

Fractal analysis measures habitat use at different spatial scales: an example with American marten

Wilis O. Nams and Maryse Bourgeois

Abstract: Habitat selection is traditionally assessed by how much time the animal spends in each habitat type; however, one can obtain additional information by analysing the structure of the movement paths. We followed and mapped snow tracks of American marten, *Martes americana* (Turton, 1806). The new method used to test the movement paths for deviations from a correlated random walk model show that these paths fail the test. This has led to an analysis of fractal dimension versus spatial scale, which showed a natural break in fractal dimension at a scale of approximately 3.5 m, suggesting that marten displayed different responses to their microenvironment in two regions of spatial scale. Marten travel was more direct at scales <3.5 m than at scales >3.5 m. Path tortuosity was affected by habitats at smaller scales but not at larger scales, indicating different responses by marten to their environment at these two ranges of scale. Multiple regression identified canopy closure and presence of conifer in the understory as variables that affect movement patterns at the 1- to 3.5-m scale. Fractal analysis of movement patterns provides a unique approach to examining habitat use, as well as a means to identify the spatial scales at which an animal responds to its habitat.

Résumé : Le temps passé par un animal dans chacun des habitats sert couramment à évaluer son choix d'habitat; cependant, l'analyse structurale des tracés des déplacements de l'animal fournit des renseignements supplémentaires. Nous avons suivi et représenté sur une carte les pistes dans la neige de martres d'Amérique, *Martes americana* (Turton, 1806). L'utilisation d'une nouvelle méthode pour déceler dans les tracés les déviations à partir d'un modèle de déplacement aléatoire corrélé a donné des résultats négatifs. Nous avons donc fait une analyse de la dimension fractale en fonction de l'échelle spatiale qui a révélé une brisure naturelle dans la dimension fractale à une échelle approximative de 3,5 m, ce qui laisse croire que les martres réagissent différemment dans deux régions de l'échelle spatiale de leur microenvironnement. Le déplacement des martres est plus direct aux échelles inférieures à 3,5 m qu'aux échelles supérieures. La tortuosité des tracés est affectée par l'habitat aux plus petites échelles spatiales, mais pas aux plus grandes, ce qui indique des réactions différentes des martres à leur environnement à ces deux échelles spatiales. Une régression multiple identifie la fermeture de la couverture arborescente et la présence de conifères dans le sous-bois comme des variables qui influencent les patterns de déplacement à l'échelle de 1-3,5 m. L'analyse fractale des patterns de déplacement fournit une méthode unique pour étudier l'utilisation de l'habitat et un moyen pour identifier les échelles spatiales auxquelles un animal réagit à son habitat.

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Introduction

Animals should prefer those habitats that maximize survival and reproductive success (Fretwell 1972), but it is difficult to assess fitness in real-world situations (Rosenfeld 2003). Instead the value of an individual animal's habitat is often assessed by habitat selection (e.g., Mosnier et al. 2003; Whittingham et al. 2003). There may even be several hierarchically organized spatial scales at which animals respond to their environment (Rettie and Messier 2000; Martinez et al. 2003). Wiens (1989) called these different regions in the range of spatial scales "domains" and the boundaries between them "transitions". Domains are often assessed by

comparing variation in specific habitat features at particular scales with the distribution of individuals at those scales (Mosnier et al. 2003).

Time spent in a habitat is a crude measure of the fitness value of a habitat, since animals may be doing different things in those habitats, but the measure is used because often visual observations of behaviour are not available; the data usually contain only locations of animals. Quantifying the movement patterns of an animal may help to compare relative values of different habitats. For example, a straight path suggests that the individual is crossing an area but is not choosing it for purposes other than travelling, whereas a tortuous path suggests increased use of an area. Thus, the degree of tortuosity may be a good measure of the importance of a habitat in terms of foraging, ability to provide cover, or other factors that could influence travel patterns.

Fractal analysis gives such a measure of tortuosity (Milne 1991) and may help to measure how an animal uses different habitats. Fractal geometry was developed as a tool to quantify objects of irregular form and is the continuous analogue of discrete geometric dimensions (Mandelbrot 1967; Milne 1991). The fractal dimension (D) for lines lies between 1, when the line is straight, and a maximum of 2,

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V.O. Nams.¹ Department of Environmental Sciences, Nova Scotia Agricultural College, Box 550, Truro, NS B2N 5E3, Canada.

M. Bourgeois. Department of Biology, Acadia University, Wolfville, NS B0P 1X0, Canada.

¹Corresponding author (email: vnams@nsac.ns.ca).

when a line is so tortuous as to completely cover a plane. One might expect D to be larger when animals are foraging more intensively.

Tortuosity can change with spatial scale (i.e., if you view an animal's movement path at a smaller scale, the line might look more or less tortuous). Thus, D is a scale-dependent measure where you specify the range of spatial scales used. If the tortuosity of a line does not change with scale, then we say that the line is self-similar, or fractal (Mandelbrot 1967), and then one D value can be validly estimated over a wide range of spatial scales.

We should clarify some potential confusion. It has often been reported that fractal dimension is scale-independent, not scale-dependent (Wiens and Milne 1989; Milne 1991; With 1994b). The inconsistency occurs because the term fractal is used in different ways; it has been used for both the concept of self-similarity and for the actual estimate calculated. The estimate must match the concept. If a movement path is self-similar, then we can use one estimate of fractal D over the whole range of spatial scales. But if a movement path is not self-similar, then it is more appropriate to estimate different D values at different spatial scales. The only purpose for one overall estimate of D would be to compare tortuosities of movement paths that are measured over the same range of spatial scales.

This potential confusion underlies Turchin's (1996) criticism of previous applications of fractal analysis to animal movement. The problem arises when movement paths are treated as both correlated random walks and also analysed with fractal analysis. With a correlated random walk, D increases with scale (Turchin 1996; specifically, it increases sigmoidally from a minimum of 1 to a maximum of 2). It is contradictory to treat a movement path as a correlated random walk (where D varies with scale) and at the same time estimate one D value for the whole path (where D is constant with scale). Turchin (1996) thus suggested initially using the correlated random walk as a null model for animal movement, and only considering fractal analysis if it can be shown that the movement pattern deviates from a correlated random walk. Past applications of fractal analysis in studying movement paths have mostly focused on estimating one D per movement path (e.g., Crist et al. 1992; With 1994a, 1994b; but see Westcott and Graham 2000). When a single estimate is suspect (i.e., when movement paths are not fractal), then it is interesting to consider how D changes with scale.

For example, one important aspect of analysing habitat selection is ensuring that we classify habitats at the same spatial scales that animals perceive them. If an animal responds qualitatively differently to its environment at different spatial scales, then we would expect the structure of its movement path to change from one scale to another (Wiens et al. 1993), signifying different domains.

We can detect this transition between domains by noting discrete breaks in the plot of D versus spatial scale. Although it has been suggested that any change in D represents a change in domain (Wiens et al. 1993; With 1994a), even within one domain a correlated random walk shows a D that increases sigmoidally with spatial scale. Likely other types of movement patterns also result in smooth changes in D with scale. Thus, we suggest that a discrete break in the plot

of D versus spatial scale represents a transition between domains.

We applied these ideas of fractal analysis and spatial scale to movement paths of American marten, *Martes americana* (Turton, 1806), in different habitats. Marten typically select habitats based on tree species (Fecske et al. 2002), overhead cover, age (Snyder and Bissonette 1987; Smith and Schaefer 2002), and structural characteristics of the stand (Payer and Harrison 2003). The reasons for habitat choice may be related to den sites (Wilbert et al. 2000), prey availability, and cover. Winter is an especially critical period for marten because of their low fat reserves (Buskirk and Harlow 1989) and their high surface area to mass ratio (Brown and Lasiewski 1972); this suggests that prey abundance may be a crucial component of marten habitat choice in winter, and thus their movement paths may especially reflect foraging differences. Anecdotal observations of snow trails suggest that marten foraging activity decreases in open areas compared with forested habitats (Hargis and McCullough 1984; Snyder and Bissonette 1987). For example, Spencer and Zielinski (1983) observed marten hunting in a zigzag search pattern. Thus, movement patterns in the snow may serve as valuable indicators of such activities.

The general purpose in this study was to find out how American marten react to habitat features during the winter at different spatial scales. The three specific objectives were (1) to test whether marten movement paths can be described by correlated random walks, and if not, then (2) to test whether movement paths show evidence of habitat selection at different spatial scales (i.e., whether there are different domains), and (3) to measure the response to habitat in each domain.

Field methods

The study was conducted in various sites within Fundy National Park, New Brunswick, Canada (centre: 45°37'N, 65°02'E). A description of the Park is given by Woodley (1985). The landscape is characterized by an elevated plateau with rolling hills and steep river valleys. The forest in the park, characteristic of the Maritime Acadian Highlands Natural Region, is made up of a variety of cover types. Much of the forest was harvested prior to the Park's establishment in 1948. Mature stands of second growth stands of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) P. Mill.) mostly cover the slopes along river valleys, while the ridges largely consist of maple (*Acer* spp.), yellow birch (*Betula alleghaniensis* Britt.), and beech (*Fagus grandifolia* Ehrh.). Regenerating birch trees (*Betula* spp.) and balsam fir are returning in many previously conifer-dominated stands, as a result of a spruce budworm (*Choristoneura fumiferana* (Clemens, 1865)) outbreak in the 1970s and 1980s. The individual sites generally included a number of stand types.

American marten snow tracks were followed during the winters of 1993–1994 and 1994–1995. Tracks were located while searching along roads and trails, by following transmitter signals of radio-collared animals, or during track transect surveys conducted by staff of Fundy National Park. Trails were measured by walking directly over the path, measuring distance with a hip chain (a surveying tool that

measures distance by releasing a thread), and turning angles with a compass. Each portion of the trail between two noticeable changes in direction was considered a straight-line move. The data were recorded with a sampling resolution for segment length of 0.25 m and for a change in direction of 5°. A path segment was determined to have ended when the trail entered a distinctly different habitat.

The habitat of each path segment was measured as follows. Overstory vegetation was defined as plants >3 m high, and understory as plants <3 m high. For overstory vegetation, percent canopy closure was measured above the track with a spherical densiometer, with readings taken and averaged over the four cardinal directions. Age was classified as young versus mature: a stand was young if >50% of the trees had a diameter at breast height of ≤ 20 cm. Presence/absence of both coniferous and deciduous trees was estimated, with presence defined as percent abundance >35%. For understory vegetation, presence/absence of coniferous and deciduous vegetation was determined in the same manner as for the overstory. The following information was recorded along with the path data: structural forest components present at the end of a segment and at sites investigated by American marten as revealed by a concentration of tracks at that spot, logs encountered, and presence of subnivean access holes.

Analyses

The general procedure we conducted was as follows. First, we statistically tested the movement paths for deviations from a correlated random walk. Then, to detect domains (i.e., to detect whether animals respond qualitatively differently at different spatial scales), we estimated D at a series of spatial scales. Then, to calculate the animals' responses in each domain detected, we calculated an overall D in each domain for each movement path. Finally, to relate the types of movement patterns to habitat types, we used those D values in regressions of D versus the habitat variables.

Correlated random walks

Turchin (1996) suggested that if an animal moves with a correlated random walk, then fractal analysis of that movement pattern is not justified. Thus, we first tested, as a null hypothesis, whether a correlated random walk model adequately describes the path segments. To do this we used an extension of the equation given in Kareiva and Shigesada (1983; Appendix A). The American marten movement paths differed significantly from those described by a correlated random walk ($t = 3.95$, $df = 58$, $p < 0.002$). The test statistic ($\bar{R}_{\text{diff}} = 0.152$), which measured (net distance travelled)² for our observed data minus that expected with a random walk model, was positive, indicating that the movement paths covered a greater distance for a given number of animal moves than a correlated random walk would.

Fractal analysis

Since we are interested in how path tortuosity changes with spatial scale, we calculated D at different spatial scales. This was done for each movement path as follows. Using a modification of the divider method (which we call the FractalMean estimator), a plot of $\log(\text{path length})$ versus

$\log(\text{spatial scale})$ was created. For the basic divider method, the length of the path is measured by stepping dividers of a certain size along the path. If this is done for larger and larger divider sizes, then the slope of $\log(\text{path length})$ versus $\log(\text{divider size})$ would be $1 - D$ (Fig. 1; Mandelbrot 1967).

One problem is that at large scales the estimates of path length vary with the starting position on the path (With 1994b; Nams 1996). To reduce this variation, the FractalMean procedure estimates mean path lengths by walking the dividers over the paths 50 times, starting at different randomly chosen points each time, and walking forwards and backwards.

Another problem with the divider method is that one is measuring a continuous variable (path length) with a discrete measure (number of divider steps). Since the end of the movement path and the divider typically do not meet, counting the number of steps to measure path length is a truncated measure. This results in an underestimate of path length, with bias increasing with divider size, leading to an increased D at larger spatial scales. We minimized this problem by estimating the proportion of a divider size needed to make up the final step.

We used divider sizes ranging from 1 to 50 m. The lower limit was chosen to be larger than the sampling precision of the recorded data (at 0.25 m) and the higher limit was based on the lengths of the longest paths recorded within a habitat.

To estimate D at various spatial scales, we applied the FractalMean procedure to a series of narrow windows of spatial scales (Fig. 1). We estimated a D at each position of the window by regressing $\log(\text{path length})$ versus $\log(\text{spatial scale})$ (Krummel et al. 1987; Nams 1996). Window sizes at each spatial scale were chosen with a minimum value of midpoint/1.35 and a maximum value of midpoint \times 1.35; this window size definition gave symmetrical, fixed-width windows on the log-transformed spatial-scale axis. Thus, measures of tortuosity at different scales were obtained for each movement path.

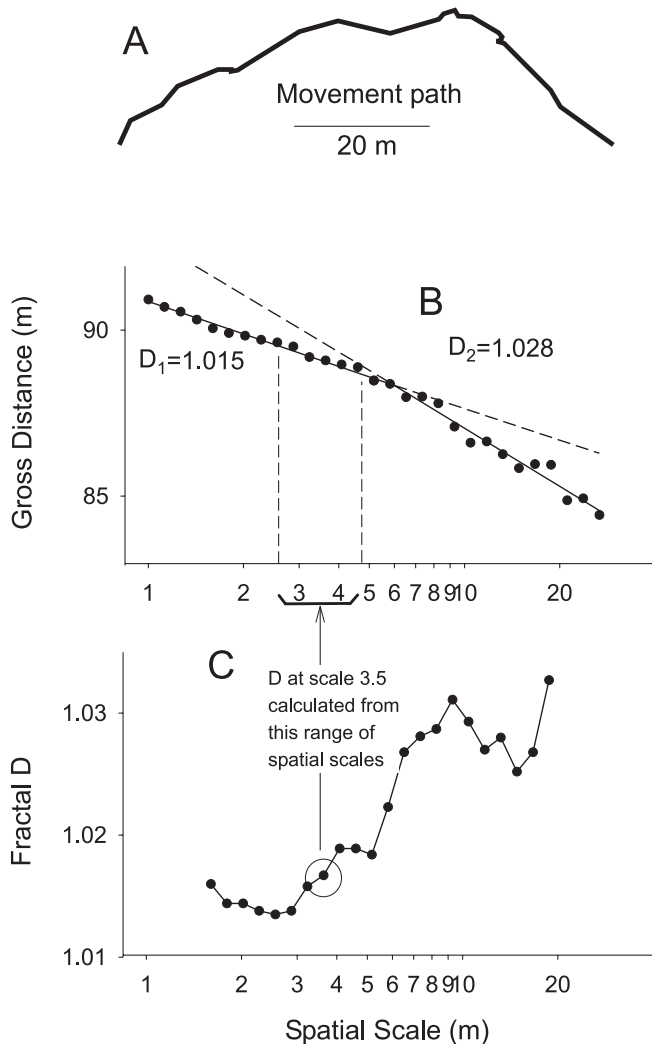
Results

Throughout the winters of 1993–1994 and 1994–1995, 3266 m of American marten tracks were followed. One example is shown in Fig. 2. This path, followed on 15 March 1995, was 84.5 m long and contained 52 moves.

The American marten movement paths differed significantly from those described by correlated random walk models ($\bar{R}_{\text{diff}} = 0.152$, $t = 3.95$, $df = 58$, $p < 0.002$). The test statistic, \bar{R}_{diff} , was positive, indicating that the movement paths covered a greater distance than a correlated random walk would. Since the movement paths could not be described by a correlated random walk model, we proceeded with the fractal analysis.

The D of the American marten paths increased with scale, with an apparent discontinuity (Fig. 3). Note that individual movement paths showed a range of patterns of D versus scale (e.g., Fig. 1 suggests three ranges of scales: <5, 5–9, >9 m); however, since we are interested in the response of marten in general, we used the mean D s over all movement paths. A broken-line regression with two line segments (Neter et al. 1996) showed a better fit ($r^2 = 0.90$, $p < 0.001$, $df = 3, 14$, breakpoint estimated at scale = 3.5 m) to the data

Fig. 1. (A) A sample American marten (*Martes americana*) movement path section from 12 February 1994 in a young coniferous stand with a sparse understory and high canopy closure. (B) The first step in calculating fractal dimension of this movement path. Gross distance of the path measured with dividers of various sizes (= scale). Note the break in the plot at 5 m. (C) Fractal D calculated from the plot in B. Fractal D calculated by first assessing the slope within a sliding window along the scale axis, and then fractal $D = 1 - \text{slope}$. Note the two distinct regions in fractal D , corresponding to the two straight-line segments in the plot in B.



set than did a linear regression ($r^2 = 0.79$, $p < 0.001$, $df = 1,16$) or a quadratic regression ($r^2 = 0.79$, $p < 0.001$, $df = 2,15$). This suggests that marten movement paths differed qualitatively for the two regions, or domains, of spatial scale: 1–3.5 m and 3.5–50 m.

We thus continued our analysis by treating each domain separately. To describe the structure of the movement path in each domain, for each path we estimated one D for each domain (D_1 for 1–3.5 m and D_2 for 3.5–50 m). In addition, to compare the results we would have obtained if we would have ignored the two domains, we also calculated one overall D (D_{all}). The D s were normalized by transforming the data by $\log(D - 0.998)$ before further analysis.

Habitat selection

The three measures of path tortuosity (D_1 , D_2 , D_{all}) were measures of what animals did in each habitat and in each domain. To see how American marten behaviour differed among habitats, we carried out stepwise regressions of each of the tortuosity measures versus the habitat variables.

Path length determined whether we would include it in the analysis. A path had to be at least 30 m long to estimate D_2 and D_{all} . This limit was determined by considering the actual range of scales that would be used in the computation: for each divider size used to measure a path, a minimum of three dividers is necessary to obtain an estimated length (With 1994a). Paths <30 m could not be measured at scales >10 m. Thus, D_2 and D_{all} were estimated for 39 paths, and D_1 for 59 paths.

There was no significant relationship between tortuosity and the habitat variables at either the larger range of spatial scales (D_2 , $p > 0.30$) or over the whole range of scales (D_{all} , $p > 0.28$). Thus, over the range of spatial scales of 3.5–50 m, the tortuosity of the American marten movement paths did not significantly change with habitat type.

However, at the small range of scales from 1 to 3.5 m, path tortuosity was significantly related to percent cover and the presence of conifer in the understory (Table 1). The model of best fit ($F_{[4,43]} = 3.12$, $p < 0.024$) contains an interaction between percent cover and understory conifer, as well as a quadratic percent cover term. Specifically, tortuosity of paths in deciduous areas increased with percent cover, but in coniferous areas tortuosity decreased with percent cover (Fig. 4). At intermediate cover values, paths were quite straight. Tortuosity was greatest in understory conifer and low percent cover.

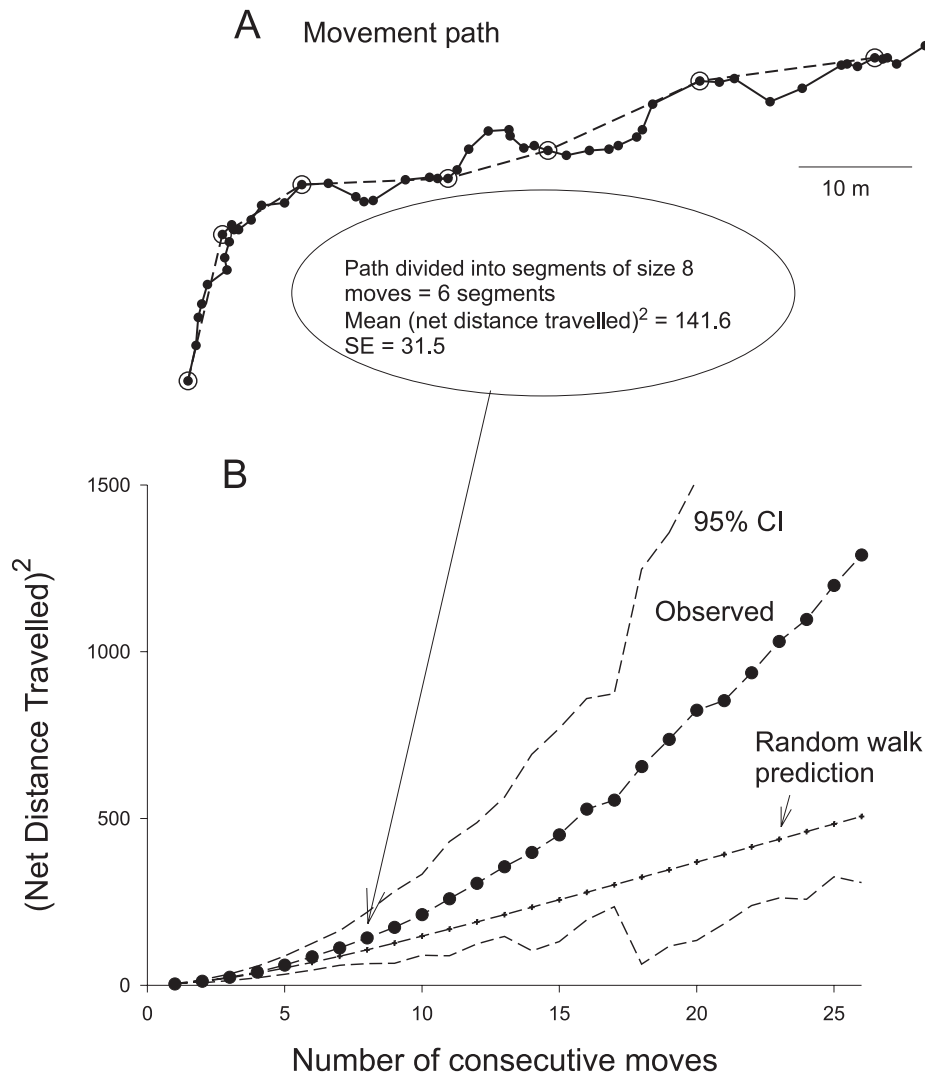
Response to forest structural components

Tree densities provide information regarding the spacing of vegetation, which may be correlated with patterns observed in American marten paths. The median densities of trees along the marten paths ranged from 12.5 to 40 per 100 m², with densities in most areas ranging from 25 to 40 per 100 m². This corresponds to an equivalent distance between trees of 2.8–1.7 m, with inter-tree distances in most areas ranging from 1.6 to 2.0 m. Out of 846 segments followed, 104 segments ended at recognisable structures (e.g., tree bases, woody debris, snags), where marten obviously changed directions. The mean segment length when this happened was 30.9 m. Only twice did martens climb trees.

Discussion

The fractal approach provides information at a much finer scale than was obtained when only the time spent in each habitat was considered, and thus complements habitat selection analyses. Examining animal interactions with their microhabitat may provide insight on the animal’s reason for selecting stand types. The apparent response of marten to their microenvironment may also account for the deviation in results noted between studies of marten habitat selection. Habitat selection at a stand level may remain undetected if animals are selecting microhabitat structures rather than forest types. For example, Hargis and McCullough (1984) did not detect differential selection of stand types, but they did

Fig. 2. (A) A sample American marten movement path section from 15 March 1995 showing an example of calculating mean (net distance travelled)² for a segment length of 8 animal moves. Under the hypothesis of a correlated random walk, the 6 segments are independent of each other. (B) The relationship of observed (net distance travelled)² to those expected with a correlated random walk model versus the number of consecutive moves. The confidence intervals (CI) are calculated by treating (net distance travelled)² for each segment of n moves as independent samples.



note the influence of specific forest components on marten activity.

The ability to detect different spatial scales of animal responses is a promising feature. Past applications of fractal analysis in studying movement paths have mostly focused on estimating one D per movement path (e.g., Crist et al. 1992; With 1994a, 1994b); in our study, if we had only calculated one D for each movement path (i.e., only used D_{all}), ignoring the possibility that American marten might view the range of scales as more than one domain, then we would have overlooked the relationship between D_1 and habitat variables, and concluded that marten do not forage differently in different habitat types.

Fractal analysis also allowed us to detect differential responses with spatial scale within the home-range scale. It has been suggested that animals select habitats in a hierarchical manner (Johnson 1980; Sallabanks 1993), that animals first select home ranges and then select habitats to use within those home ranges. In studying this, researchers typi-

cally choose a few different spatial scales that seem biologically important, and then measure animal response. For example, Bissonette et al. (1997) studied habitat use of pine marten (*Martes martes* (L., 1758)) at microhabitat, stand, and landscape spatial scales among different study sites, and Rondinini and Boitani (2002) studied habitat use by beech martin (*Martes foina* (Erxleben, 1777)) at the home range and within-home-range scales. We detected two domains for American marten and these both lie within Bissonette et al.'s (1997) microhabitat spatial scale and Rondinini and Boitani's (2002) within-home-range spatial scale. Fractal analysis of movement patterns provides a unique approach to examining habitat use as well as a means to identify the spatial scales at which an animal responds to its habitat.

Our analysis avoids some of the pitfalls that other ecological fractal analyses have shown (e.g., Halley et al. 2004). We detected two distinct domains despite the decreased power caused by our narrow range of scales. We treated individual path segments as independent sampling units, rather than in-

Fig. 3. Combined fractal D_s from all movement paths. There is a discontinuity in the fractal D curve at a spatial scale of 3.5 m as estimated by nonlinear regression (the solid and broken lines show the two fitted straight lines). This suggests that American marten move qualitatively differently at spatial scales <3.5 and >3.5 m. Each data point is a mean of fractal D_s over all movement paths. Dotted lines represent 95% CI and were calculated using data that were transformed by $\log(D - 0.998)$.

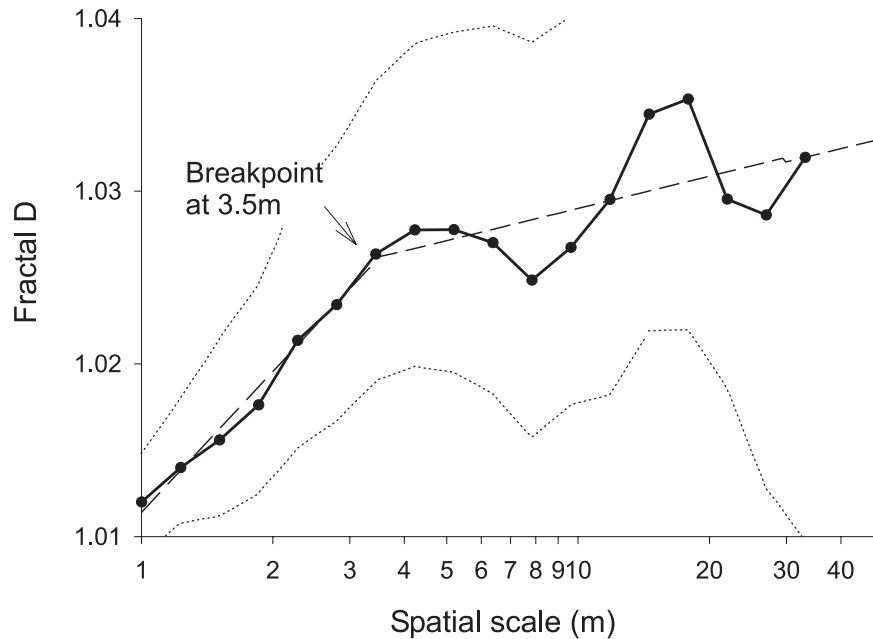


Table 1. Regression model relating fractal D at a scale of 1–3.5 m to several habitat variables of American marten (*Martes americana*).

Effect	df	F	p
Constant	1,43	22.3	0.00002
Understory conifer	1,43	5.13	0.029
Percent cover	1,43	3.05	0.088
(Percent cover) ²	1,43	5.28	0.027
Understory conifer × percent cover	1,43	4.41	0.042

Note: Understory conifer refers to the proportion of conifer in the understory and overstory conifer refers to the proportion of conifer in the overstory. A backward stepwise regression was carried out. See Fig. 4 for a plot of this relationship.

dividual points at each scale; however, we could not assign path segments to individual American martens. Finally, we estimated fractal D for a scale-specific section of the curve to detect deviations from fractality.

Response to habitat characteristics

American marten displayed different responses to their microenvironment at two regions of spatial scale. The discrete difference in the path tortuosities between the 1- to 3.5-m scale and the 3.5- to 50-m scale suggests that different processes are occurring at these two regions of scales of observation, and that these represent two domains of response. Marten movements are straighter at the smaller scale than at the larger scale. Furthermore, marten responded to habitat at the smaller scale (Fig. 4) but not at the larger one.

What causes these two domains of response? There are several possibilities. First is that the 3.5-m division represents the grain of the American marten’s response to its habitat; i.e., 3.5 m is the smallest scale at which an animal responds to patchiness in its environment (Kotliar and Wiens

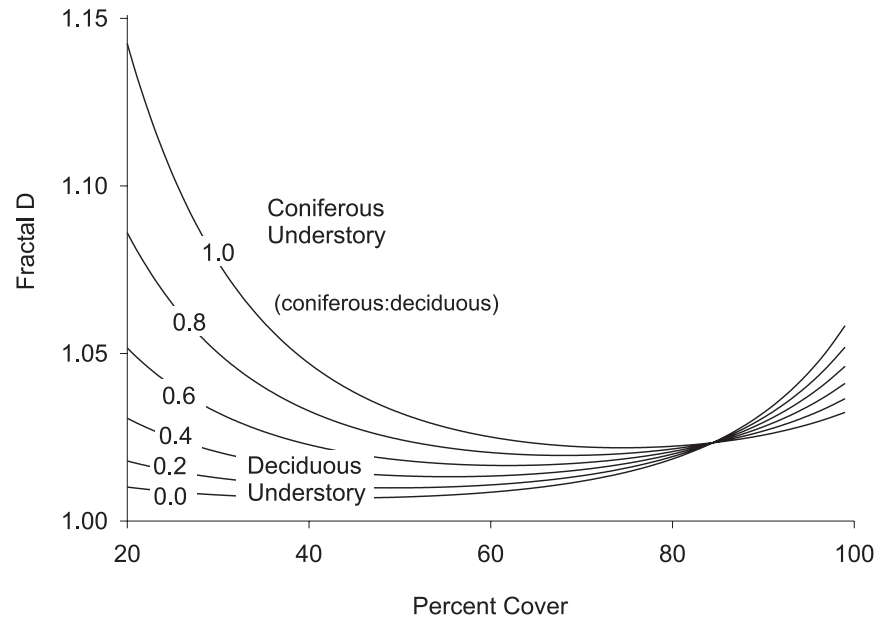
1990). This is unlikely because path tortuosity at smaller scales differed among habitat types (Fig. 4), implying that the marten did respond to habitat at that smaller scale.

A second possibility is that American marten walk from some object (e.g., trees) to another, with a spacing of 3–4 m between objects encountered (i.e., this determines the breakpoint between the two ranges of scales). Such behaviour has been observed in wood mice, *Apodemus sylvaticus* (L., 1758), which travel in a directed path toward individual bushes (Benhamou 1990); however, at a larger scale they move from bush to bush randomly. Because the wood mouse’s path is essentially a straight line at the smaller scale, this would give the pattern we observed in our data (i.e., a straighter path at the smaller scales). However, this process is unlikely for marten because <1/8 of the path turns occurred at recognisable habitat structures. In addition, although we did not record whether trees affect marten movement path in more subtle ways, trees were spaced much closer together than 3.5 m.

A third possibility is that American marten respond to habitat features differently at the smaller scale of 1–3.5 m than at 3.5–50 m. This is most likely; information on various habitat features along the paths was recorded, and the densities of trees coincided with the 1–3.5 m scale. It is difficult to tell whether such a response would be active or passive. For example, an active response would be if marten are attracted to low overhanging tree branches (Hargis and McCullough 1984; Corn and Raphael 1992), whereas a passive response would be if marten had to change their direction slightly to avoid trees or depressions in the snow caused by trees.

It is not clear what would affect the large-scale movement pattern. There were no correlations with habitat types; thus, no support for the idea of prey densities (which would differ

Fig. 4. Plot of regression model relating movement path tortuosity over a scale of 1–3.5 m to percent cover and the type of understory vegetation. The range for the percent-cover axis was set by the range of the habitat data. Note the interaction between cover and type of understory, as well as the quadratic effect of the understory type. See Table 1 for specific details of the analysis.



in different habitat types) affecting movement patterns. Many other factors, such as directed travel or active selection for specific habitat types not recorded, may affect movement patterns in the 3.5- to 50-m size range. However, our small sample reduced the power of our statistical tests, making it difficult to judge the relevance of nonsignificant results.

The responses at the small scale might be governed by foraging. For example, American marten often investigate various habitat features such as low conifer branches (Raine 1987), coarse woody debris (Corn and Raphael 1992), and logs and root plates of fallen trees (Raine 1987). This investigation has been interpreted to be searching for access to prey in the subnivean layer. Thus, smaller scale patterns that marten show might be driven by searching for individual prey items. This is corroborated by the habitat analyses, which showed that at the small scale movement paths were more tortuous in habitats containing more conifer in the understory and lower overstory canopy closure (Fig. 4). Also, we noted that marten trails tended to pass under the cover of low conifer branches. Low conifer branches intercepting the snow surface may form crevices, thus providing greater accessibility to the subnivean layer (Hargis and McCullough 1984; Corn and Raphael 1992). However, only one marten path entered the subnivean layer.

Path tortuosity at the small spatial scale differed significantly among habitats, but the total range of 0.1 seems quite small (Fig. 4). However, this small difference in D can represent a large biological difference because D represents an exponent in scaling relationships, and a small change in an exponent can have a big impact on the distance travelled (Milne 1997). For example, suppose two animals each travelled a net distance of 1 km per day (Hickey et al. 1999), with a difference in D of 0.1. The animal with the more tortuous path would have travelled a gross distance that is twice as far, measured at a scale of 1 m. This is a huge difference

in energy expenditure that is especially important in the winter (Brown and Lasiewski 1972; Buskirk and Harlow 1989). This large difference in energy use suggests that there must be strong benefits to travelling in those habitats with higher D values.

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Appendix A. Testing for correlated random walks²

If an animal path can be described by a correlated random walk, then after n consecutive moves the expected square of the net distance travelled, $E(R_n^2)$, is given by (Kareiva and Shigesada 1983):

$$[1] \quad E(R_n^2) = nE(l^2) + 2E(l)^2 \frac{c}{1-c} \left(n - \frac{1-c^n}{1-c} \right)$$

where c is $E(\cos\theta)$ and θ is the turning angle, and l is length of one move. $E(\cos\theta)$ is estimated by the mean $\cos(\theta)$, $E(l)$ is estimated by the mean move length, and $E(l^2)$ is estimated by the mean (move length)².

To compare the expected square of net distance to the observed, one can divide the movement path into s segments of length n consecutive moves. Then, for each segment estimate (net distance travelled)², and then the mean (net distance travelled)² over all segments. Doing this for each n , one can then plot the observed versus expected (net distance travelled)² as a function of n .

We will show how to statistically test whether the observed differs from the expected. Under the null hypothesis of a correlated random walk the distances moved in each segment are independent of each other. Thus, one can calculate the mean (net distance travelled)², and SE of that mean, over all segments. Being a mean, this statistic will be normally distributed.

As a first step in the analysis, for each n , one can now calculate confidence intervals (CI = SE t_{s-1}) for the observed mean (net distance travelled)². Plotting these on the same graph as the expected (eq. 1), one can visually see where the expected values deviate from the observed values.

²Computer programs used to carry out all of these analyses are available from the senior author.

However, it is not clear how to interpret the results if only some of the values deviate from the expected values, because the estimates of mean (net distance travelled)² are not independent among the different move sizes n . Thus, it would be useful to have an overall test for significance.

To test for significance, first, we will calculate one statistic measuring the overall deviation of the observed from the expected, over all n . Let R_n^2 represent the mean (net distance)² for each number of n consecutive moves. For each n , calculate the difference between observed and expected (net distance travelled)², but scaled by the expected. Then, take the mean of this over all step sizes. We will represent this statistic by R_{diff} , as follows:

$$[2] \quad R_{diff} = \frac{1}{k} \sum_{n=1}^k \frac{\overline{R_n^2} - E(R_n^2)}{E(R_n^2)}$$

Since the individual $\overline{R_n^2}$ are normally distributed, then so is R_{diff} . Under the null hypothesis of a correlated random walk, R_{diff} will have a zero mean.

Next we need to estimate $\sigma_{R_{diff}}^2$ the variance of this statistic. For brevity let us represent

$$[3] \quad \text{Var} \left(\frac{\overline{R_n^2} - E(R_n^2)}{E(R_n^2)} \right) \text{ by } \sigma_{nm}$$

$$[4] \quad \sqrt{\sigma_{nm}} \text{ by } \sigma_n$$

and

$$[5] \quad \text{Covar} \left(\frac{\overline{R_n^2} - E(R_n^2)}{E(R_n^2)}, \frac{\overline{R_m^2} - E(R_m^2)}{E(R_m^2)} \right) \text{ by } \sigma_{nm}$$

where n and m are segment lengths, then

$$[6 \text{ and } 7] \quad \sigma_{R_{diff}}^2 = \text{Var} \left(\frac{1}{k} \sum_{n=1}^k \frac{\overline{R_n^2} - E(R_n^2)}{E(R_n^2)} \right) \\ = \frac{1}{k^2} \sum_n \sum_m \sigma_{nm}$$

The $\overline{R_n^2}$ estimates for the various number of moves are not independent of each other, and thus the covariances σ_{nm} are nonzero. We do not have estimates for these covariances because each one is calculated at a different n . However, the maximum for $\sigma_{R_{diff}}^2$ will occur when all $\overline{R_n^2}$ are completely positively correlated with each other; i.e., when

$$[8] \quad \sigma_{nm} = \sigma_n \sigma_m$$

then

$$[9] \quad \sigma_{R_{diff}}^2 \leq \frac{1}{k^2} \sum_n \sum_m \sigma_n \sigma_m$$

Finally,

$$[10] \quad \sigma_n = \sqrt{\frac{1}{E(R_n^2)^2} \text{Var}(\overline{R_n^2})}$$

which we can estimate by

$$[11] \quad \hat{\sigma}_n = \frac{SE(\overline{R_n^2})}{E(R_n^2)^2}$$

Therefore, for a conservative estimate of $\sigma_{R_{diff}}^2$, we will combine eqs. 9 and 11 to yield

$$[12] \quad \hat{\sigma}_{R_{diff}}^2 = \frac{1}{k^2} \sum_n^k \sum_m^k \frac{SE(\overline{R_m^2})}{E(R_m^2)^2} \frac{SE(\overline{R_n^2})}{E(R_n^2)^2}$$

with $E(R_n^2)$ being given by eq. 1.

Since R_{diff} is normally distributed, we can calculate the maximum 95% CI for it by

$$[13] \quad 95\% \text{ CI} = R_{diff} \pm 1.96 \hat{\sigma}_{R_{diff}}$$

Under the null hypothesis of a correlated random walk, the expected value of R_{diff} is zero. Thus, to calculate a probability level for testing the null hypothesis, use the standard normal distribution.

Note that the statistic R_{diff} measures the deviation from the correlated random walk in one consistent direction (i.e., whether the observed (net distances travelled)² are consistently higher or lower than the expected ones). Thus, it will not detect situations such as the observed (net distance travelled)² being smaller at shorter step lengths and larger at longer step lengths. We have not found it to be a problem, because all of the movement paths we have analysed have had consistently positive or negative deviations; however, one should still realise that this statistic is conservative in this way.

This discussion has centred on statistically testing one movement path. If one now wants to test a sample of movement paths (as we have done in this study), then calculate the statistic R_{diff} (given in eq. 12) for each movement path. The variance estimates for each movement path ($\sigma_{R_{diff}}^2$) are ignored because we need an estimate of variation among movement paths. Since the paths are independent of each other, and R_{diff} is normally distributed, then use a traditional parametric statistic such as a t test, using each path as one sample, to test for a significant deviation between mean R_{diff} and 0.

Example

Consider the American marten movement path in Fig. 2A, which was followed on 15 March 1995. This path is 84.5 m long, containing 52 moves. The mean move length, $E(l)$, is 1.63 m, the mean square of the move length, $E(l^2)$, is 3.56 m, and the mean cosine of the turning angle, $E(\cos\theta)$, is 0.786. Figure 2B shows how the path is divided into segments for $n = 8$ animal moves, with the first segment starting at step 1. Note that if the first segment was started at one of the other datum points, then slightly different estimates would be obtained for these statistics. We minimized this variation by carrying out a bootstrap procedure for each n , starting the sampling at different starting points for each bootstrap sample.

For $n = 8$ animal moves, there were 6 segments. The mean (distance travelled²) was 142 m², with a SE of 31.5. Using a t value of 2.57 for $df = 5$, this gives a 95% CI of 142 ± 81 m². Figure 2 shows results of these calculations for n ranging from 1 to 26.

For testing whether overall this movement path can be described by a correlated random walk, we estimated $R_{\text{diff}} = 0.747$ and $\sigma_{R_{\text{diff}}}^2 = 0.346$. A two-tailed probability level for a z value of $R_{\text{diff}}/\sigma_{R_{\text{diff}}} = 2.16$, giving a p value of 0.03. Thus, this movement path differs significantly from one generated by a correlated random walk at a significance level of 0.03.

Note the apparent contradictions. At no point did the ex-

pected (net distance travelled)² fall outside of the observed 95% CI (Fig. 2), yet the overall test of significance showed that the movement path differed from a correlated random walk. This happened because R_{diff} combines all of the deviations, and all of the observed (net distance travelled)² deviated in the same direction from the expected.