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Using animal movement paths to measure response to spatial scale

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Abstract Animals live in an environment that is patchy and hierarchical. I present a method of detecting the scales at which animals perceive their world. The hierarchical nature of habitat causes movement path structure to vary with spatial scale, and the patchy nature of habitat causes movement path structure to vary throughout space. These responses can be measured by a combination of path tortuosity (measured with fractal dimension) versus spatial scale, the variation in tortuosity of small path segments along the movement path, and the correlation between tortuosities of adjacent path segments. These statistics were tested using simulated animal movements. When movement paths contained no spatial heterogeneity, then fractal D and variance continuously increased with scale, and correlation was zero at all scales. When movement paths contained spatial heterogeneity, then fractal D sometimes showed a discontinuity at transitions between domains of scale, variation showed peaks at transitions, and correlations showed a statistically significant positive value at scales smaller than patch size, decreasing to below zero at scales greater than patch size. I illustrated these techniques with movement paths from deer mice and red-backed voles. These new analyses should help understand how animals perceive and react to their landscape structure at various spatial scales, and to answer questions about how habitat structure affects animal movement patterns.

Keywords Fractal · Domain · Heterogeneity · Hierarchy · Tortuosity

Introduction

Animals live in an environment that is patchy and hierarchical—that is, there are patches within patches. Animals perceive and react to this structure at many different spatial scales, and each aspect of their biology (e.g. foraging behaviour (Fritz et al. 2003), dispersal patterns (Blums et al. 2003), animal orientation (Benhamou 1989), and population dynamics (Lewis and Murray 1993) relates to specific sections of this scale. Wiens (1989) called such sections “domains” and called the boundaries between them “transitions”.

There can be heterogeneity both along spatial scale and through space—domains refer to heterogeneity along spatial scale. For example, an animal may travel towards a certain place and forage for food on the way. There would be two domains: at the large scale the animal travels, and on the small scale the animal forages. In the large domain the movement pattern is homogeneous, as the animal travels in a directed walk; in the small domain the movement pattern is heterogeneous, as the animal enters and leaves patches of food. Scale and pattern intertwine.

In order to understand how animals perceive and react to their landscape structure, we need to detect the boundaries of these domains of scale (i.e. locations of transitions), and then study how the animals react to their landscape within each domain. Thus we need to address both spatial scale and spatial heterogeneity.

Most current techniques of analysis of animal movement paths do not successfully incorporate both spatial scale and heterogeneity. For example, fractal analysis of movement paths (With 1994; Mårell et al. 2002) has been used to study how animals respond to their environment at different spatial scales, but does not deal with the issue of spatial heterogeneity. On the other hand, modelling animal movements with state space models (Blackwell 1997; Jonsen et al. 2003) has represented animals' switching from one type of movement to

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another, but these models have not dealt with the aspect of spatial scale.

This paper presents new methods to analyse animal movement paths. Fauchald and Tveraa (2003) suggested that the distance at which variance in first-passage time is a maximum, indicates the spatial scale at which individuals concentrate their search effort. I extend their method, incorporating fractal analysis and correlations, in order to detect the transitions between domains of scale and incorporate the effects of spatial heterogeneity. I illustrate these techniques with computer simulations of animal movements as well as data from deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*).

Techniques of analysis

Spatial scale

Since different aspects of animal biology are involved in different domains, we might expect the structure of an animal's movement path to change qualitatively from one domain to another. To detect this change, we need to measure path structure as a function of spatial scale, with some measure that reflects animals' behaviour.

One measure of path structure proposed for this use is fractal dimension (Wiens 1989; With 1994). Fractal D is one measure of tortuosity, and for lines is the continuous analogue of discrete geometric dimensions (Mandelbrot 1967). The fractal D for movement paths lies between 1 and 2— i.e. D is 1 when the path is straight and 2 when the path is so tortuous as to completely cover a plane. Fractal D would be influenced by

behavioural aspects such as foraging intensity, navigational ability, and microhabitat selection.

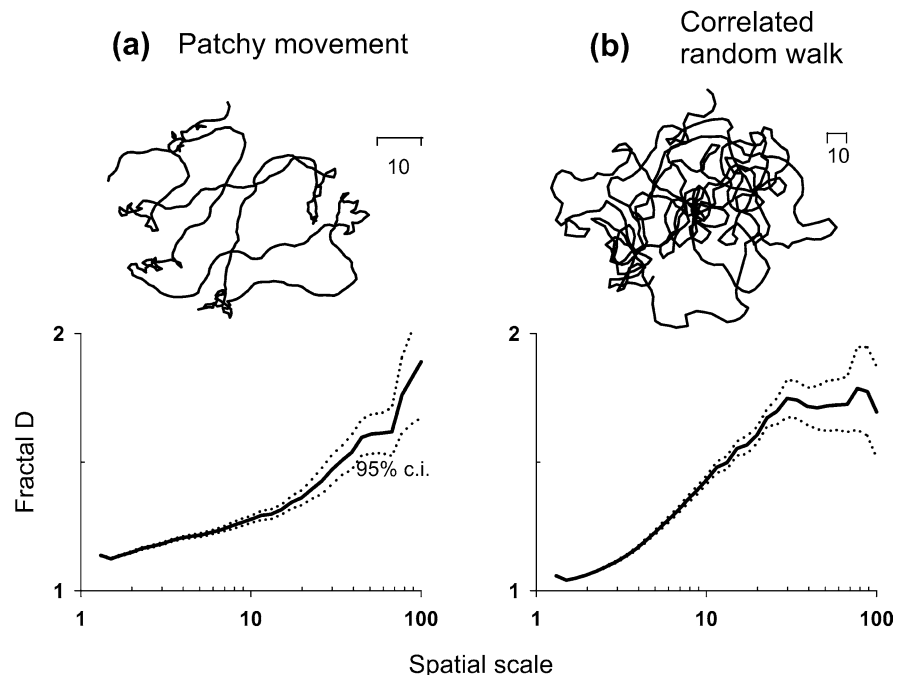
Fractal D is also scale-specific, in that it is calculated over a specific range of spatial scales. Estimates of D versus spatial scale can be obtained by using a narrow range of scales, and then sliding this range along the spatial scale axis. This gives the potential to detect transitions and domains.

What types of changes in D would imply a transition? The expectation of a *qualitative* change in path structure from one domain to another suggests a *discontinuity* in D versus scale (i.e. a “mixed fractal”, *sensu* Russ (1994)); within domains any change in D would be *continuous*. It is difficult to prove whether this holds for all types of animal movements, but all animal movement models (homogeneous and heterogeneous) tested so far that show only continuous changes within domains (V.O. Nams, unpublished). Thus, one might use fractal analysis to separate the range of spatial scales into separate domains, by noting discontinuities in the plot of D versus scale. Note that unlike other applications of fractal analysis to biology (Halley et al. 2004), this does not assume that movement paths are fractal—in fact, it makes use of the changes in D .

Spatial heterogeneity

Variation in space may, however, affect the ability of fractal D to detect transitions. In a patchy environment animals often travel differently in different types of habitats. For example, animals might turn around more often where there is more food (Smith 1974), or they might move slower where there is more protection from

Fig. 1 The movement path in a (a) patchy habitat shows a similar fractal D pattern (Eq. 2) as does the correlated random walk in a (b) homogeneous habitat. Thus, with heterogeneous movement paths, the absence of discontinuities in the plot of fractal D versus scale does not imply the absence of transition points



predators (Berggren et al. 2002). Thus, as an animal goes in and out of different habitats, the fractal D of its movement path may change. However, the calculations of D at each scale, estimate one value over the whole trail—i.e. they assume that path tortuosity remains constant over the whole trail. This combines the D -values from the different habitats into one overall measure.

This combining may hide transition points from one domain to another. For example, Fig. 1a shows a simulated animal travelling in a patchy habitat with patches of size 15 and a spacing of 100. Inside those patches, the animal turns around quite often, but walks quite straight between them. Here there are three domains: below 15, representing movement inside the small patches; between 15 and 100, representing movement between the patches; and above 100, representing large scale movement. We expect the plot of D versus spatial scale to show discontinuities at the transitions between these domains, but there is little difference between this plot and an analysis of a correlated random walk of similar length and tortuosity (Fig. 1b); the tortuous sections inside the patches and the straighter sections outside of the patches averaged out, giving intermediate D values. Thus spatial heterogeneity might decrease the statistical power to detect transitions using fractal D .

This decrease in power not only affects fractal analysis but any method of analysis that explicitly does not consider spatial heterogeneity. For example, Turchin (1996) suggested that instead of analysing movement patterns with fractal analysis, a simulation approach be carried out, using a null hypothesis of a correlated random walk. However, the statistical tests for deviation from a correlated random walk also assume homogeneity along the movement path, and application to

patchy movement might also give false negatives. Consider the example in Fig. 2, of a simulated animal travelling in a habitat with patches of size 5 and a spacing of 10. Inside those patches, the animal turns around quite often, staying inside the patch for 50 steps, but walks quite straight between them. It is obvious that this is not a correlated random walk (Fig. 2), yet the observed net distance travelled per step is not significantly different from the specific values expected (Kareiva and Shigesada 1983) with a correlated random walk model. Thus spatial heterogeneity can decrease the power of this test; the deviations from a correlated random walk model were not detected because of variation along the path. To detect all transitions, we need a way of measuring that variation, not obscuring it.

Variances

One way of measuring movement path heterogeneity is by dividing the path into segments, and estimating the variance in tortuosities among the segments. If the segments are smaller than patches, then variation in tortuosity would be high because some segments would be inside (high D) and some would be outside of patches (low D). If the segments are much larger than patches, then variation in tortuosity among those segments would be low because they would contain both inside and outside patch movement. Thus we would expect variation to be high at and below the scale of patch size, and drop as scale gets larger than patch size.

However, it is not clear what would be the null pattern—i.e. what variation would one expect if there is no patch use? Would it increase or decrease with scale? It would likely depend on the type of movement pattern. For example, if an animal travels with a directed walk on a large scale, but forages quite tortuously on a small scale, then variation in tortuosity can decrease with scale, even without spatial heterogeneity. It is also not known whether a peak necessarily implies patchiness, since variance can change for reasons other than patchiness. More research is needed on these types of relationships.

Correlations

The next measure does give a specific null hypothesis. Suppose we compare tortuosities of pairs of adjacent path segments. If one uses small path segments that are much smaller than the patch size, then likely, both path segments would be either inside or outside of a patch. Thus one would expect a high correlation between the two, because both would have either a high or low tortuosity. When segments are larger, approximately equal to patch size, then when one segment is in a patch (and therefore tortuous), the next is outside of a patch (and therefore straight). Thus, we would expect a negative correlation. Finally, when segments are large

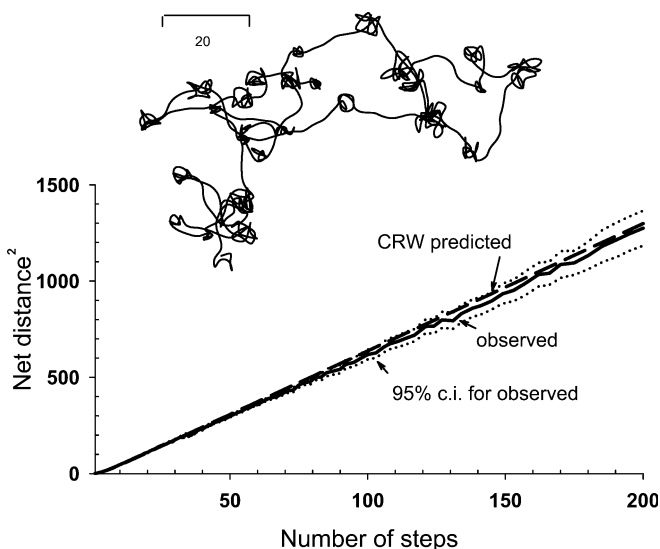


Fig. 2 The predicted net distance values for a correlated random walk (CRW predicted), as a function of the numbers of steps, are similar to the observed values for a simulated movement path in a patchy habitat (given above the panel). Dashed lines represent 95% confidence intervals

enough to cover several patches, then we would expect a zero correlation.

Thus we would expect the following pattern of correlation of tortuosities of adjacent path segments versus scale: positive correlations at sizes below patch size, then dropping to negative at the patch size, and back up to zero as scale gets much larger than patch size. The null hypothesis is clear—if there is no patch use, then we expect zero correlations at all scales, no matter whether animal is walking a random walk, directed walk, or other type.

Methods

Simulations

These methods were tested with simulated animals moving with different movement models, in various types of habitats. The first set of simulations represents the null hypothesis—animals travelling with homogeneous movement paths. I tested both non-directed and directed travel.

To model non-directed travel I used a correlated random walk (Kareiva and Shigesada 1983). At each step there is a certain probability of turning, and if an animal turns, then the direction it turns is chosen randomly from a circular normal distribution. The environment it moves in is homogeneous. This is a *correlated* random walk, because the directional angle is always chosen relative to the previous directional angle. I used Cain's (1985) algorithm for generating the movement, but with steps of equal length. K denotes the turning angle concentration, where a smaller K -value gives a more tortuous walk.

To model directed travel, I considered the following assumptions. Many animals, especially mammals, do not travel completely randomly; they often go towards specific points (Benhamou 1990). Furthermore they have to avoid obstructions, which occur at various spatial scales and often are distributed similarly over a range of scales (i.e. they are fractally distributed; Lathrop and Peterson 1991). Finally most mammals have a home range in which they learn habitat features (Stamps and Krishnan 1999).

Consider the following example that uses these assumptions. Suppose a deer is walking to a certain point. Considering first obstructions at the largest scale, the deer may have to walk around a large hill. On the way to that hill it would encounter smaller obstructions—for example, it may have to walk around a smaller hill. On the way to the smaller hill it may have to avoid even smaller obstructions—e.g. a ravine. And so on, down to the scale of individual footsteps. At the smallest scale, the deer must avoid individual shrubs. The larger obstructions the deer remembers, while the smaller ones it sees as it walks. If the obstructions the deer encounters are fractally

distributed (meaning that at each scale they have the same spatial distribution) then at each scale, we could represent the deviations from the intended path in a similar manner.

I modelled this situation by first choosing starting and ending points. Then I represented the effect of the largest obstruction on the path by randomly selecting a perpendicular deviation at the middle of the path and splitting the path into two around this deviation. I then represented the effect of the next largest obstructions by taking each of the two path segments and repeating the above. This was repeated down to the scale of the animal's step size. The deviations were drawn from a normal distribution with a constant coefficient of tortuosity,

$$C_T = \frac{\sqrt{\text{Variance}}}{\text{Segment length}}, \quad (1)$$

which is analogous to the coefficient of variation. The fractal nature of the habitat is incorporated by having a constant C_T at all scales, where a lower C_T -value gives a straighter path. The algorithm is similar to the group of mid-point displacement algorithms for generating fractal lines (Saupe 1988).

For each model, I tested five different path tortuosities, using paths of length 10,000 steps, replicated 50 times, with step sizes of 1. For the correlated random walk I used K -values of 1, 4.5, 10, 20, 50, and for the directed walk I used C_T values of 0.1, 0.2, 0.3, 0.4, 0.5.

The second set of simulations represent the alternate hypothesis—animals moving with heterogeneous movement paths. I modelled four different situations, each with a path of length 2,000 steps, replicated 50 times. Animals moved with correlated random walks both within and between patches. The patch size and distribution were determined dynamically as the simulated animal walked—they were not pre-defined. The four situations are:

(a) Animals travel towards a destination on a large scale, but forage in patches on the way. Animals walk for 50 steps between patches, with a quite a straight path ($K=50$). After 50 steps the animals enter a square patch of size 15x15 steps and forage inside it ($K=5$). Within the patch the animals reflect from the patch edge. After 50 steps they exit the patch and resume the direction of previous travel.

(b) Animals live in an area with small food patches, sparsely distributed. This simulation is similar to (a), except that when exiting a food patch, animals do not resume the direction of previous travel.

(c) and (d) The previous simulations use constant patch sizes. However, more often there is a range of sizes. These simulations were the same as (a) and (b), except that patch sizes and distances between patches varied randomly. Patch size and distance were chosen from a loguniform distribution, with a range of $\pm \log 3$; thus, patch size varied from 15/3–15x3, and distances between patches from 50/3–50x3.

Statistics ¹

I estimated fractal D by two different methods. The first was based on the divider method (Mandelbrot 1967; Milne 1991). The length of the path is measured by walking a pair of dividers of a certain size along the path. If this is done for larger and larger dividers, then the slope of the plot for log (path length) versus log (divider size) is $1-D$, yielding one overall estimate for fractal D over a range of scales (here, “scale” is the size of the dividers). To estimate how D changes with scale, I used a sliding window along the x axis of the log–log path length plot, and used regression to measure the slope of the line within the window (e.g. Krummer et al. 1987). This process was carried out both forwards and backwards along the pathway (V.O. Nams, unpublished).

The second method was the VFracal (Nams 1996). The path is discretized into steps of a fixed length, and a mathematical transformation estimates fractal D from the mean cosine turning angle between those steps (here, “scale” is the length of the two steps together), as follows:

$$D = \frac{2}{1 + \log_2(\cos \theta + 1)} \quad (2)$$

The scale is then the net displacement of the two steps.

The first D estimate is more intuitive and can estimate fractal D over a narrower size range, but the second gives error estimates for individual movement paths, and allows you to combine movement paths measured at different spatial scales. I used the first for the simulations, to get error estimates for many replicate paths, and the VFracal for the field data, to get error estimates for individual paths.

To measure variances and correlations of tortuosities, I used variances and correlations of cosines of the turning angles (since cosine can be transformed into a fractal D).

Error estimates

Errors were estimated in two ways. For the simulations, each path was treated as an individual sample. Thus, each statistic was estimated for each path at each spatial scale, and then estimates were averaged over all paths, with standard errors of means calculated from among-path variation.

For the example mouse and vole paths, I calculated error estimates for each path, using a bootstrapping procedure (as done in Nams 1996). Bootstrapping allows one to calculate estimates that are normally distributed from any estimate of a sample of independent points (Efron and Tibshirani 1991).

Results

The first set of simulations represent the null hypothesis—animals travelling with homogeneous movement paths. For the correlated random walk both fractal D and variance increased sigmoidally with spatial scale (Fig. 3). For the directed walks, fractal D and variance were more constant, with slight changes for the more tortuous paths (Fig. 4). For both types of movement patterns, fractal D and variance plots showed gradual changes, while correlation plots show zero correlation at all scales.

The second set of simulations represented animals moving with heterogeneous movement paths. The fractal D analysis detected (by showing statistically significant peaks) the appropriate patch size for three of the

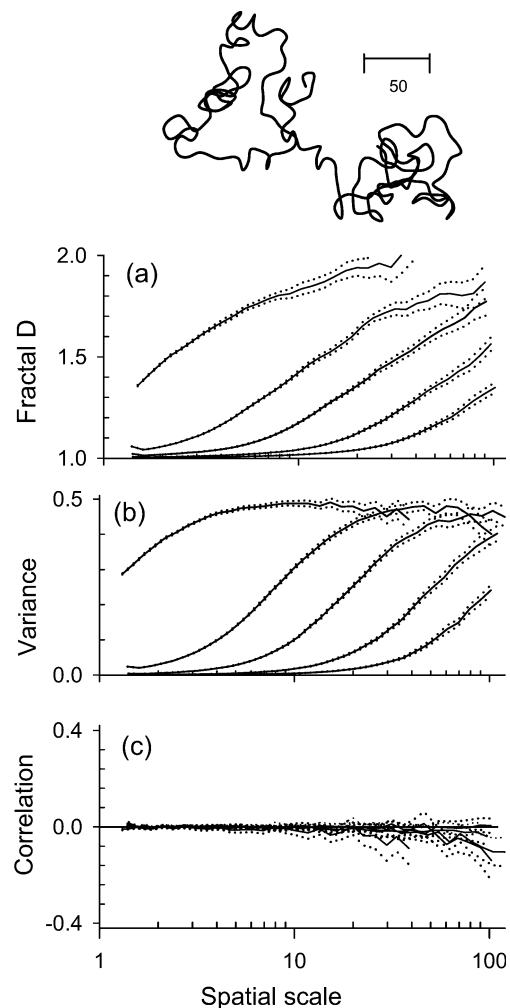


Fig. 3 Analyses of simulated correlated random walks of animals moving in a homogeneous habitat (an example path is given at the top—i.e. a null hypothesis of no heterogeneity). (a) Tortuosity (fractal D , Eq. 2) versus spatial scale. (b) Variance in tortuosity among path segments of length “spatial scale”. (c) Correlation in tortuosity between adjacent path segments of length “spatial scale”. Dashed lines represent 95% confidence intervals

¹Computer programs to carry out all of these calculations can be freely downloaded by contacting the author

types of heterogeneity [(a), (b) and (c); Fig. 5]. Fractal D decreased with scale for (a) and (c), showing the straighter paths on a larger scale, which was caused by the animal travelling in an overall general direction. However for (d), fractal D did not detect the appropriate path size, and showed a similar pattern as the plots for the correlated random walks (Fig. 3). Thus the fractal analyses are a conservative tool for detecting transitions.

The variance analyses also detected (by showing statistically significant peaks) the appropriate patch size for (a), (b) and (c). The peaks were smaller when animals came out of the patch and did not resume the direction they had been previously travelling in (Fig. 5b), or when patch size varied (Fig. 5c, d). When both happened (Fig. 5d) the variance plot showed no peak at all, giving similar results as some of the variance plots from the correlated random walks (Fig. 3). Thus the variance

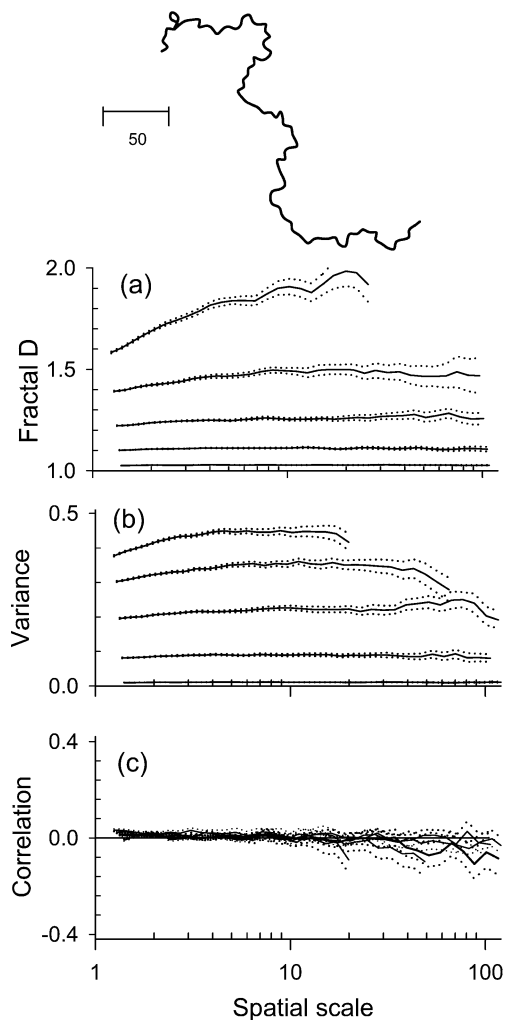


Fig. 4 Analyses of simulated directed travel of animals moving in a homogeneous habitat (an example path is given at the top—i.e. a null hypothesis of no heterogeneity). (a) Tortuosity (fractal D , Eq. 2) versus spatial scale. (b) Variance in tortuosity among path segments of length “spatial scale”. (c) Correlation in tortuosity between adjacent path segments of length “spatial scale”. Dashed lines represent 95% confidence intervals

analyses are also a conservative tool for detecting transitions.

However, in every simulation the correlation plot detected the appropriate patch sizes, showed significant positive values just before the patch size, and usually showed a drop to below zero at the patch size. In simulation (b) the analysis even detected the 50-unit distance between patches. This response is quite robust to varying patch sizes, showing it even when patch size varied by six times. Note that when patch size varied, the correlation did drop below zero, but not always significantly (Fig. 5d). This is likely because the spatial scale at which the smaller patches showed a negative correlation corresponded to the scale at which larger patches showed a positive correlation. Thus transitions would be indicated by a positive correlation at a segment length less than patch size and/or negative at a segment length just greater than patch size.

Field data

I applied these techniques to movement paths from small mammals. The paths are from red-backed voles and deer mice near Truro, Nova Scotia, Canada. Both of these mammals live in the boreal forest, with home ranges of about 50×50 m. They live on the forest floor and in burrows just under the forest floor.

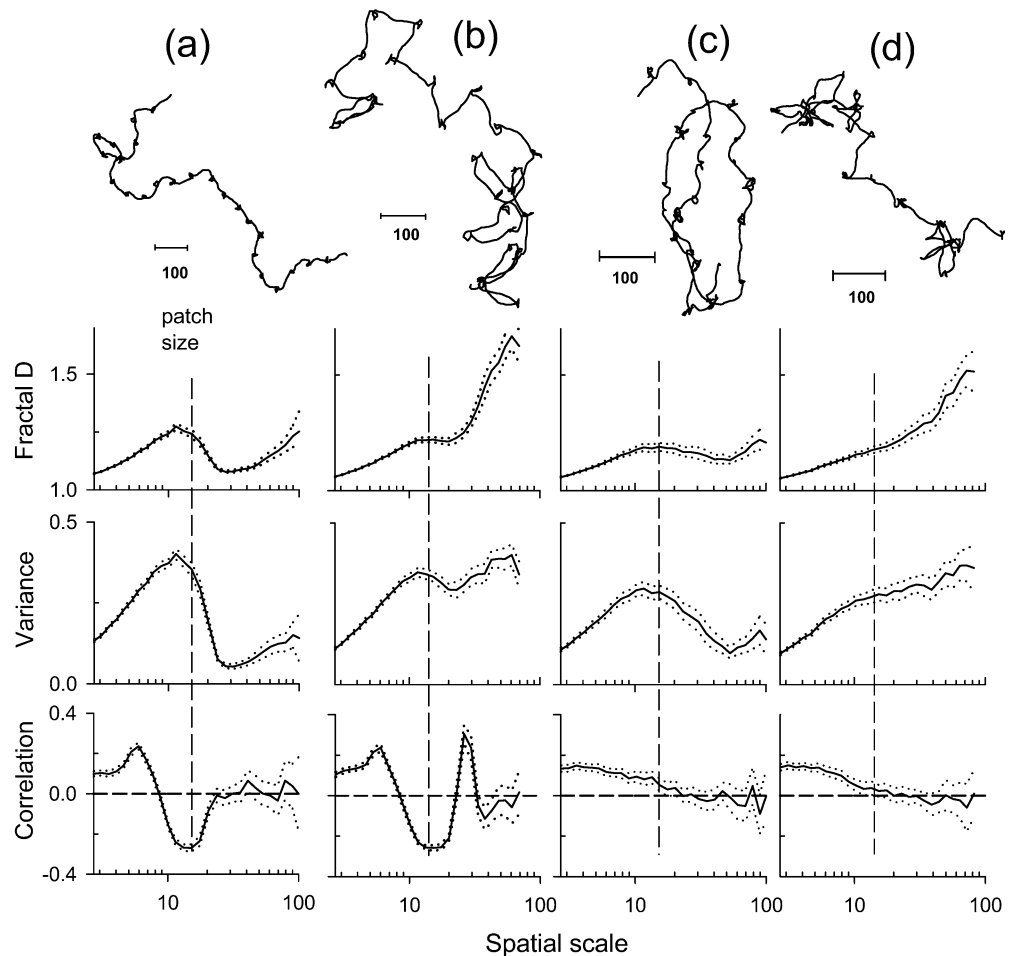
I tracked the animals by following a thread spool attached to their backs (Boonstra and Craine 1986). As the thread plays out, it snags in grass and other vegetation on the forest floor, thus retaining the shape of the movement path. I mapped the trails by first laying a thick bright rope on the thread trail, then video-taping the rope and digitising the images. This gave the x and y co-ordinates for the trails with an accuracy of ± 5 cm.

Deer mouse

The first path (Fig. 6) is from a male deer mouse, 17 g in weight, with a 25 m long trail and 607 data points. The trail is very linear, with some smaller-scale tortuosity, but no other obvious pattern. The plot of fractal D versus scale shows how movement path tortuosity changes with the scale at which it is viewed. The mouse plot shows a peak in D at 100 cm, suggesting that this mouse has two domains of scale, with qualitatively different movement patterns in each domain; in some way the mouse is moving differently at spatial scales of 15–100 cm versus 130–450 cm. The drop in variance at 100 cm confirms the pattern found in the fractal D plot, but adds nothing new.

The correlation plot shows some new results. The drop in correlation to a significantly negative value, at a scale of 22–27 cm, allows us to split the lower domain into two, with a transition at approximately 25 cm. Thus

Fig. 5 Various types of simulated movement paths in patchy habitats. For all of them the correlation plots show a significantly positive correlation below the patch size or a significantly negative correlation above the patch size. Only some of them show a discontinuity in fractal D or a peak in variance at the patch size. Types of movement: (a) when animal exits patches of diameter 15, it continues in the general direction of travel it was going before entering the patch; (b) the animal forgets the general direction of travel upon entering a patch; (c) and (d) are the same as (a) and (b), but with patch diameters that vary from 3–45. Dotted lines represent 95% confidence intervals



we now have three domains: 15–25, 30–100 and 100–350 cm. Note that while I listed specific values for the transition points, they are quite broad. The drops in correlations suggests that this path shows patchiness at both the lower and middle domains. The positive correlation is much lower for the lower domain than the middle one, suggesting the patch use is less intense.

For the spatial scales larger than 100 cm, the confidence intervals for the correlation plot are too wide for it to indicate anything. However, the very low fractal D values show a straight path, and the very low variance shows a homogeneous path at that large scale.

In summary, we see three potential domains of scale. From 10–25 cm the mouse's path shows a slight use of patches, from 30–100 cm, stronger use of patches, and above 100 cm a straight, homogeneous path.

Comparing this to the actual movement path (Fig. 6), we see the more linear path at a larger scale, and some of the bends at the medium and small scales. Note that the bends at the smaller scales just look like increased tortuosity at that scale, but the analysis shows that there is actual heterogeneity—that is, sections of straighter versus more tortuous segments, which suggest reactions to habitat structure. The analysis discovered interesting structure in this visually uninteresting movement path.

Red-backed vole

The second path (Fig. 7) is from a male red-backed vole, 23 g in weight, with a 74-m long trail and 2,373 data points. This trail is more tortuous than the mouse's trail, with a few areas where the animal turned back and forth. The plot of fractal D versus scale simply shows an increase in D with scale. The variations around this increase are not statistically significant (as shown by the wide confidence intervals). Thus, we see only evidence of one domain for the vole in the size range of 15–500 cm. The variance plot shows similar results—a gradual increase, suggesting one domain only.

The correlation analysis allows us to split that domain. The correlations are significantly positive below 55 cm, and then drop below zero just past that scale, indicating use of patches of size less than 55 cm. The slight drop to below zero at ~150 cm suggests a slight use of patches. At 400 cm there is a large drop in correlation, but the confidence interval is too broad to draw any conclusion—more data at larger scales is needed to increase precision.

In summary, we see three potential domains of scale: 10–55, 55–150, and above 150 cm. Comparing this to the actual movement path (Fig. 7), we can see the tortuous-

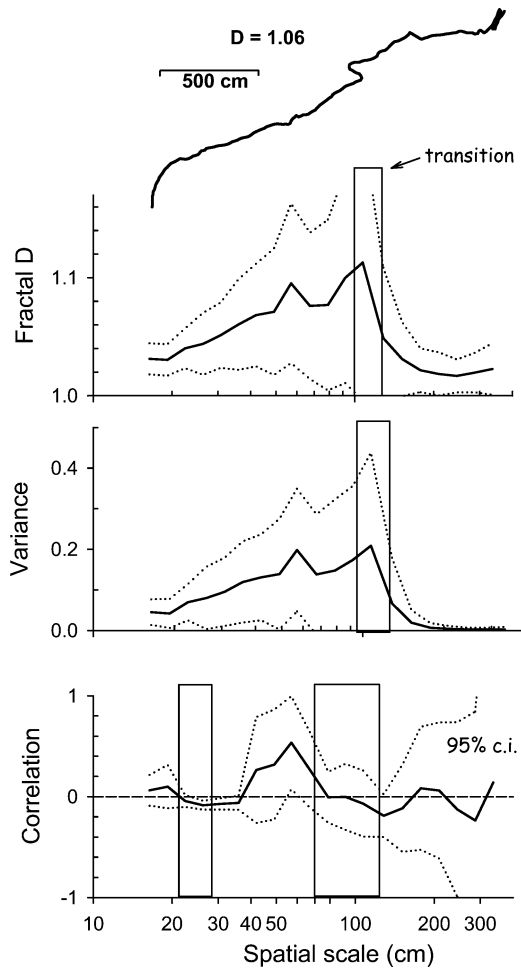


Fig. 6 Movement path of deer mouse (*Peromyscus maniculatus*). Patch use is shown by a peak in fractal D (Eq. 2) or variance, or by a positive correlation dropping to a negative correlation. There are three domains, divided by transitions within the regions 22–27 cm and 80–130 cm

sity at the three different ranges of scales. As with the mouse plot, by eye the bends at the smaller scale just look like increased tortuosity, but the analysis shows that there is actual heterogeneity, suggesting reactions to habitat structure.

Discussion

The variance method is similar to Fauchald and Tveraa's (2003) methods, but instead of path tortuosity, they estimated the travelling time (which they refer to as "first-passage time"). They compare in several ways. First, the measure of travelling time might detect effects missed by path tortuosity, because travelling time incorporates both path tortuosity and speed. For movement data that is not time stamped, speed is irrelevant, and thus travelling time would be equivalent to tortuosity.

However, the measure of travelling time might be adversely affected by smaller domains. Travelling time

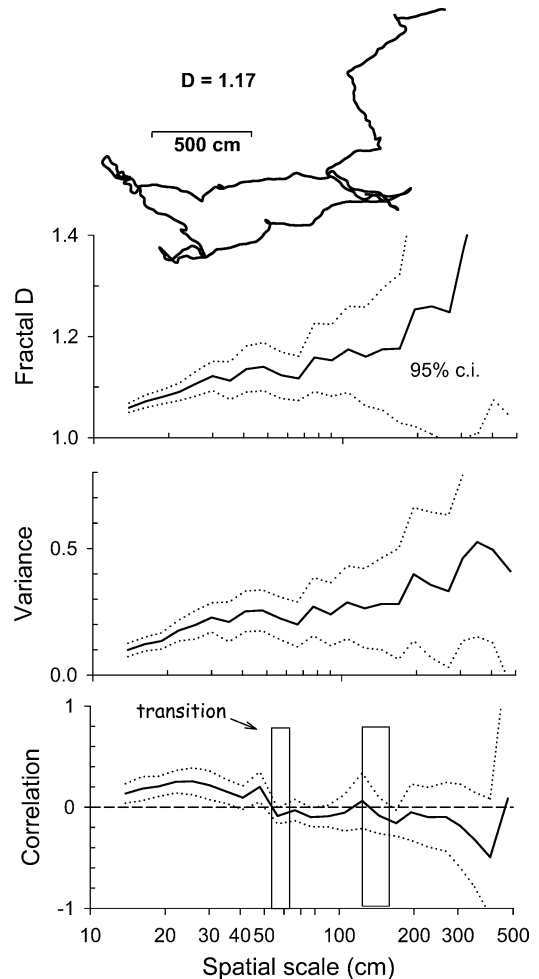


Fig. 7 Movement path of red-backed vole (*Clethrionomys gapperi*). Patch use is shown by a peak in fractal D (Eq. 2) or variance, or by a positive correlation dropping to a negative correlation. There are three domains, divided by transitions within the regions 55–60 cm and 150–165 cm

incorporates effects from all shorter spatial scales, whereas the measure of path tortuosity, based on the cosine of the turn angle at a given step size, ignores effects below the scale of step size. If there are several domains of size below the current scale, then using travelling time would include their effects—but it is not clear what result this would give.

Finally, and most importantly, variation in travelling time has the same limitations as variation in tortuosity: that the null hypothesis is unknown, and it is also not known whether other factors/models can create peaks. It might be of interest to investigate the usefulness of correlations of tortuosities versus correlations of travelling times.

Error estimates

My analyses allow one to combine many movement paths from one individual animal. At each scale, the

Table 1 Expected shapes of the plots of each estimator versus spatial scale

Type of estimator	Within one domain—no transitions	Between domains—across a transition
Fractal D	Continuous plot	A discontinuity in the plot or a continuous plot
Variation in tortuosity among path segments	Unknown	A drop in variation at segment length just greater than patch size
Correlation in tortuosity among pairs of segments	Zero	Positive at segment length less than patch size and/or negative at length just greater than patch size

VFracal, variance and correlation algorithms divide the movement path into short segments. Thus, the data do not have to be in one continuous movement path—many sections can be combined. We can also combine movement paths measured at different resolutions. For example, the mouse movement path was measured at an accuracy of ± 5 cm. If that animal had also been tracked using fluorescent dusting (Lemen and Freeman 1985) at an accuracy of ± 1 cm, and using radio-telemetry at an accuracy of about ± 500 cm, then all these paths could be combined into one analysis over a wide size range. For size 1–5 cm, only the dusted data would be used, for 5–500 cm, both dusted and threaded data, and for > 500 cm all the data could be used.

Appropriate estimation of errors depends on the type of data. For individual movement paths, one can base error measures on variation among path segments. I used a bootstrapping procedure to do this for the example mouse and vole paths (Figs. 6, 7). However one should view these with caution because there is the potential for patchiness to create spatial autocorrelation, biasing the measures of variation downwards.

For individual animals, one should base error measures on variation among movement paths. For different animals, with various numbers of movement paths for each, one should base the error measures on variation among animals. Thus, for each animal, one should first combine results of all movement paths, calculating values for fractal D , variance and correlation versus spatial scale for each animal. Then one should combine results from all animals, estimating appropriate confidence intervals from among-animal variation. Thus these methods address the difficulties that Halley et al. (2004) have shown for fractal analyses in estimating errors.

Strategy of analysis

The assumptions of the various analyses create a natural order to analysing animal movement paths. For example, estimating one fractal D over a range of scales assumes that D is constant over that range, and thus this assumption must be tested first. Estimating fractal D over a whole path assumes that D is homogeneous in space, and thus this assumption must be tested first.

Our analysis should start by viewing the whole range of spatial scales, and then narrowing in as needed. The

first step is to detect transitions between domains, by using a combination of fractal D , variance, and correlation, analyses (Table 1). Then within each domain, use correlation analysis to determine whether the movement path is heterogeneous.

If the movement path is heterogeneous within a domain, then further studies are needed to understand the pattern of heterogeneity—e.g. what are the different types and sizes of patches, and how they affect the animal. This might require more detailed analysis of movement paths, such as modelling animal movements with state space models (Blackwell 1997; Jonsen et al. 2003) which represent animals switching from one type of movement to another.

If the movement path is homogeneous within a domain (or within each patch type of a heterogeneous domain), then use the relationship of fractal D versus scale to learn about the rules underlying the movement pattern. More work is needed on describing the D versus scale relationships for various types of movement paths. Finally, the overall size of D tells us how finely the animal is searching/moving in that range of spatial scales.

Recent technological advances have made these types of analyses feasible. Although these analyses require many data points (correlation estimates especially require large sample sizes for narrow confidence intervals), gathered over a wide range of spatial scales, those are now possible. In the last decade animal-mounted GPS tracking devices have been developed to automate the collection of movement data (Edenius 1997; Moen et al. 1997; Johnson et al. 2002). As with all computer-based technology, smaller devices are being developed, allowing them to be used on smaller animals. Furthermore, the accuracy of locations has increased since selective availability was removed from the GPS system on 1 May 2000. Now one can automatically track larger mammals, recording 10,000 positions per movement path to an accuracy of ± 10 m.

These analyses that I have proposed should help us understand how animals perceive and react to their landscape structure at various spatial scales, and to answer questions about how habitat structure affects animal movement patterns.

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