cover the pattern. This procedure is repeated at various values of δ. A simpler approach is to superimpose a grid of non-overlapping boxes over the pattern, and count how many boxes are occupied. The fractal dimension D is given by the limit:

$$D = -\lim_{\delta \to 0} (\log N_\delta / \log \delta), \tag{6.1}$$

where N_δ is the number of boxes of diameter δ containing at least one point. The limit $\delta \to 0$ is not defined for discrete point patterns; instead, one plots $\log N_\delta$ against $\log \delta$. The point pattern is fractal if a straight line is obtained over the range of δ values: the negative of the gradient of this line is the fractal dimension. The grid method is somewhat sensitive to grid location, particularly for small sample sizes ($n < 500$). Grid placement should therefore be randomly replicated to ensure stability of results (Appleby 1996, Milne 1997).

GENERALIZED ENTROPY

The fractal dimension described above considers only presence-absence of points in the boxes: the number of occupied boxes is counted but the number of points in a given occupied box is not considered. By considering the distribution of point counts within boxes, a set of q dimensions is defined that more fully characterizes the fractal pattern. The dimension described above is known as the cluster fractal dimension, which is defined at $q = 0$. More generally, counts of the number of points (n_i) in each of N_δ occupied grid boxes are obtained and expressed as proportions ($p_i = n_i/n$) of the sample size n. These are used to determine the generalized entropy (Renyi 1970) expressed as:

$$I_q(\delta) = 1/(1 - q) \log \sum_{i=1}^{N_\delta} p_i^q. \tag{6.2}$$

The generalized entropy defines a family of functions, each of which is referenced by the parameter q. From this, the generalized dimension D_q for the qth fractal moment is given by:

$$D_q = -\lim_{\delta \to 0} [I_q(\delta) / \log (\delta)]. \tag{6.3}$$

A plot of the generalized entropy $I_q(\delta)$ against $\log \delta$ is used to estimate D_q (Hentschel and Procaccia 1983). If a straight line is obtained over the range of δ, D_q is given by the negative of the gradient. Varying q generates a family of generalized dimensions (Table 6.1).

TABLE 6.1 Common Generalized Entropy Functions

q	$I_q(\delta)$	Dimension
0	$\log N_\delta$	Cluster
$\rightarrow 1$	$-\sum p_i \log p_i$	Information
2	$-\log \sum p_i^2$	Correlation

Measuring dimension as a function of q reveals the multifractal aspects of a pattern (Stanley and Meakin 1988, Scheuring and Riedi 1994). Consider the effect of varying q. At $q = 0$, each occupied box is weighted equally irrespective of the number of points it contains. For positive values of q, greater weight is given to boxes containing more points, while negative q values result in greater weight given to boxes containing few points. In analyzing statistical fractals, it is generally recommended that $0 \leq q \leq 3$ (Appleby 1996).

DILUTION EFFECT AND MONTE CARLO TEST

For fractal patterns of finite size, the log-log plot (e.g., log N_δ vs. log δ, cluster fractal dimension) will deviate from linear at small δ values since N_δ necessarily approaches the sample size n as δ decreases (Gautestad and Mysterud 1993). In fact, the maximum possible number of occupied boxes is $N_\delta = n$ and is therefore independent of δ. In a slightly different context, Gautestad and Mysterud (1994) refer to this as the dilution effect. Resolving the dilution effect problem requires careful selection of a lower bound for δ that is appropriate to the resolution of the data (i.e., sample size). An objective procedure to determine this lower bound is to generate known fractal patterns (e.g., using the Lévy flight model) of sample size n and derive the δ value at which the log-log plot deviates from linear.

A finite sample will also underestimate the true fractal dimension. For example, a random spatial pattern has a theoretical fractal dimension $D = 2$, but this value is only achieved as n approaches infinity (Gautestad and Mysterud 1993). For an empirical random pattern of finite size, $D < 2$. The smaller the sample size n, the further the deviation from $D = 2$. An observed D value (obtained from an empirical point pattern of size n) must therefore be compared against values obtained from random patterns of the same size to determine whether the observed pattern deviates significantly from random (Hastings and Sugihara 1993:106).

An appropriate null model is that the observed point pattern is statistically random (i.e., all areas of the landscape are used equally). This hypothesis is readily tested using a Monte Carlo procedure (Manly 1997):

1. Generate a random point pattern of n points.
2. Compute D for this randomly generated pattern.
3. Repeat the above steps 100 times to generate a distribution of expected D values under the null hypothesis.

If the observed D value is less than the 100 random D values, the null hypothesis is rejected and one concludes that the observed pattern deviates significantly from random. This is a conservative test; confidence limits based on 100 simulations are considered adequate for tests at the conventional 5% level (see Kenkel 1993).

MODELING FRACTAL PATTERNS: LÉVY FLIGHTS

Animal movements over finite time intervals rarely achieve a strictly random pattern (Gautestad and Mysterud 1993). Animal positions are determined in part by previous locations, since travel distances are constrained by organism mobility. Movement patterns therefore have a memory component. The Lévy flight power law contains such a memory component making it well suited for modeling animal movements. The Lévy flight model can be used to simulate fractal patterns (Mandelbrot 1983), and time series animal movement data (Viswanathan et al. 1996). The model is a special case of the random walk, in which "step" lengths are selected randomly from a power law probability distribution. Conventional random walks, by contrast, assume that step lengths are constant. A fractal point pattern, termed Lévy dust, is obtained by plotting the set of landing points between Lévy flights. Sequentially connecting the points generates a path (Lévy flight random walk) of the same fractal dimension as the corresponding point pattern (Mandelbrot 1983). In this sense, there is a close relationship between the path and point pattern approaches to fractal analysis.

Although mathematically rigorous, Lévy dust cannot be simulated. However, an approximate realization on a two-dimensional torus is obtained from a set of n finite steps of a random walk (Ogata and Katsura 1991). Specifically, each flight is a random vector with polar coordinates $(R;\Theta)$. The azimuth Θ is selected uniformly and independently from the interval $[0, 2\pi]$, while the radius R is chosen independently according to conditional probability:

$$\Pr(R > r|R > r_0) = 1 \text{ if } r \leq r_0, \text{ otherwise } = (r_0/-r)^D, \qquad (6.4)$$

where r_0 is the minimum flight distance, and D is the fractal dimension of the simulated pattern.

This is implemented by generating R values according to the power law distribution:

$$R = r_0(1 - x)^{-1/D}, \tag{6.5}$$

where x is a random uniform value (0,1). Provided that n is very large, the resulting point pattern has fractal dimension D and is self-similar over a range of scales from r_0 to the torus distance. Different degrees of self-similar contagion are readily simulated by varying the parameter D in Eq. (6.5).

EXAMPLE: SAGE GROUSE LOCATION DATA

To illustrate the fractal approach, we examined the utilization distribution of a sage grouse population in northwest Colorado. Sage grouse may travel large distances between winter and summer habitat, but movements of 1–5 km are typical within a season (Beck 1977, Connelly et al. 1988, Hagen 1999). Annual movement patterns are closely linked to the availability and spatial distribution of suitable habitat, as sage grouse generally select large, landscape-scale habitat patches (Patterson 1952, Oyler-McCance 1999). Within these large patches, habitat selection is a function of vegetation composition and quality (Beck 1977, Fischer et al. 1996) and topographic features (Hupp and Braun 1989). This hierarchy in habitat selection makes the species well suited for testing the fractal approach to radiotelemetry data analysis. Here we use the generalized entropy and Lévy flight modeling to test the hypothesis that sage grouse locations exhibit self-similar fractal properties. Specifically, we address the following questions:

1. Is the sage grouse utilization distribution statistically self-similar?
2. If the utilization distribution is self-similar, what is the degree of spatial contagion?
3. What factors contribute to the degree of spatial contagion?

Study Area

The sage grouse population studied occurs within a 1400 km^2 area of the Piceance Basin and Roan Plateau region, northwest Colorado. Suitable sage grouse habitat in this region is highly fragmented, the result of both natural and human-induced processes. The study area is a structural basin dissected by parallel undulating ridges, producing a highly fragmented and scale-invariant habitat landscape. Elevation ranges from 1800 to 2700 m, but sage grouse are generally restricted to middle and upper elevational regions where sagebrush (*Artemisia* spp.) is most abundant. Agricultural practices have altered or degraded sagebrush habitat at the periphery of the study area, and fossil fuel exploration and extraction have resulted in localized habitat degradation. Colonization by pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus utahensis*), the invasion by nonnative weeds, and domestic cattle grazing have also contributed to habitat fragmentation in the area.

POPULATION SAMPLE

Male and female grouse were night-trapped on or near lek sites during the breeding season, using spotlights and long-handled nets (Giesen et al. 1982). In total, 44 individuals were trapped at six of eight known active leks. Each bird was fitted with a 14-g lithium battery or a 20-g solar-powered radio ($< 3\%$ of body mass). To ensure that the sample was representative of the population, 25 individuals having inadequate relocation information (fewer than 15 radiotelemetry fixes) were excluded from consideration. The remaining 19 individuals had 27 ± 5 relocations and were representative of all six of the sampled leks. We feel that these individuals are representative of the population as a whole, particularly given that sage grouse are capable of traveling considerable distances (Fig. 6.1). Sage grouse locations were documented from April 1997 to December 1998. Attempts were made to relocate radio-marked individuals every week from June to August, and every 2 weeks otherwise.

DATA ANALYSIS

Self-Similarity and Fractal Dimension Estimation

We obtained fractal dimension estimates for the population using the box counting method. A 96×96 grid was placed over the 44×44 km study area and occupancy at box sizes 4, 6, 8, 12, and 16 determined. Smaller box sizes were not used, as Lévy flight fractal simulations at $n = 519$ revealed a strong dilution effect. The cluster ($q = 0$), information ($q = 1$), and correlation ($q = 2$) fractal dimensions were determined from these data.

Random Simulations

We used Monte Carlo simulation to obtain 100 realizations of a random spatial pattern of $n = 519$ points. For each realization, a 96×96 grid and box sizes of 4, 6, 8, 12, and 16 were used to estimate the cluster, information, and correlation dimensions. Upper and lower limits of the D estimates were

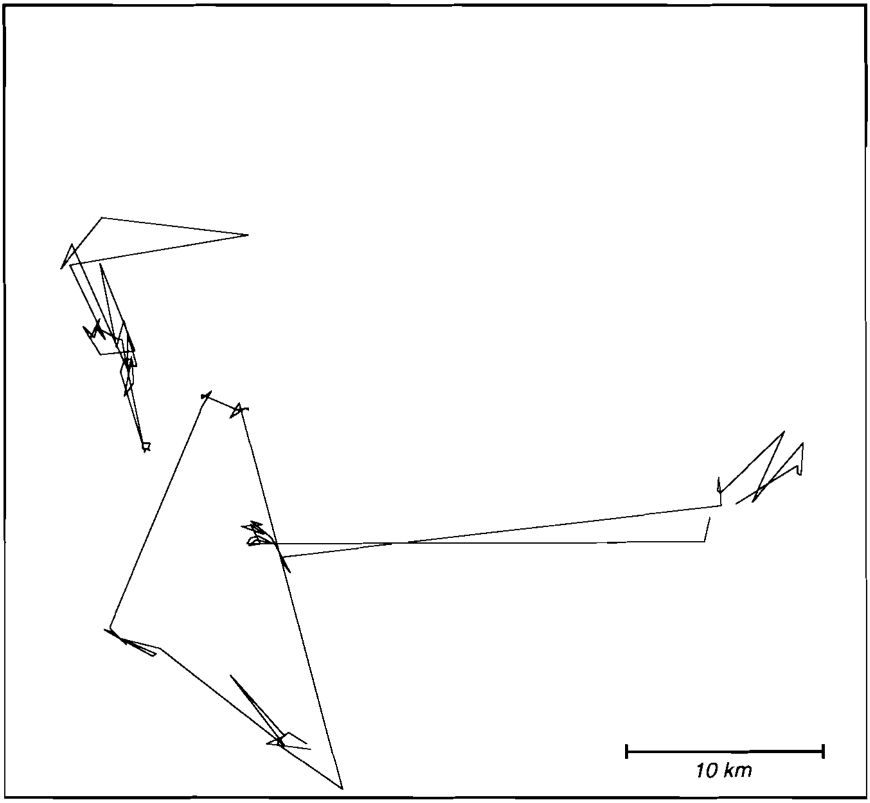

FIGURE 6.1 Movement paths for three individual sage grouse tracked between April 1997 and December 1998 in the Piceance Basin – Roan Plateau region of northwestern Colorado.

determined for the 100 random simulations and compared to the observed D values. In this test, the null hypothesis is that the observed pattern of sage grouse locations is statistically random.

We also statistically compared the observed pattern to a random Lévy dust pattern by simulating Lévy flights at $D = 2$. One hundred realizations of random Lévy dust at $n = 519$ points were obtained and analyzed as above. In this test, the null hypothesis is that sage grouse are randomly foraging on the landscape.

Lévy Flight Model

We tested the appropriateness of the Lévy flight model by comparing the empirical distribution of sage grouse movement distances to that expected from the Lévy flight power law conditional probability, Eq. (6.5). The model was developed at $n = 519$ and $D_0 = 1.06$ (i.e., the empirical fractal dimension of the sage grouse radiotelemetry data).

RESULTS

The observed pattern of sage grouse locations ($n = 519$) displays evidence of strong spatial contagion (Fig. 6.2). Furthermore, the pattern appears scale invariant because the same overall degree of spatial contagion occurs across scales (Fig. 6.3). These empirical observations were confirmed by the fractal analysis. The log-log scatterplots for the q dimensions are linear (Fig. 6.4), and

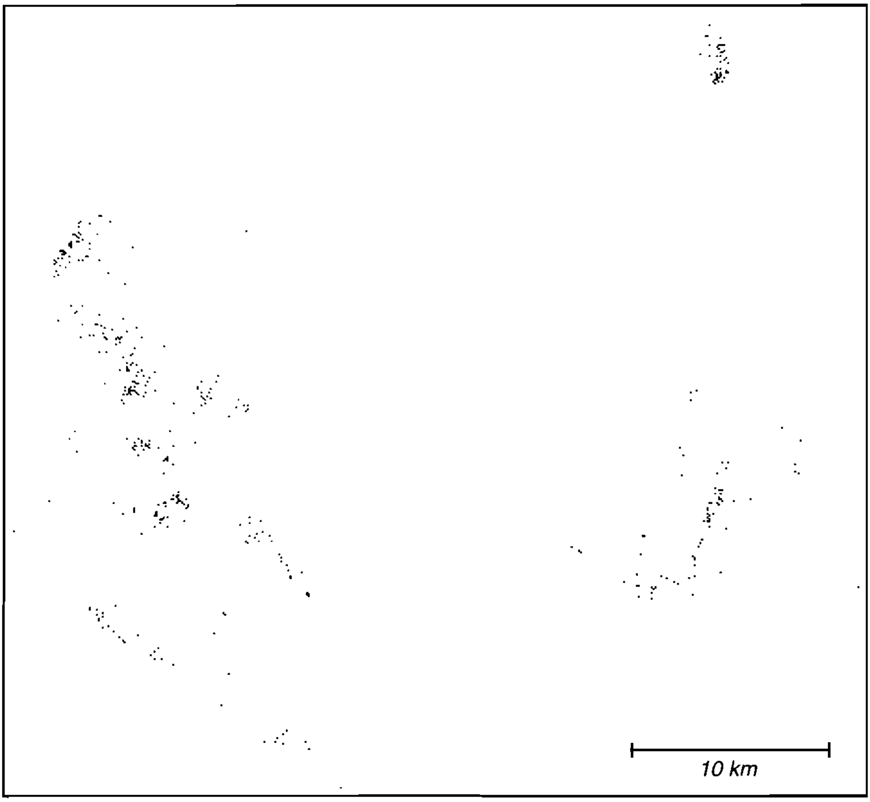

FIGURE 6.2 Spatial pattern of sage grouse relocations ($n = 519$) for all individuals tracked within the study area.

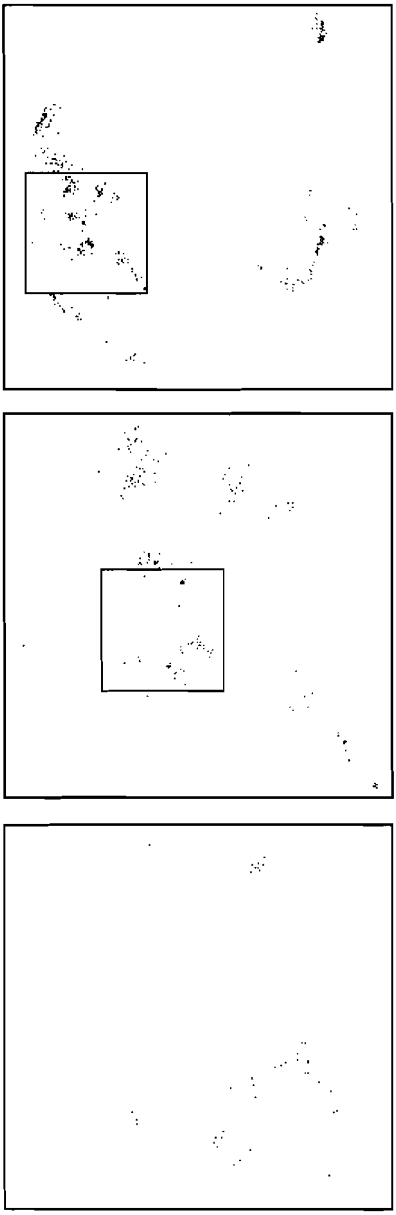

FIGURE 6.3 Sage grouse relocations at three spatial scales, illustrating the self-similar properties of the spatial point pattern. Note how successive magnification (top to bottom) resolves a similar pattern. The middle and lower panels are magnifications of the small box areas in the upper and middle panels, respectively.

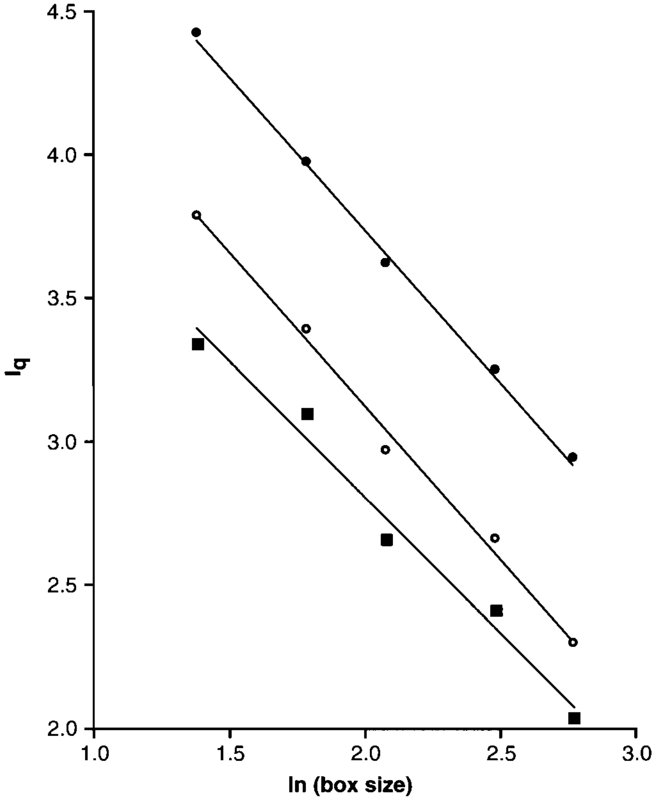

FIGURE 6.4 Power law relationships between I_q and box size (natural log scale) for $q = 0$ (cluster dimension, filled circle), $q = 1$ (information dimension, open circle), and $q = 2$ (filled square, correlation dimension). The fitted lines are principal components.

the Monte Carlo tests indicate significant deviations from both empirical random and random Lévy flight patterns (Table 6.2). For these random patterns, the finite sample size problem ($n = 519$) results in q dimensions that deviate strongly from the theoretical value of $D = 2$. However, the observed q dimensions are much lower still, indicating strong spatial contagion of grouse locations.

The empirical distribution of movement distances adheres closely to the Lévy flight power law model (Fig. 6.5). This confirms that movements are statistically self-similar at $D_0 = 1.06$ (i.e., the frequency distribution of sage grouse dispersal distances is log-log linear). For example, 195 movements were less than 0.5 km, but only 7 were between 5.0 and 5.5 km. Deviations

TABLE 6.2 Observed q-Dimensions (Cluster, Information, and Correlation) for the Sage Grouse Point Pattern ($n = 519$)

	D_q		
Data	$q = 0$	$q = 1$	$q = 2$
Observed	1.06	1.07	0.95
Random[a]	1.59–1.67	1.53–1.63	1.44–1.58
Lévy[a]	1.51–1.63	1.55–1.66	1.51–1.66

[a] Range of 100 simulations, $n = 519$.

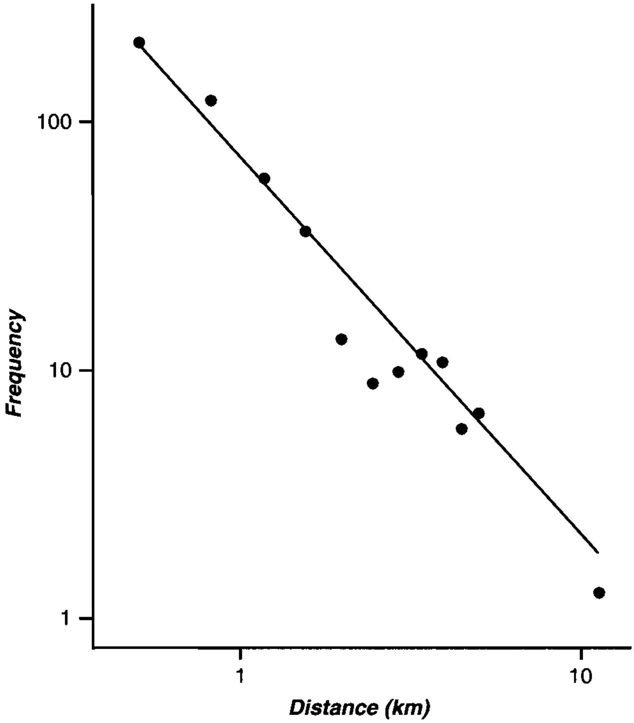

FIGURE 6.5 Empirical frequency distribution of sage grouse movement distances (filled circles) and the theoretical Lévy flight power law model at $D = 1.06$ (line).

from expectation at intermediate distances (3 to 4.5 km, Fig. 6.5) are likely attributable to the small sample size and the comparative rarity of longer distance dispersal events.

For illustrative purposes, we simulated Lévy flight point patterns for fractal dimensions $D_0 = 2.0, 1.5$, and 1.06 at $n = 519$ (Fig. 6.6). The simulation at $D_0 = 1.06$ results in a pattern that is statistically similar to the sage grouse location data (also $D_0 = 1.06$, Fig. 6.2). At $D = 1.5$ the pattern is somewhat less strongly contagious, whereas at $D = 2.0$ points are well dispersed.

DISCUSSION

Self-Similarity

The utilization distribution of the sage grouse population is statistically self-similar, as demonstrated by both the linear log-log plot of spatial location data and adherence of dispersal distances to the Lévy flight model. A statistically self-similar pattern is consistent with hierarchical habitat selection, an idea that has allowed researchers to synthesize resource use studies into a single approach (Johnson 1980). Just as Johnson's (1980) selection order has unified resource selection studies, self-similarity has the potential to unify the study of movements through time and across individuals. Self-similarity may be an adaptive strategy for optimal foraging in habitats where resource availability is also scale invariant (Viswanathan et al. 1996) and may be of adaptive significance in avoiding predators (Bascompte and Vila 1997). While Johnson (1980) provides a quantitative approach to the problem of scaling and habitat selection, his approach is aspatial. Our results indicate that a full understanding of the hierarchical nature of habitat selection requires examination of the scaling properties of location data. The fractal power law distribution is appropriate here because, scale-invariant patterns cannot be properly characterized using a Poisson random walk model (Viswanathan et al. 1996).

Degree of Contagion

The sage grouse movement data are highly contagious across scales ($D_0 = 1.06$). Unlike standard home range estimators, the fractal dimension explicitly characterizes the scaling properties of a species' utilization distribution (Gautestad and Mysterud 1993). Utilization distributions are often characterized by voids (i.e., unvisited areas within the home range), but these are not fully characterized in standard two-dimensional home range analysis (see Chapter 5). Fractal analysis, by contrast, explicitly quantifies the spatial features of voids in the species home range. In this sense, home range and

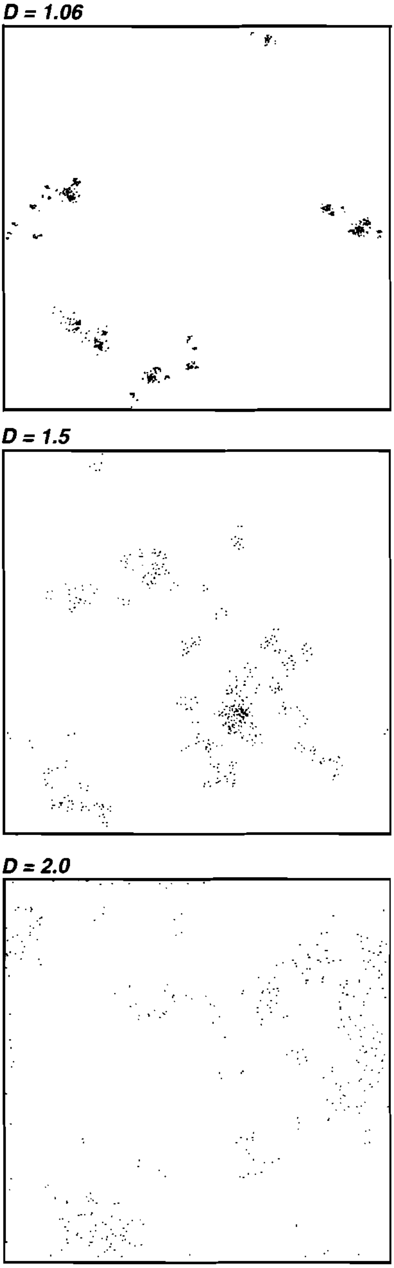

FIGURE 6.6 Example Lévy flight point patterns at $n = 519$, for three cluster fractal dimensions ($D = 1.06$, $D = 1.5$, and $D = 2.0$).

fractal analysis are complementary approaches to characterizing utilization distributions.

Factors Affecting Spatial Contagion

The observed contagion of sage grouse locations is best understood in terms of the spatial configuration of available habitat, landscape physiography, and distribution of leks. Sage grouse generally select relatively large patches of sagebrush at the landscape level (Patterson 1952, Oyler-McCance 1999), while movements within patches are determined by a suite of finer scale variables (Hupp and Braun 1989). While apparently suitable sage grouse habitat (sagebrush/deciduous shrub, sagebrush, and grassland communities) comprises about two-thirds of the Piceance Basin study area, only a very small proportion of this is consistently used by the population. An observational study in the North Park region of Colorado found that sage grouse use only 7% of the available winter habitat (Beck 1977). Landscape-scale habitat features appear to be important in explaining these findings. For example, the central region of our study area consists of long but very narrow (< 0.5 km) patches of sagebrush surrounded by agriculture and pinyon-juniper woodlands (Fig. 6.7). Such a spatial configuration is apparently unsuitable for sage grouse, as few birds used these patches and no birds were recorded traversing this area.

Self-similarity in the sage grouse utilization distribution indicates that movements within large sagebrush patches are also highly contagious. Preferred sage grouse habitat (sagebrush and grassland) is patchy across scales, and habitat use analyses (using the selectivity index; Manly et al. 1993) revealed strong habitat selection by sage grouse at all spatial scales (Hagen 1999). This result suggests that sage grouse movements are strongly affected by scale-invariant features of the habitat (Viswanathan et al. 1996, Etzenhouser et al. 1998, Ferguson et al. 1998). Physiography may also play a role, as sage grouse are most often found on the upper reaches of sagebrush-covered ridges of the study area (Hagen 1999). In addition, seasonal congregation at lek sites may contribute to coarse-grained spatial contagion (Bradbury et al. 1989). What emerges is a picture of a population subjected to numerous scale-invariant factors that affect movement patterns across all spatial scales.

FUTURE DIRECTIONS

Many ecologists have embraced fractal geometry as the rationale for spatial extrapolation and interpolation of natural phenomena (Hastings and Sugihara 1993, Milne 1997). While a strong case can be made for using the power law

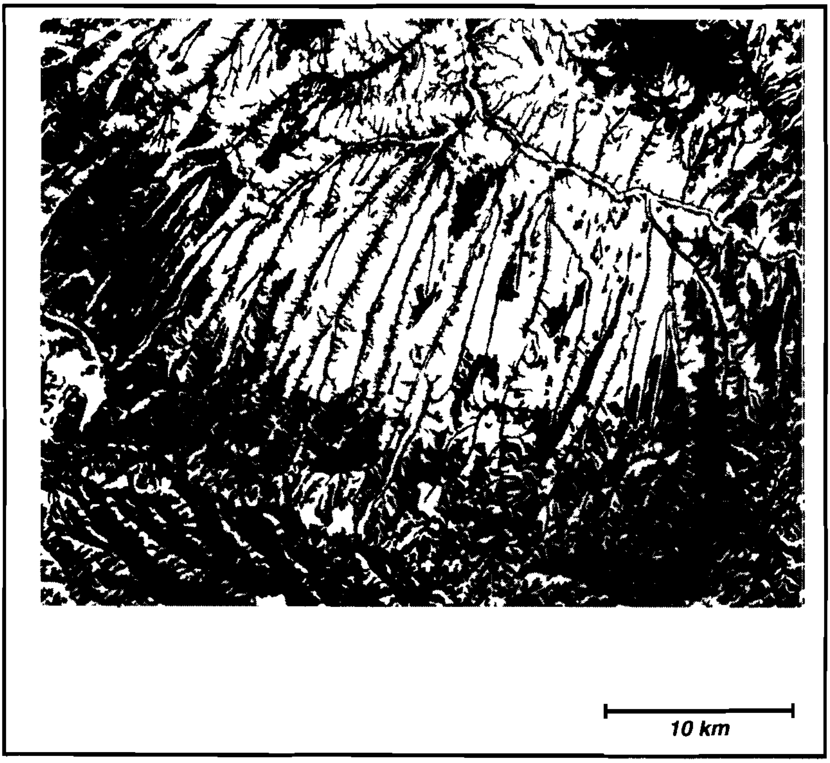

FIGURE 6.7 Spatial distribution of sagebrush habitat (gray) in the main portion of the study area.

distribution to quantify animal movements, does this application have a more fundamental basis? Certainly both the Gaussian and power law distributions have wide applicability in describing and modeling nature (Turcotte 1997). If spatio-temporal events are statistically independent, the central limit theorem provides the basis for application of the Gaussian distribution; examples include classic home range analyses and random walk models. Unfortunately, animal movement data must be simplified to achieve statistical independence (Swihart and Slade 1985a, Turchin 1998), suggesting that this basic assumption is untenable. By contrast, scale invariance of spatio-temporal events provides the rationale for applying the power law distribution (Gautestad and Mysterud 1993). In describing and modeling animal movements, we believe that scale invariance is a more reasonable assumption than statistical independence (Viswanathan et al. 1996).

Fractal geometry provides new and valuable insights into animal movement data that cannot be obtained from traditional home range analyses, first-order spatial statistics, and habitat selection estimation. The fractal dimension quantifies and characterizes the habitat available to a species at different scales, in both space and time (Milne 1997). In this respect, fractal analysis can be viewed as complementary to more traditional approaches. The Lévy flight model produces statistically self-similar clusters of used habitat and voids of unoccupied habitat (Viswanathan et al. 1996), a pattern that wildlife biologists may find intuitive and appealing. Scale-invariance of utilization distributions thus has far-reaching consequences for radiotelemetry data analysis and the modeling of animal movements.

A limitation of the fractal approach is that a large sample size is required to overcome the dilution effect. Point pattern analysis requires a minimum of about 500 radiotelemetry fixes (although thousands are needed to completely overcome the dilution problem). Similarly, movement path analysis requires finely detailed temporal data to properly characterize a path's fine-scale features. Insufficient sampling exacerbates the dilution effect and may lead to the possibly erroneous conclusion that a fractal structure is not statistically self-similar (cf. Panico and Sterling 1995, Turchin 1996). Recent advances in global positioning system tracking and microchip technology have made it possible to collect large amounts of spatially accurate and temporally continuous location data from marked individuals (Cohn 1999). Large data-sets will allow us to explore the self-similar scaling features of animal movements with more confidence.

Many ecological studies have used fractal geometry as a descriptive tool, but most have stopped short of prediction (Kenkel and Walker 1996, Milne 1997). A major challenge for the near future is to determine the processes underlying observed animal movements. Recent studies have hypothesized that movements are matched to the self-similar complexity of habitat and resource availability in space and time (e.g., Viswanathan et al. 1996, Etzenhouser et al. 1998), but the specific mechanism by which this occurs is unclear. A second challenge is to incorporate self-similarity and hierarchical scaling into wildlife biology models and management tools. There has been much theoretical progress in this area (e.g., Ritchie 1998, With et al. 1999, references therein), but such models require field-testing and validation. While it is difficult to predict with certainty the future of fractal analysis in wildlife biology, we are confident that self-similarity and the power law will have important roles in describing and modeling animal movements.

SUMMARY

Animal location data are commonly obtained by tracking radio-marked individuals. Recent technological advances in radiotelemetry offer the potential to collect large amounts of spatially accurate location data, allowing researchers to formulate new and fundamental questions regarding animal movement patterns and processes. We outline a fractal-based approach for analyzing spatial location data that uses Lévy flight modeling and generalized entropy. In this approach, each animal location is viewed as a sampled coordinate from an underlying spatio-temporal distribution. The set of radiotelemetry fixes constitutes a constellation of points known as a utilization distribution. Fractal analysis quantifies and characterizes the degree of spatial contagion of a utilization distribution and determines whether the distribution is statistically self-similar. As such, it offers valuable insight into how a population uses the landscape. The method is illustrated using radiotelemetry data ($n = 519$ locations) from a disjunct population of sage grouse in northwest Colorado.

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