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FRACTAL ANALYSES OF ANIMAL MOVEMENT: A CRITIQUE¹

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Abstract. Several recent papers developed and applied a novel approach for the analysis of animal movement paths, based on calculating the paths' fractal dimensions. The estimated fractal dimension is used to describe the pattern of the interaction between animal movement and landscape heterogeneity, and possibly to extrapolate movement patterns of organisms across spatial scales. Here, I critically examine the key assumption of the fractal approach: that the estimated fractal dimension is constant over some biologically relevant range of spatial scales. Use of a correlated random walk as a null hypothesis for movement suggests that the fractal dimension should grade smoothly from near 1 at very small spatial scales to near 2 at very large spatial scales. Several empirical data sets exhibit a qualitative pattern in agreement with this prediction. I conclude that ecologists should avoid calculating and using the fractal dimension of movement paths, unless self-similarity (a constant fractal dimension) for some range of spatial scales is demonstrated. An alternative approach employing random-walk models provides a more powerful framework for translating individual movements in heterogeneous space into spatial dynamics of populations.

Key words: *animal movement; correlated random walk; fractal dimension; quantitative analysis of movement; spatial scales.*

INTRODUCTION

How can we meaningfully extrapolate ecological information across spatial scales? This is one of the central issues in landscape ecology (Gardner et al. 1989, Turner and Gardner 1991, Levin 1992, Wiens et al. 1993a). Ecologists are attempting to understand and predict processes occurring at landscape, continental, or even global scales (Turner and Gardner 1991), yet most experimental data are collected at much smaller spatial scales (Kareiva and Anderson 1988). This difficulty is especially acute when we consider studies designed to quantify movement of organisms in heterogeneous environments. Movement is the glue that connects local population dynamics in space, and it is now widely appreciated that quantitative studies of population redistribution in the field are a necessary component of any research program aiming to understand spatial population dynamics. However, movement studies, and especially detailed analyses of paths traced by animals, are typically done at small spatial scales.

It was recently proposed that ecologists can usefully employ a novel approach, relying on *fractals* (Mandelbrot 1983) to describe and extrapolate patterns of individual movement (Jander 1982, Dicke and Burrough 1988, Milne 1991). A number of empirical applications and theoretical investigations of this approach have appeared in the last few years (Crist et al. 1992, Fourcassie et al. 1992, Johnson et al. 1992a, b, Wiens et al. 1993a, b, 1995, With 1994). Fractal analysis of paths extends the hope that, by identifying scale-

independent properties of movement process, we will be able to use the path data collected at patch or within-habitat scale to gain insights into the spatial population dynamics at the landscape level. The key question, however, is whether or not the fractal dimension of movement paths is constant over some meaningful range of scales. Such self-similarity is required if one wants to extrapolate mechanisms from a small to a large spatial scale (Sugihara and May 1990). Unfortunately, many recent articles (see Wiens et al. 1995 for a summary) simply assume that the fractal dimension of a movement path is scale-independent. Here, I argue that before the fractal model is used in an analysis of animal movement, this critical assumption must be tested.

DEFINING AND ESTIMATING THE FRACTAL DIMENSION

The logic of the fractal approach can be intuitively understood by considering two extreme representations of organism movement. One extreme is an organism moving along a perfectly linear path. Since the path is a line, its spatial dimension is $d = 1$. No matter what the resolution at which we measure this path, its measured length will always be the same. The second, and opposite, extreme is the Brownian motion of, for example, dye particles in a solution. A dye particle traces a very convoluted path. Depending on how finely we sample particle positions, we will get different estimates of the path length. Thus, a Brownian path and the coast of England are alike, in that the smaller our measuring stick, the longer their apparent length. Actually, Brownian paths in the plane have the fractal dimension $d = 2$, suggesting that such paths visit all points in a portion of two-dimensional space, leaving

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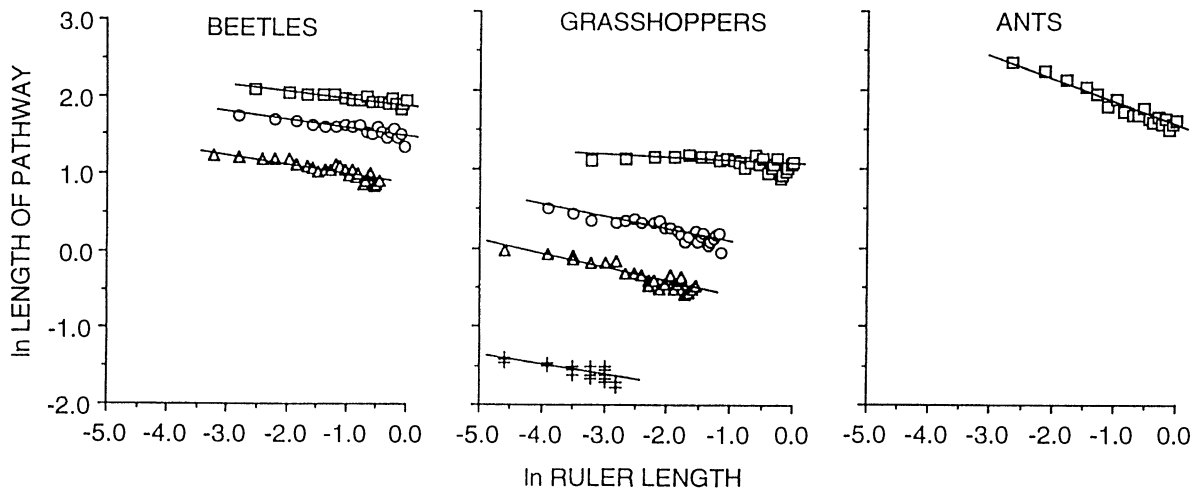


FIG. 1. Regressions showing the relationship between length of insect path (L) and measurement scale (λ) for representative beetles, grasshoppers, and ants. Beetles: *Eleodes hispilabris* (squares), *E. obsoleta* (circles), *E. extricata* (triangles). Grasshoppers: *Xanthippus corallipes* (squares), *Psoloessa delicatula* (circles), *Opeia obscura* adult (triangle) and nymph (cross). Ants: *Pogonomyrmex occidentalis* (squares). (From Wiens et al. 1995.)

no areas unfilled. (A very helpful discussion of the nature of Brownian motion can be found in Segel 1978: 171; see also Mandelbrot 1983 and Hastings and Sugihara 1993.)

Linear and Brownian motion are two theoretical "limiting cases," and we might expect that the dimension characterizing paths of real organisms will lie somewhere between the extremes $d = 1$ and $d = 2$. This suggests that the dimension d may provide a measure of the path "sinuosity" or "tortuosity," with d near 1 characterizing fairly linear movement, and d closer to 2 being characteristic of "Brownian-like" movement. We will call d the *fractal dimension* of movement. The key assumption here, as I have stated, is that d is a *scale-independent* parameter. That is, if we measure d for paths of some organism that are several centimetres long, it will be the same as d measured for paths measured on the scale of metres and hundreds of metres. Such paths can be modeled as a modified Brownian process, with appropriately scaled increments in space and time to ensure a constant fractal dimension (see Sugihara and May 1990: Box 3). I will refer to such models as "fractal Brownian processes."

In practice, the fractal dimension of a path is estimated by the "dividers" method (Sugihara and May 1990), using the following formula:

$$L(\lambda) = k\lambda^{1-d}, \quad (1)$$

where $L(\lambda)$ is the length measured using a particular length scale λ , d is the fractal dimension, and k is some constant of proportionality. A range of λ is used, and fractal dimension is estimated by a log-log regression of $L(\lambda)$ on λ .

An example of a fractal analysis of path data is given by With (1994). She used estimated d to assess how different species of grasshoppers may perceive land-

scape structure. Regressions of path length on λ indicated that movement patterns of smaller species were characterized by higher fractal dimensions (Fig. 1). With (1994) suggested that the two smaller species are interacting with patch structure at a finer scale of resolution than the large species.

A similar analysis of paths of three species of *Eleodes* beetles was performed by Crist et al. (1992) (Fig. 1). They found that, although net displacement increased markedly with beetle size and decreased with habitat complexity, the fractal dimensions of paths were similar across vegetation types and among species. Crist et al. (1992) concluded that the three species interacted with the heterogeneous landscape in essentially similar ways, despite differences in the overall scale of dispersal. A third example is the work of Crist and Wiens (1994) on ant movement (Fig. 1).

Johnson et al. (1992a) investigated the fractal nature of movement using computer models. They simulated correlated random walk in a spatially uniform environment on the computer, and observed that the slope of the curve relating net squared displacement to time (on a double-log plot) changed with time. They interpreted this shift as a discrete crossover from one kind of movement pattern to another. Another model investigated by Johnson et al. (1992a) was a simple random walk in a fragmented environment that was modeled by a percolation process (in which some proportion of positions was made inaccessible to the random walker). Again, Johnson et al. (1992a) suggested that a crossover is evident. Finally, Johnson et al. (1992a) analyzed paths of *Eleodes* beetles and claimed that there was a discrete shift in the fractal exponent at the spatial scale characterizing environmental heterogeneity (the size of grass and bare soil patches), with a second shift at scales characterizing home range activity.

IS THE FRACTAL DIMENSION SCALE-INDEPENDENT?

I now turn to a critical examination of the key postulate on which validity of the fractal analysis is based. In order to extrapolate ecological information across spatial scales using the fractal dimension, one has to demonstrate that paths are characterized by strict self-similarity; in other words, that there is a scale-independent fractal dimension. In practical terms, this means that we have to show that the data patterns on various log-log plots are linear: the slope does not change with scale. The analyses of Crist et al. (1992), Crist and Wiens (1994), and With (1994) have implicitly made this linearity assumption, whereas Johnson et al. (1992a) assumed that patterns are piecewise linear, with breaks corresponding to some biologically meaningful scales. Wiens et al. (1993a) go further and state this assumption as a conclusion: "because the fractal dimension has the desirable feature of being constant over a finite range of measurement scales, it is useful in comparing movements of insects that may respond to the patch structure of the environment at different absolute scales."

An alternative hypothesis is that *the fractal dimension is not constant, but changes continuously with scale*. A simple, but very powerful framework for representing organism movement is the correlated random walk (Kareiva and Shigesada 1983, Turchin 1996). Correlated random walk (CRW) behaves like linear movement at very small spatial scales (specifically, at the scale comparable to the organism's body size), and like Brownian motion at very large scales (Turchin 1996). Thus, we should expect that the dimension d estimated from a CRW path would grade smoothly from 1 to 2 as the spatial scale λ is increased. To illustrate this idea, I used the computer to generate a CRW path and then applied the fractal analysis to the simulated path. To generate the path, I assumed that organisms moved one spatial unit per time step (that is, with constant speed), and that the distribution of the turning angle between successive moves was a circular normal, with the standard deviation of $\pi/9$ radians (20°). A strong correlation in the direction between successive steps was chosen to ensure that the path would be close to linear at the smallest scale.

The fractal analysis of a path consisting of 10 000 steps is shown in Fig. 2. For log ruler lengths <1.0 , the estimated slope is very close to 0, whereas for log ruler lengths >1.5 , the estimated slope is ≈ -1 . Thus, the fractal dimension d at very small λ is ≈ 1 ; and at very large λ , d is ≈ 2 . It is evident in Fig. 2 that the gradation is smooth; in other words, there is no scale-invariant slope for any range of measurement scales.

When working with real data, we are likely to be limited to a restricted range of λ , within which the degree of curvature will not be very noticeable. We may confidently estimate a fractal dimension from the path data, but this measure will have little biological

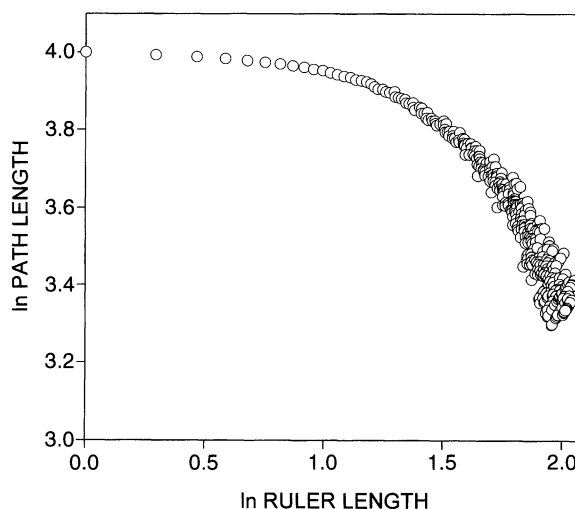


FIG. 2. Calculating the fractal dimension of a simulated path resulting from a correlated random walk.

meaning. Any particular estimate of d will reflect not how animals interact with a fragmented landscape, but rather will be an artifact of the scale at which the investigator happened to measure paths, and where that scale fits within the spectrum of d from 1 to 2 for each species. Moreover, unless the estimated d is already close to 2, any extrapolation to greater spatial scales will be in error.

Certain features of data in Fig. 1 suggest that paths of real organisms may exhibit the patterns predicted by the CRW model. In particular, in all species but two (the ants and the top regression for beetles), there appears to be a slight downward curvature; the data points at both small and large λ tend to be below the fitted line. Similarly, Dicke and Burrough (1988) reported that the estimated d was affected by the range of ruler lengths used in their analysis; increasing the maximum value of λ resulted in an increased estimate of d (see Dicke and Burrough 1988: Fig. 4). These qualitative patterns are suggestive and can be explored graphically by plotting fractal dimension as a function of scales (e.g., Krummel et al. 1987), but there is a need for a formal statistical test to distinguish between the hypotheses of a fractal Brownian process and a CRW process. One possible approach is to test whether or not adding a quadratic term to the log-log regression will significantly increase the proportion of explained variance. The problem with this approach, however, is that it assumes a fractal Brownian process as the null hypothesis (it may be argued that, instead, we should start with CRW as a null hypothesis, since it has already proved its worth in many applications: see Kareiva and Shigesada 1983, Cain 1990, 1994, Turchin 1991). If the power of the test is low (because of high variability and/or low sample size), then we may accept the null hypothesis by default. Another difficulty is that data points in log-log regressions coming from the same

path are probably autocorrelated, so that standard statistical tests would be inappropriate. Thus, we should use each path as a single data point (Turchin et al. 1991, Wiens et al. 1993a). Based on these considerations, I propose the following test for downward curvature in log-log plots. First, a quadratic curve is fitted to the data, separately for each individual pathway. Next, one counts the number of negative vs. positive fitted coefficients associated with the quadratic term. Finally, one determines whether or not the number of negative coefficients is significantly greater than would be expected under the null hypothesis that negative and positive coefficients are equally likely.

CONCLUSION

If paths of study organisms are better described by the CRW framework than by a fractal Brownian process, then attempting to estimate a constant fractal dimension from such data will not likely lead to meaningful results. Thus, it is imperative to statistically test the assumption of the constant slope before proceeding with the rest of the fractal analysis. Which of the two models, CRW or fractal Brownian, provides a better framework for analyzing movement paths is an empirical question that can, and should, be resolved using the data on movements of actual organisms.

Here, my primary focus has been on whether or not the fractal dimension is constant over some biologically relevant range of spatial scales. I also have a broader concern: the fractal analysis of paths is designed to yield a phenomenological, rather than a mechanistically-based measure. I completely agree with Wiens et al. (1995) that translating individual movements in heterogeneous space into the spatial distribution of populations is a valid goal. Unfortunately, an index of path sinuosity does not really accomplish this goal. The alternative approach that I advocate (Turchin 1989, 1991, 1996) is based on detailed descriptions of individual movements as random walks. Although called "random," these models can be made very complex and nonrandom, limited only by the capacity of computers to simulate them and the capacity of the human brain to assimilate the results. Predictions about spatial population dynamics can be obtained either by computer simulation or by a more elegant technique, diffusion approximation, that translates random walks into generalized population redistribution models. The latter approach has an advantage in that it connects the detailed descriptions of individual behaviors to a growing theory of spatial population dynamics based on reaction-diffusion models (this theme is developed in greater detail in Turchin 1996).

It is interesting to note that theoretical predictions about what fractal patterns we might expect in nature (e.g., Crist et al. 1992, Johnson et al. 1992a) are based on simulations of random walks. I suggest that we should be applying random walk models directly to movement data, instead of a more complicated ap-

proach that first predicts theoretically, and then estimates empirically, the fractal dimension of paths.

Finally, I am pessimistic that any analysis, fractal or otherwise, will generally be able to identify scale-independent properties of movement patterns useful for translating information gathered at smaller spatial scales into inferences about larger scale phenomena. In principle, a CRW model can be used to predict movement patterns of organisms at a larger scale of spatial heterogeneity than was observed. In practice, higher scale of patchiness is likely to introduce some novel, unpredictable effects. For example, we may understand how an individual insect responds to spatial heterogeneity in host plant distribution within a field. But when attempting to predict spatial redistribution of insects in a patchwork of field and forest, can we simply assume that movement pattern will be unchanged in the forest, or that insects would not perceive and respond to the field-forest boundary? Thus, I doubt that simple rules will solve the problem of translating across the scales. More likely, it will be necessary to do it the hard way, collecting the data, modeling the processes, and testing the models at each appropriate spatial scale.

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