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FRACTAL PATTERNS OF INSECT MOVEMENT IN MICROLANDSCAPE MOSAICS

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How individuals move, whether in short-term searching behavior (Bell 1991) or long-term dispersal (Bunce and Howard 1990, Stenseth and Lidicker 1992), influences the probability that individuals will experience physiological stress or encounter appropriate habitat, potential mates, prey, or predators. These influences translate into effects on the spatial dynamics of populations and metapopulation structure, gene flow, or the distribution of nutrients in ecosystems. Indeed, an understanding of movement behavior can contribute to the resolution of many ecological questions (Swingland and Greenwood 1984, Wiens et al. 1993*a*).

Because of their variety and complexity, however, it is often difficult to make sense of movements. Organisms that differ in size, structure, or taxonomy often move at different rates and trace different movement pathways. Because movement pathways are strongly influenced by environmental structure, they may reflect differences in how organisms perceive habitat heterogeneity over a given range of scales (Kotliar and Wiens 1990, With 1994). Comparisons among such organisms are complicated by the scale-dependence of movement patterns. Because the fractal dimension of a movement pathway is scale-independent, however, it may provide

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TABLE 1. Fractal dimension (D) and intercept (K) values for ant, beetle, and grasshopper movement pathways. Pathways in both low-heterogeneity and high-heterogeneity mosaics are combined in this analysis. Values for K are for pathway length expressed on a natural log scale.

Species	N	Fractal dimension (D)		Intercept (K)	
		Mean	SD	Mean	SD
Ants					
Pogonomyrmex occidentalis	34	1.31	0.15	0.62	0.79
Beetles					
Eleodes extricata	15	1.17	0.09	−0.31	1.22
Eleodes obsoleta	14	1.19	0.11	0.53	1.08
Eleodes hispilabris	15	1.17	0.09	0.40	1.19
Grasshoppers					
Opeia obscura nymph	15	1.10	0.11	−2.01	0.84
Opeia obscura adult	15	1.21	0.15	−1.59	2.15
Psoloessa delicatula	15	1.12	0.07	−1.04	1.62
Xanthippus corallipes	19	1.09	0.05	−0.15	1.35

a useful measure for comparing dissimilar taxa. Here, we use fractal measures to compare the movement pathways of individual beetles (Coleoptera: Tenebrionidae: *Eleodes hispilabris, E. obsoleta, E. extricata*), grasshoppers (Orthoptera: Acrididae: *Xanthippus corallipes, Psoloessa delicatula, Opeia obscura*), and harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex occidentalis*) occupying semiarid shortgrass steppe in north-central Colorado.

Our focus was on fine-scale movement and its relationship to microlandscape structure rather than on long-range dispersal (Wiens and Milne 1989, Crist et al. 1992, Crist and Wiens 1994, With 1994). We tracked individuals for 5–30 min in 25-m^2 areas using small numbered flags to mark the locations of individuals at 5–20 s time intervals. Flag locations were then electronically surveyed and the coordinate data used to generate pathway maps (additional details are given in Wiens et al. 1993*b*). The observation areas varied in microlandscape heterogeneity, from plots dominated by bare ground and low grass (low heterogeneity) to those containing a mixture of grasses, cactus, and low shrubs (high heterogeneity) (Crist et al. 1992).

We derived several measures to characterize pathways. Scale-dependent measures, such as net displacement (the straight-line distance from beginning to end of a pathway), characterize movement in terms of absolute distance; individuals that travel faster or farther have larger values. Fractal dimension, on the other hand, is a scale-independent measure of the complexity or tortuosity of a pathway. The measured length of a pathway (L) decreases as the measurement scale (δ) increases according to the relation

$$L(\delta) = K\delta^{1-D}, \tag{1}$$

where D is the fractal dimension (Mandelbrot 1983). In practice, D is derived by regressing ln L on ln δ, where δ represents a measurement scale or "ruler length" (Dicke and Burrough 1988). The fractal dimension of movement pathways over a plane surface lies between 1.0 (a straight line) and 2.0 (Brownian motion, which, continued unabated, fills a two-dimensional plane) (Dicke and Burrough 1988, Milne 1991). The intercept of the regression, K, is rarely considered in discussions of fractal patterns, but it may also contain important information (Milne 1992). In this case, it estimates the length of a movement pathway at a standardized measurement scale.

We have previously reported the results of our separate analyses of pathways of beetles (Crist et al. 1992), grasshoppers (With 1994), and ants (Crist and Wiens 1994). In general, the scale-dependent pathway measures varied significantly among species and with variations in the spatial heterogeneity of the mosaic. Among the *Eleodes* beetles, for example, net displacement was greater for larger than for smaller species and was greater in areas dominated by bare ground and continuous grass cover than in more heterogeneous areas that contained cacti or shrubs. The fractal dimension of beetle pathways, however, did not differ significantly either among species or among microlandscapes. Simulation analyses (Crist et al. 1992) showed that these results did not stem from any inherent insensitivity of the fractal index, but reflected basic similarities in the complexity of pathways despite their differences on an absolute scale.

Because we recorded the movements of beetles, grasshoppers, and ants in the same microlandscapes using the same procedures, we can use fractal measures to compare pathways of these taxa. The fractal dimensions of pathways varied significantly among the major taxa (ANOVA, F = 4.85, df = 13, 113, $P < 0.0001$). Ant pathways had a greater D than those of beetles and grasshoppers (Table 1, Fig. 1). Beetle species as a group

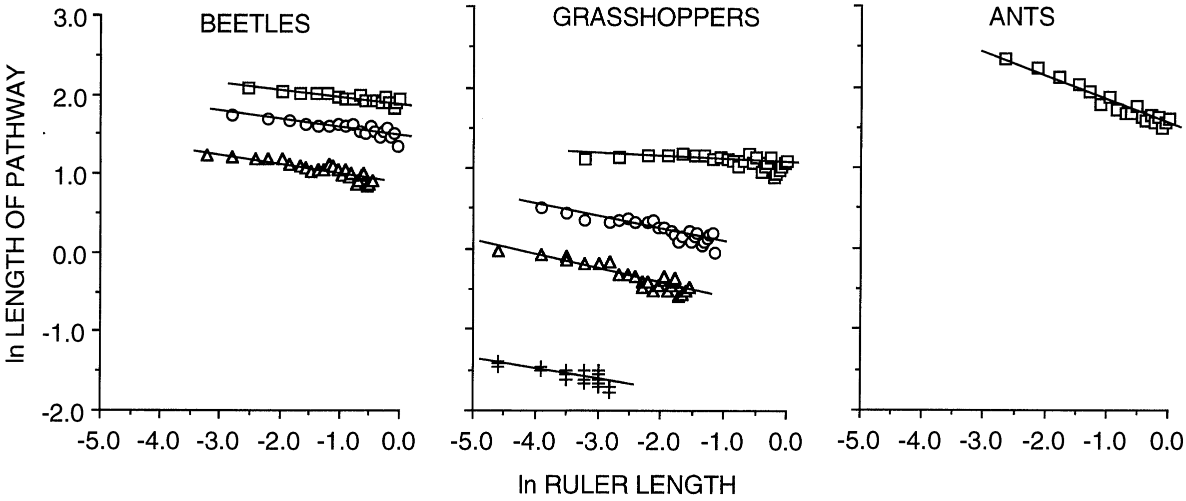

FIG. 1. Regressions showing the relationship between insect movement pathway length (L in Eq. 1) and measurement scale (δ in Eq. 1) for representative beetles, grasshoppers, and ants in a low-heterogeneity, grass-dominated mosaic. The fractal dimension of the pathway (D) is given by 1.0 minus the slope of the regression. Key: beetles: □ *Eleodes hispilabris,* ○ *E. obsoleta,* △ *E. extricata*; grasshoppers: □ *Xanthippus corallipes,* ○ *Psoloessa delicatula,* △ *Opeia obscura* adult, + *O. obscura* nymph; ants: □ *Pogonomyrmex occidentalis.*

had more complex pathways than did the grasshoppers (ANOVA, $F = 2.04$, df = 11, 81, $P = 0.03$), but there were no significant differences among the beetle species. Among the grasshoppers, values of D for pathways of adult *Opeia obscura* were greater than those of *Psoloessa delicatula* and *Xanthippus corallipes,* as well as those of nymphal *Opeia obscura,* but were similar to values of D for the beetle species (Table 1). Fractal dimensions of movement patterns across major taxa or species did not vary systematically with microlandscape heterogeneity.

The fractal dimension, D, indexes the overall complexity of pathway configuration over a range of spatial scales, whereas K provides a standardized measure of total pathway length. Values of K for grasshoppers as a group were lower than those of beetles and ants (ANOVA, $F = 5.79$, df = 13, 113, $P < 0.0001$; Table 1), although one of the grasshopper species, *Xanthippus corallipes,* had an intercept value similar to that of *Eleodes extricata* (Fig. 1). Among the beetle species, K was significantly greater for pathways of *Eleodes hispilabris* and *E. obscura* than of *E. extricata.* Intercept values for the beetle species were also significantly lower in the high-heterogeneity than in the low-heterogeneity grassland mosaics, but heterogeneity had no direct effect on K for the other taxa.

These cross-taxa comparisons reveal that, after accounting for differences among species in the absolute scale of their movements (e.g., rates, net displacement), there were in addition differences in the scale-independent (fractal) configuration of their movements. These differences in the fractal dimensionality of pathways may reflect differences in the ways the taxa perceive environmental heterogeneity and may be related to differences in resource use. The movements of harvester ants, for example, are directed toward searching for small seeds that have patchy distributions. In contrast, *Eleodes* beetles feed upon a broad range of plant material and detritus (Allsopp 1980, Crawford 1981), and the grasshoppers feed primarily on *Bouteloua gracilis* (Pfadt and Lavigne 1982), the dominant grass in this system. These resources are widespread and abundant. An organism walking in a straight line through an area with an evenly distributed resource encounters it at a rate $q = ct^{D_r}$, where the fractal dimension of the resource along the line is $D_r = 1$ and c is a concentration. Since the reward for searching is constant with time, the only way to increase q is to move to another environment with a higher concentration. The fastest way to reach a higher concentration is to take the shortest path out of the current environment, i.e., use a search path with $D_r = 1$. In contrast, an organism searching for sparse but highly clumped resources while walking a straight line encounters them at a rate $q = ct^{D_r}$, with $D_r < 1$. In this case, it pays (on average) to search a subregion where resources have been found in the past. Consequently, a more convoluted path is appropriate (Crist and MacMahon 1991). Following this same argument, the greater linearity of beetle and grasshopper pathways (lower values of D) may also increase the likelihood of encounter and mating among widely dispersed (but uniformly or randomly distributed) individuals. Nymphal *Opeia obscura* do not reproduce. In this case, selection of locations that provide shelter from predators or favorable microclimates may reduce their movement rates (low *K*) and relatively rapid and direct movements between sheltering locations may reduce pathway complexity (low *D*) relative to that of adults.

Within the range of spatial scales considered in a study, the parameters *D* and *K* may indicate how an organism responds to or perceives environmental pattern. In the grassland system we studied, for example, similarities in the values of *K* suggest that ants may travel just as far as the larger beetles and grasshoppers during a time interval (i.e., they have similar extents, sensu Wiens 1990, Kotliar and Wiens 1990). The greater value of *D* (a more tortuous pathway) suggests that ants may interact with environmental heterogeneity on a finer scale (smaller grain). Differences in these measures among species in the same system or for a given species in different environments may indicate different constraints on movement and/or differences in behavior. Conversely, similar dimensions across systems or species would be consistent with similarities in landscape effects or behaviors.

Because a given fractal dimension is a statistical summation of many interacting phenomena, however, different combinations of ecological and behavioral features may produce the same value of *D*. Fractals do not give a complete representation of movements by themselves and should be used in concert with other, scale-dependent measures. Nonetheless, they provide a way to assess similarities or differences in how organisms respond to heterogeneity that is independent of differences in body mass, physiology, diet, life history, or vagility. Similarities in *D* among species operating across quite different spatial scales suggest that their movements might be described by a common model, and this observation may provide an impetus for a more probing examination of the mechanisms underlying these similarities.

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