

MOVEMENT RESPONSES TO PATCH STRUCTURE IN EXPERIMENTAL FRACTAL LANDSCAPES

KIMBERLY A. WITH,¹ SEAN J. CADARET, AND CINDA DAVIS

Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA

Abstract. Neutral landscape models predict that habitat loss will abruptly disrupt landscape connectivity. We performed a series of simulation experiments to explore whether thresholds in landscape connectivity affect movement attributes (path length, net displacement, and fractal dimension of pathway) within fractal neutral landscapes. We then tested these assumptions by generating fractal landscape patterns in the field across a range of habitat abundances (0%, 20%, 50%, and 80% grass) and patchiness (clumped vs. patchy) and quantified how patch structure affected movement behavior in a generic organism, the common cricket *Acheta domestica* (Orthoptera: Gryllidae).

In the simulation experiment, individuals constrained to move only through adjacent grass cells (neighborhood size = 4 cells) exhibited abrupt thresholds between 50% and 80% grass cover for all movement parameters in clumped fractal landscapes but exhibited a linear decline in movement with decreasing habitat in patchy landscapes. Individuals constrained to move in sand within these same landscapes did not exhibit thresholds in movement with decreasing sand habitat. The exception is for the fractal dimension of pathways (a measure of tortuosity) in which a threshold occurred between 50% and 80% grass (50% and 20% sand) in patchy landscapes. Increasing the scale of movement by allowing individuals to move through unsuitable habitat (neighborhood size = 12 cells) reduced or eliminated any effects of patch structure on movement.

Live crickets can traverse both grass and sand, and thus threshold effects in movement behavior were generally not evident in the field experiment. Only small crickets (15–25 mm) exhibited a threshold response in net displacement (straight-line distance traversed) between 50% and 80% grass cover (50% and 20% sand). Crickets did exhibit significant responses to patch structure, however. Crickets moved faster and with less tortuosity in the control (0% grass) and less-vegetated (20% grass) plots than in plots with greater habitat coverage. Crickets used grass cells significantly more (73%) than expected in the 20% patchy fractal microlandscape; crickets were reluctant to leave isolated cells of grass. Grass provided cover, but sand facilitated movement. While experimentation at the landscape scale is generally intractable or impossible, computer simulation and field experiments founded on neutral landscape models permit initial assessment of how disrupting landscape connectivity affects movement behavior.

Key words: animal movement; crickets; experimental model systems; fractal geometry; habitat fragmentation; landscape connectivity; landscape ecology; neutral landscape models; percolation theory; spatial patterns.

INTRODUCTION

One of the more immediate consequences of habitat fragmentation is the disruption of dispersal among populations. “Dispersal is the glue that keeps populations together” (Hansson 1991), especially in terms of maintaining metapopulation dynamics. Increasing isolation among populations, which leads to reduced dispersal success and patch colonization rates, results in a decline in the persistence of individual populations and an enhanced probability of regional extinction for the entire metapopulation across the landscape (e.g., Lande 1987, With and King 1999a). Maintaining landscape

connectivity has thus been identified as the key to preserving dispersal among populations (Taylor et al. 1993, Pearson et al. 1996, With et al. 1997). “Connectivity” is often taken literally to mean the physical connectedness among habitat patches, as evidenced by the recommendation and establishment of habitat corridors for the conservation of some species (but see Mann and Plummer 1995). Nevertheless, landscape connectivity need not imply *structural connectivity*, the actual connection of habitat patches by corridors, but may instead result from *functional connectivity*, the connection of habitat patches (and populations therein) by dispersal. For example, species capable of crossing gaps of unsuitable habitat (e.g., a neotropical migrant bird) may perceive landscapes as connected across a greater range of habitat availability than species constrained to move only through suitable habitat (e.g., a

Manuscript received 30 January 1998; revised 23 June 1998; accepted 24 June 1998.

¹ E-mail: kwith@bgnet.bgsu.edu

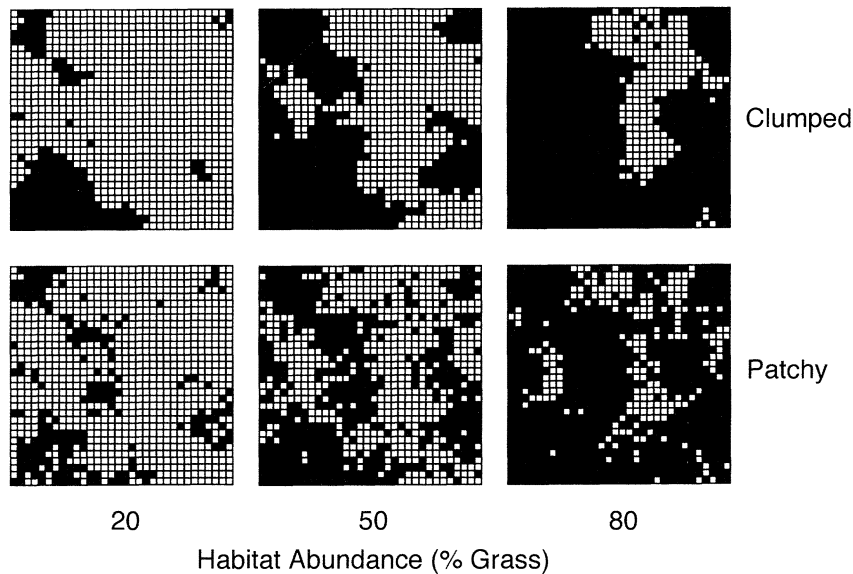


FIG. 1. Experimental model system. Fractal microlandscapes (5×5 m) were generated in the field as grass (shaded cells) and sand mosaics. These grid-based landscape patterns (32×32 cells) were generated as sectioned fractional Brownian surfaces based on the midpoint displacement algorithm (Saupe 1988, Keitt and Johnson 1995, With et al. 1997). This enabled us to produce landscape maps across a range of grass-habitat abundance (20%, 50%, and 80% grass) and fragmentation severity (patchy [$H = 0.1$] and clumped [$H = 0.9$]). A control plot consisting of 100% sand is not shown.

plethodontid salamander restricted to moist forest floors) (e.g., Dale et al. 1994).

Neutral landscape models, developed in the field of landscape ecology from percolation theory, have been employed to identify when landscapes become fragmented (Gardner et al. 1987, Gardner and O'Neill 1991, Gardner et al. 1993, With 1997, With and King 1997). In these grid-based percolation models, landscape connectivity is defined by the presence of a habitat cluster that spans the entire landscape (the "percolating cluster"). Landscape connectivity is defined as a threshold phenomenon, in which the landscape initially becomes fragmented abruptly over a very small range of habitat loss (Gardner et al. 1987, Gardner and O'Neill 1991, Plotnick and Gardner 1993, With 1997, With and King 1997). Above this threshold, the landscape is dominated by the percolating cluster, and habitat loss has little effect on connectivity until the critical threshold is reached (Andr en 1994). Below the threshold, the landscape is fragmented and is comprised of small, isolated patches of habitat. Such a dramatic transition in the overall patch connectivity of the landscape should have a major impact on dispersal, in terms of affecting the ability of organisms to move between patches.

Landscape connectivity depends not only on the degree of habitat loss (p), but also upon the pattern of loss. For example, if habitat is removed at random in small, isolated cells across the landscape (i.e., fine-scale habitat loss), connectivity is disrupted sooner (at higher levels of p) than if habitat is removed as a single

large "clearcut" (broad-scale habitat loss [Pearson et al. 1996]). This can be demonstrated by considering another theoretical habitat distribution—fractal neutral landscape models—in which the spatial contagion or clumping of habitat (the Hurst dimension H , a measure of the degree of spatial autocorrelation) can be varied in addition to p (Fig. 1). The point at which the extremely clumped (e.g., $H = 0.9$) landscape becomes disconnected or fragmented occurs at $p_{\text{crit}} = 0.45$, in which patch connectivity is defined as habitat cells that are connected along at least one edge, excluding diagonals (structural connectivity, Rule 1, Fig. 2). Thus the landscape remains connected across a greater range of habitat loss than in patchy fractal landscapes ($H = 0.1$), in which habitat loss occurs at a finer scale ($p_{\text{crit}} = 0.54$; Patchy, Fig. 2). To complicate matters further, assessment of landscape connectivity also depends upon the scale at which patch structure is assessed, which may relate to the scale of movement or the gap-crossing abilities of the species. Landscapes remain functionally connected, even if not structurally connected, across a greater range of habitat abundance if individuals are able to cross cells of unsuitable habitat; this has the effect of shifting the threshold (p_{crit}) to lower levels of p (Plotnick and Gardner 1993, Pearson et al. 1996).

Because neutral landscape models have been presented as a tool for quantifying patch connectivity in landscapes (a threshold phenomenon) and a disruption in connectivity is predicted to have significant ecological effects, it is only natural to ask how dispersal or

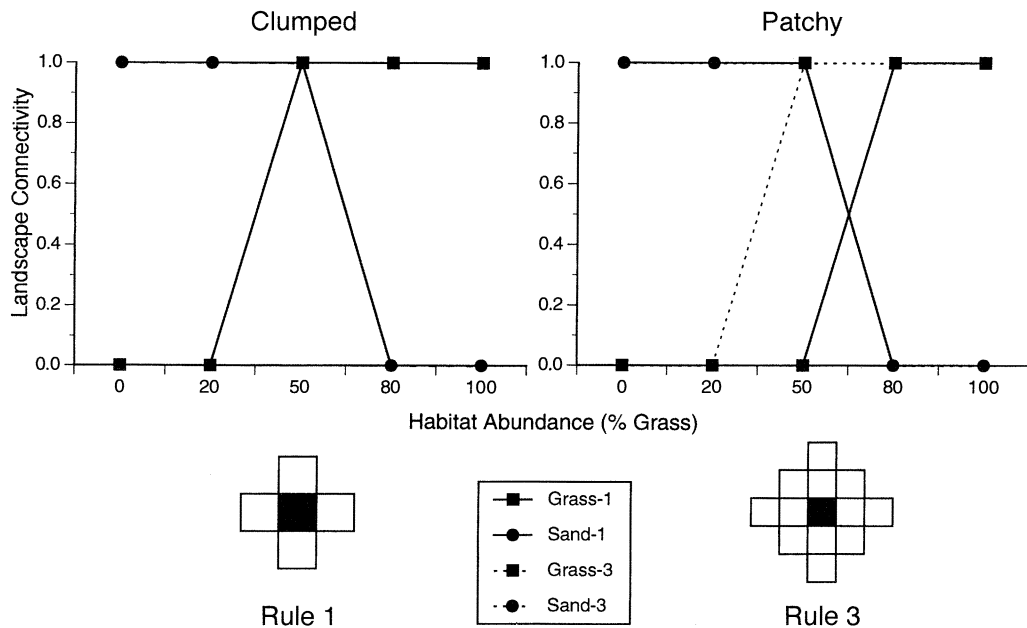


FIG. 2. Landscape connectivity for fractal landscape patterns (see Fig. 1) used in the simulation and field experiments (Clumped [$H = 0.9$], Patchy [$H = 0.1$]). Patch connectivity is the probability that a single large patch of habitat spans the entire microlandscape plot. Patches are defined either by assuming structural connectivity (neighborhood size = 4 cells, excluding diagonals; Rule 1) or in terms of functional connectivity, assuming that a species has gap-crossing abilities (neighborhood size = 12 cells; Rule 3). Connectivity is assessed separately for grass (Grass-1 and Grass-3) and sand (Sand-1 and Sand-3) at each of these two scales (Rule 1 vs. Rule 3).

movement behavior might be affected by a disruption in landscape connectivity or patch structure, whether thresholds also exist in movement behavior, and whether they coincide with thresholds in landscape connectivity. Recently, John Wiens and his colleagues (Wiens et al. 1997) developed an experimental model system (EMS) inspired by neutral landscape models, in which they studied the movement responses of tenebrionid beetles in microlandscapes consisting of randomly distributed grass cells at varying levels of abundance. Beetles demonstrated abrupt changes in movement behavior, not at the predicted threshold in landscape connectivity ($p_{\text{crit}} = 0.59$ if defined by Rule 1 for random landscapes), but at much lower levels of habitat abundance ($p < 0.2$). It is intriguing that ecological responses to habitat loss may occur at lower thresholds than expected on the basis of landscape connectivity (e.g., Andr n 1994).

We expand upon the study of Wiens et al. (1997) by considering how movement behavior is differentially affected by habitat loss, as opposed to the pattern of habitat loss or resulting patch structure (i.e., fragmentation). We first develop a simulation experiment to explore how patch structure (degree of habitat clumping) and habitat abundance are expected to affect the movement responses of organisms moving as a percolation process (movement constrained to suitable habitat cells within a given neighborhood size) in fractal landscapes. Fractal neutral landscape models have

the advantage of permitting control over the amount (p) as well as the spatial contagion (H) of habitat (With 1997, With et al. 1997). In addition, we studied the movement responses of a generic organism, the cricket *Acheta domestica* (Orthoptera: Gryllidae), in fractal microlandscape plots we created in the field. We can then compare predicted and observed movement responses to patch structure in experimental fractal landscapes.

Experimental model systems have become a valuable tool for exploring the ecological consequences of spatial complexity within the field of landscape ecology (Wiens and Milne 1989, Johnson et al. 1992a, Wiens et al. 1993), because they permit the rigorous testing of hypotheses emanating from neutral landscape models at experimentally tractable scales and with a degree of replication that is difficult to obtain at more traditional, human-defined landscape scales. Furthermore, there is an emerging recognition that "landscape" is a scale-independent entity, which must be defined at a scale relevant to the process and organism being studied (Wiens 1989, Wiens and Milne 1989, With 1994a). General principles of landscape ecology should apply to landscapes of all scales. Because movement is a fundamental ecological process that is known to be affected by spatial complexity, it is reasonable to adopt neutral landscape models as a null model to explore how patch structure (landscape connectivity) affects movement.

METHODS

The simulation and field experiments are each realizations of the “ant in the labyrinth” scenario, in which an individual is released in the center of a landscape and then permitted to move through the habitat maze. The simulation experiment was not intended to provide a general treatment of movement in spatially complex landscapes, but it was meant to generate quantitative predictions of movement behavior specific to the fractal landscape patterns that were generated in the field.

Generation of landscape patterns

Landscape patterns were created as two-dimensional grids (32×32 cells) in which the proportion of habitat (grass) covered either 0% (control), 20%, 50%, or 80% of the landscape. We generated landscape patterns using a fractal algorithm (midpoint displacement [Saupe 1988]) in which habitat distributions were produced as segmented fractional Brownian surfaces (Keitt and Johnson 1995, With et al. 1997). Midpoint displacement produces a continuously varying surface across the landscape (e.g., topography), which can be sectioned at some “elevation” such that a given proportion of the distribution lies above the elevation filter and is classified as “habitat.” The resulting landscape is a binary contour map of habitat patches. By adjusting the degree of spatial autocorrelation (H) among sites (cells) on the landscape, we can vary the fractal dimension ($D = 3 - H$) of the landscape pattern, and hence the degree of clumping of the habitat distribution. For this experiment, we generated fractal habitat distributions that were either clumped ($H = 0.9$) or patchy ($H = 0.1$; Fig. 1). A total of seven landscape configurations (1 control and 3 habitat levels \times 2 levels of clumping) were thus used in these simulation and field experiments to assess how patch structure affects movement (Fig. 1).

Description of landscape connectivity

Patch structure can be defined simply as the adjacency of neighboring habitat cells; in the parlance of percolation theory, this coincides with the “nearest-neighbor rule” used to define the structural connectivity of landscapes (i.e., Rule 1 [Plotnick and Gardner 1993, With 1997]). Attempts have been made to define patch connectivity on the basis of the dispersal or “gap-crossing” abilities of species in order to develop organism-centered definitions of landscape connectivity (i.e., functional connectivity [Dale et al. 1994, Pearson et al. 1996, With 1997, With and King 1997]). The size of the neighborhood presumably reflects either the area requirements of the species (e.g., minimum territory size), the area across which individuals are able to integrate information on patch structure (which might influence their movement decisions), or the size of the gap they are willing to traverse in search of suitable

habitat. Species capable of crossing gaps thus may perceive the landscape as connected (patches are functionally connected by dispersal) even if habitat patches are not physically connected (i.e., structural connectivity). A neighborhood size of 12 cells (Rule 3) allows individuals to cross at least one cell of unsuitable habitat.

Thus, whether or not the landscape is perceived as connected depends on the scale (Rule 1 vs. Rule 3) at which the organism interacts with spatial pattern and the underlying patch structure (patchy vs. clumped). For the fractal landscapes used in this study, connectivity is disrupted between 20% and 50% grass cover in clumped fractal landscapes at whatever scale it is assessed (Fig. 2). The threshold for grass is shifted in patchy fractal landscapes (50–80% grass) if patch structure is measured at a fine scale (Rule 1, Fig. 2). At a broader scale (Rule 3), the threshold for grass patch connectivity shifts back to between 20% and 50%. At what scale might crickets be perceiving patch structure in these fractal landscapes?

Movement responses to patch structure

It is difficult to assess a priori the scale across which crickets might be integrating information on patch structure or the gap size that crickets might be willing to cross in search of more suitable habitat (e.g., grass cover). We have no evidence to suggest that crickets are integrating information on spatial pattern beyond the cells immediately adjacent to them and which might therefore influence their movement behavior (e.g., Rule 1 movement). Nevertheless, crickets, like many animals, are not restricted to move only within a single habitat type. Grass provides cover, but movement is facilitated on sand (see *Results: Field experiment*). Crickets are thus capable of crossing “gaps” between grass cells, which suggests that a larger neighborhood rule (e.g., Rule 3) is more appropriate for modeling their movement responses to patch structure. Because the effect of patch structure on movement parameters (e.g., path length, net displacement, tortuosity) has not been quantified previously in a percolation framework, we present the simulation results for both neighborhood rules (Rule 1 and Rule 3) as a basis for comparison.

Although percolation theory assumes that movement occurs only within a single habitat type (the percolating medium), it provides a useful null hypothesis for understanding movement responses to patch structure in grid-based (raster) landscapes and for making comparisons to rule-based definitions of landscape connectivity (p_{crit}). Movement in crickets is facilitated by extensive areas of sand (see *Results: Effect of habitat abundance on movement*) and thus sand might be considered the primary percolating medium. Nevertheless, crickets do move in grass and we therefore bracketed the range of expected behavior by simulating movement in each medium (grass and sand) within these landscapes (Fig. 1).

Simulation experiment.—A single individual (“cybercricket,” $n = 40$ individuals) was positioned in the center of each landscape map (7 landscapes \times 40 cybercrickets = 280 runs) and was permitted to move either to (1) an adjacent habitat cell (neighborhood size = four cells; Rule 1), or (2) a habitat cell within a 12-cell neighborhood (gap-crossing; Rule 3). Movement continued until the individual reached the edge of the landscape or until 50 moves had been made or attempted. The direction of movement was assigned at random with equal probability into one of the neighboring cells.

Two series of experiments were run: (1) grass as the percolating medium, and (2) sand as the percolating medium, with sand covering 20%, 50%, 80%, or 100% (control) of the landscapes (Fig. 1). Movement into a neighboring cell was permitted only if it was the appropriate habitat type. We retained information on the x , y coordinates of the cells through which the cybercricket moved in its traverse of the grid for subsequent analysis (see *Methods: Analysis of movement pathways*). A total of 1120 cybercricket pathways (280 runs \times 2 movement rules \times 2 experiments) were generated in the simulation experiment.

Field experiment.—We established a series of experimental microlandscapes (5 \times 5 m plots) at the Ecology Research Station, located just north of the Bowling Green State University campus. Microlandscapes were fractal mosaics of grass and sand (32 \times 32 cells; each cell = 15.6 \times 15.6 cm²) in which the proportion of grass constituted either 0% (control plot); 20%, 50%, or 80% of the plot (Fig. 1). Plots were bordered with wood furring strips, along which monofilament line was attached to nails at 15.6-cm intervals to create a 1024-cell microlandscape grid. The height of the grass cover within the plots (~7–9 cm) was maintained by periodic mowing. Fractal microlandscape patterns were maintained by manual weeding and herbicide application as needed.

We used crickets as generic organisms in this study of animal movement responses to patch structure. Crickets were obtained from Fluker Farms (Baton Rouge, Louisiana) as 15-mm nymphs and were housed in plastic, covered tubs in the laboratory with ad libitum access to food (dog kibble, orange wedges) and water under constant temperature, humidity, and lighting conditions. Because nymphal crickets grew in size and matured before we concluded our field experiment, it was necessary to order crickets in two separate batches (~4 wk apart). Body size affects how terrestrial arthropods interact with spatial complexity (Crist et al. 1992, With 1994a, b), and thus we incorporated the effect of cricket size (small = 15–25 mm, large = 26–35 mm) in the design of our statistical analyses (see *Methods: Statistical analyses*).

We observed the movement responses of $n = 20$ –22 individuals from each of the two size classes (small vs. large) within each plot during summer (June–Au-

gust) 1996. Crickets were randomly assigned to a plot to minimize potential intraseasonal effects on movement owing to weather changes or differences between cricket batches (i.e., crickets of one size class did not come from a single batch and were not all observed at a particular time in the season). We used each cricket only once in experimental trials. We released individual crickets into a randomly selected cell within the center of the plot (a region of nine cells); each cricket was then allowed to acclimatize for 5 min beneath a plastic cup before we began observations. Crickets were released within the center of plots so as to maximize the extent to which individuals could interact with landscape patterns. Because surface temperatures might have affected the movement responses of crickets, we restricted our observations to periods when surface temperatures (of sand) were 20–30°C; this temperature range was found to bracket the activity periods of other orthopterans (Anderson et al. 1979, With 1994a, b) and is consistent with our preliminary observations of reduced activity levels in crickets above or below this range.

As each cricket traversed the microlandscape, we marked its location on the grid with numbered toothpick flags as it moved from cell to cell. This was done at a lagged interval to ensure that we did not influence the cricket’s movement behavior. We continued mapping the movement pattern until the cricket either left the grid or remained motionless for ≥ 5 min. We observed a total of 298 crickets for an average of 9.6 ± 8.49 min per individual (mean ± 1 SD). Crickets made an average of 32 ± 16.7 cell transitions per trial (range = 5–128 cell transitions), before reaching the edge of the plot (71%), remaining motionless for ≥ 5 min (27%), or disappearing from sight (2%). After each trial, we recorded the cell coordinates (x , y) and habitat types (grass or sand) through which the cricket moved. Because we have quantified the cricket’s movement pattern on the basis of cell transitions, the grain of the movement response is the same as the landscape pattern (i.e., raster-based). We are not interested in the fine-scale movements that occur within cells, as this occurs below the resolution of the grid-based landscape pattern.

Analysis of movement pathways.—We measured a number of parameters for each movement pathway generated in either the simulation or field experiment. These measures included net displacement (linear distance between the midpoint of the first and last cell through which the cricket moved, in meters), path length (sum of distances across all cells, in meters), and fractal dimension (D), a measure of the tortuosity of the movement pathway, which was calculated using the dividers method (Dicke and Burrough 1988, Wiens and Milne 1989, Crist et al. 1992, With 1994a, b, Wiens et al. 1995). Although Turchin (1996) has recently criticized the use of fractal analysis to characterize animal movement pathways, his main point of contention was

TABLE 1. Analysis of variance of cricket movement parameters in experimental fractal microlandscapes as affected by body size (small vs. large) and habitat abundance (0%, 20%, 50%, and 80% grass).

Movement parameter Source of variation	df	MS	F	P
Movement rate				
Model ($R^2 = 0.295$)	7	0.13	17.36	0.0001
Size	1	0.17	23.87	0.0001
Habitat abundance	3	0.23	31.79	0.0001
Size \times habitat abundance	3	0.02	2.33	0.075
Error	290	0.01		
Net displacement				
Model ($R^2 = 0.120$)	7	0.18	5.67	0.0001
Size	1	0.65	20.69	0.0001
Habitat abundance	3	0.09	2.76	0.042
Size \times habitat abundance	3	0.11	3.34	0.020
Error	290	0.03		
Path length				
Model ($R^2 = 0.046$)	7	0.08	2.00	0.055
Size	1	0.12	3.15	0.077
Habitat abundance	3	0.09	2.22	0.09
Size \times habitat abundance	3	0.08	2.01	0.113
Error	290	0.04		
Fractal dimension				
Model ($R^2 = 0.124$)	7	0.03	5.87	0.0001
Size	1	0.02	3.18	0.076
Habitat abundance	3	0.07	11.65	0.0001
Size \times habitat abundance	3	0.00	0.60	0.618
Error	290	0.01		
Habitat use (proportion of grass cells)				
Model ($R^2 = 0.713$)	7	6.37	102.69	0.0001
Size	1	0.02	0.33	0.566
Habitat abundance	3	14.82	238.98	0.0001
Size \times habitat abundance	3	0.02	0.39	0.757
Error	290	0.06		

Note: ANOVA used Type III sums of squares.

the potential for scale-dependent shifts to occur in the fractal dimension, which would compromise the ability to extrapolate fine-scale information on movement responses to broader spatial scales. We use the fractal dimension of movement pathways merely as a descriptor of pattern complexity in this analysis and not as a mechanistic model of animal movement or as a scale-independent measure for translating individual movement into the spatial dynamics of populations. In addition to these three measures, we also calculated movement rate (number of cells traversed per minute) and the proportion of grass cells through which crickets moved, to compare the use of habitat relative to its abundance in the field experiment.

Statistical analyses.—Formal statistical analyses were conducted on the pathways generated by real crickets in the field experiment to address how habitat fragmentation (H), apart from habitat abundance (p), affected cricket movement responses to spatial complexity. The statistical model was a three-way analysis of variance (ANOVA, using Type III sums of squares; PROC GLM, SAS Institute, Cary, North Carolina) with body size (small vs. large), habitat abundance (20%, 50%, and 80%), and degree of clumping ($H = 0.1$ or 0.9) as the independent variables. The movement parameters analyzed individually as dependent variables

were movement rate, path length, net displacement, fractal dimension of pathway, and proportion of grass cells traversed during movement ([number of grass cells traversed]/[total cells traversed], a measure of habitat use).

A separate series of ANOVAs was required to evaluate how crickets performed in the control plot (0% grass) relative to plots with varying amounts of habitat; the degree of habitat clumping is obviously moot in the control plot, and thus it was not possible to evaluate fully the effects of habitat abundance in the previous three-way model. Consequently, we performed separate two-way ANOVAs to assess how body size and habitat abundance (0%, 20%, 50%, or 80%) interacted to affect cricket movement parameters. The effects of cricket size and habitat abundance reported throughout the text and figures are based on this latter analysis because of the larger sample sizes resulting from inclusion of pathways from the control plot, although significance levels were similar in the two analyses (Tables 1 and 2).

For all analyses, data were transformed as necessary to produce normality and homogeneity of variances. Tukey tests were used to distinguish among means where significant differences were found in the ANOVAs.

TABLE 2. Analysis of variance of cricket movement parameters in experimental fractal microlandscapes as affected by body size (small vs. large), habitat abundance (20%, 50%, and 80% grass), and habitat fragmentation (patchy [$H = 0.1$] or clumped [$H = 0.9$]).

Movement parameter Source of variation	df	MS	F	P
Movement rate				
Model ($R^2 = 0.142$)	11	0.026	3.65	0.0001
Size	1	0.068	9.66	0.0021
Habitat abundance	2	0.088	12.53	0.0001
Habitat fragmentation	1	0.008	1.20	0.274
Size \times habitat abundance	2	0.003	0.40	0.670
Size \times fragmentation	1	0.000	0.00	0.963
Habitat abundance \times fragmentation	2	0.003	0.39	0.680
Size \times habitat abundance \times fragmentation	2	0.010	1.46	0.234
Error	242	0.007		
Net displacement				
Model ($R^2 = 0.131$)	11	0.109	3.31	0.0003
Size	1	0.539	16.31	0.0001
Habitat abundance	2	0.118	3.56	0.0298
Habitat fragmentation	1	0.056	1.70	0.193
Size \times habitat abundance	2	0.157	4.75	0.0094
Size \times fragmentation	1	0.003	0.09	0.765
Habitat abundance \times fragmentation	2	0.014	0.42	0.657
Size \times habitat abundance \times fragmentation	2	0.015	0.46	0.631
Error	242	0.033		
Path length				
Model ($R^2 = 0.038$)	11	0.034	0.88	0.561
Size	1	0.001	0.04	0.844
Habitat abundance	2	0.057	1.49	0.227
Habitat fragmentation	1	0.012	0.32	0.575
Size \times habitat abundance	2	0.015	0.40	0.671
Size \times fragmentation	1	0.012	0.31	0.579
Habitat abundance \times fragmentation	2	0.086	2.24	0.109
Size \times habitat abundance \times fragmentation	2	0.014	0.35	0.702
Error	242	0.038		
Fractal dimension				
Model ($R^2 = 0.107$)	11	0.016	2.64	0.003
Size	1	0.029	4.67	0.0317
Habitat abundance	2	0.054	8.66	0.0002
Habitat fragmentation	1	0.000	0.01	0.9156
Size \times habitat abundance	2	0.004	0.66	0.519
Size \times fragmentation	1	0.015	2.36	0.126
Habitat abundance \times fragmentation	2	0.007	1.07	0.343
Size \times habitat abundance \times fragmentation	2	0.006	1.01	0.365
Error	242	0.006		
Habitat use (proportion of grass cells)				
Model ($R^2 = 0.545$)	11	1.79	26.40	0.0001
Size	1	0.039	0.57	0.450
Habitat abundance	2	9.04	132.88	0.0001
Habitat fragmentation	1	0.297	4.37	0.038
Size \times habitat abundance	2	0.035	0.51	0.602
Size \times fragmentation	1	0.118	1.73	0.190
Habitat abundance \times fragmentation	2	0.314	4.61	0.011
Size \times habitat abundance \times fragmentation	2	0.231	3.39	0.035
Error	242	0.068		

Note: ANOVA used Type III sums of squares.

RESULTS

Expected movement responses in fractal landscapes

Effect of habitat abundance on movement.—Movement responses are not symmetrical in these fractal landscapes and are dependent upon the percolating medium preferred by the organism. Thresholds in movement are only evident between 50% and 80% grass for cybercrickets without gap-crossing abilities (i.e., Rule 1) that were constrained to move on grass. Path lengths

are nearly five times longer, resulting in a net displacement that is nine times greater, in the 80% landscapes than in the 50% landscapes (Grass-1, top and center panels of Fig. 3). Tortuosity of pathways declines linearly with decreasing habitat, however (values of $D \rightarrow 0$ indicate cybercrickets did not move beyond their original point in the center of the plot). Movement cannot occur for grass cybercrickets in the 20% and 50% plots (and obviously in the 0% control plot) because of the absence of grass cells within the center of these land-

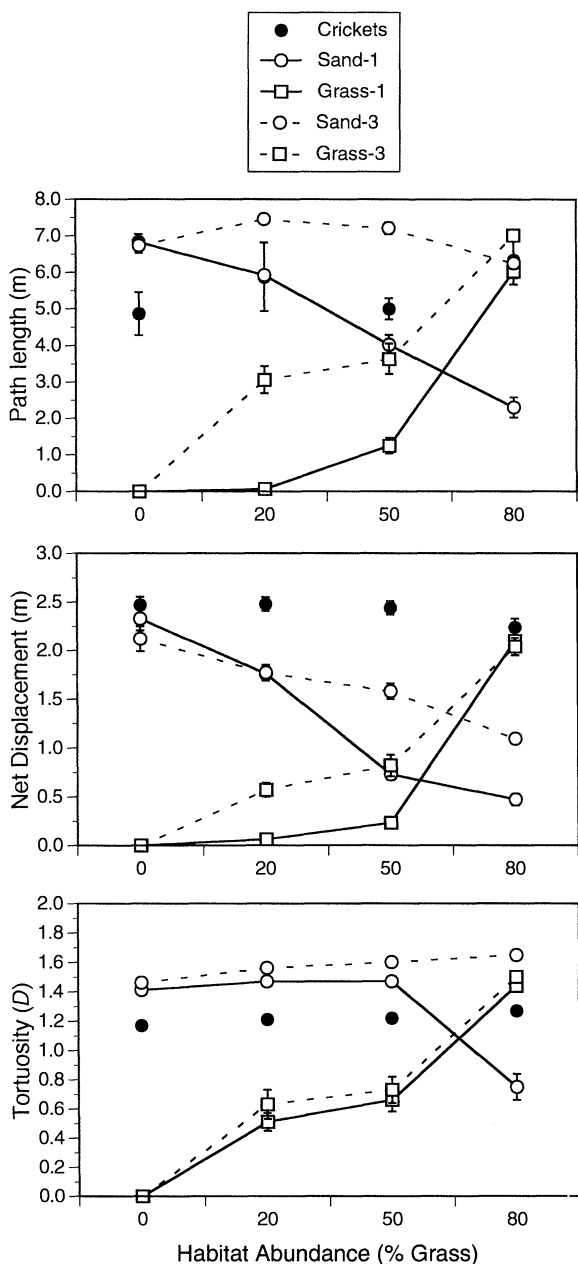


FIG. 3. Comparison of movement responses between cybercrickets on either grass or sand and real crickets ("Crickets") in fractal landscapes that differ in habitat abundance (% grass cover). Movement was simulated as a percolation process for cybercrickets at two scales (Rule 1 or Rule 3). Thus, "Sand-1" refers to cybercrickets constrained to move as a nearest-neighbor process (Rule 1) on sand, and "Grass-3" refers to cybercrickets with gap-crossing abilities (Rule 3) that must move among grass cells.

scapes where they were "released" (Fig. 1). This suggests that the threshold effect is sensitive to the starting condition and the specifics of the landscape pattern, especially since sand cybercrickets exhibited a linear decline in movement distance with increasing grass

(and thus decreasing sand) coverage and the effect of increasing the scale of movement (Rule 3) is to produce more linear responses to changing levels of habitat abundance (e.g., Grass-3, top and center panels of Fig. 3).

Nevertheless, a threshold is evident between 50% and 80% grass (20% and 50% sand) for movement tortuosity in cybercrickets without gap-crossing abilities that are percolating on sand (Sand-1, bottom panel, Fig. 3). Sand cybercrickets maintain near-maximum tortuosity ($D = 1.5$ for a random walk) when grass covers 0–50% of the landscape (or, alternatively, when sand covers 50–100% of the landscape), but movement is restricted in the 80% grass plots (particularly in the 80% patchy landscape, Fig. 4). The effect of increasing the scale of movement (Rule 3) is to reduce or eliminate the effect of habitat abundance on movement (Sand-3, Fig. 3).

Effect of habitat fragmentation on movement.— Movement was differentially affected by the degree of fragmentation or patchiness of the landscape (Fig. 4). Threshold effects were evident between 50% and 80% grass for cybercrickets moving on grass in clumped fractal landscapes, regardless of the scale of movement (Grass-1 and Grass-3, left-hand panels for Clumped landscapes, Fig. 4). Again, this threshold results from the inability of grass cybercrickets to move in these landscapes because of the absence of grass cells in the center of the plot (Fig. 1). In contrast, grass cybercrickets without gap-crossing abilities (Rule 1) in the patchy landscapes exhibited a linear decline in movement parameters with decreasing grass coverage (Grass-1, right-hand panels for Patchy landscapes, Fig. 4). Sand cybercrickets without gap-crossing abilities (Rule 1) generally exhibit linear declines in these movement parameters, particularly in the patchy fractal landscapes. The exception is the threshold evident in movement tortuosity between 50% and 80% grass (50% and 20% sand, respectively) in the patchy landscape (Sand-1, bottom-right panel, Fig. 4). Note that it is in these patchy landscapes that habitat abundance has little effect on movement for good dispersers (Rule 3). Furthermore, movement in patchy landscapes is similar on either percolating medium for dispersers with gap-crossing abilities, except when grass covers only 20% of the landscape (Grass-3 and Sand-3, Patchy landscapes, Fig. 4). Sand cybercrickets with gap-crossing abilities (Rule 3) have path lengths that are 20% longer, resulting in a net displacement that is 60% greater, than grass cybercrickets in 20% patchy landscapes.

Field experiment

Large crickets moved significantly farther and faster than small crickets through the experimental fractal microlandscapes (net displacement: large, 2.6 ± 0.60 m [mean \pm 1 SD], $n = 147$ crickets; small, 2.2 ± 0.71 m, $n = 151$ crickets; movement rate: large, 0.1 ± 0.12 cells/min; small, 0.08 ± 0.07 cells/min; Tables 1 and

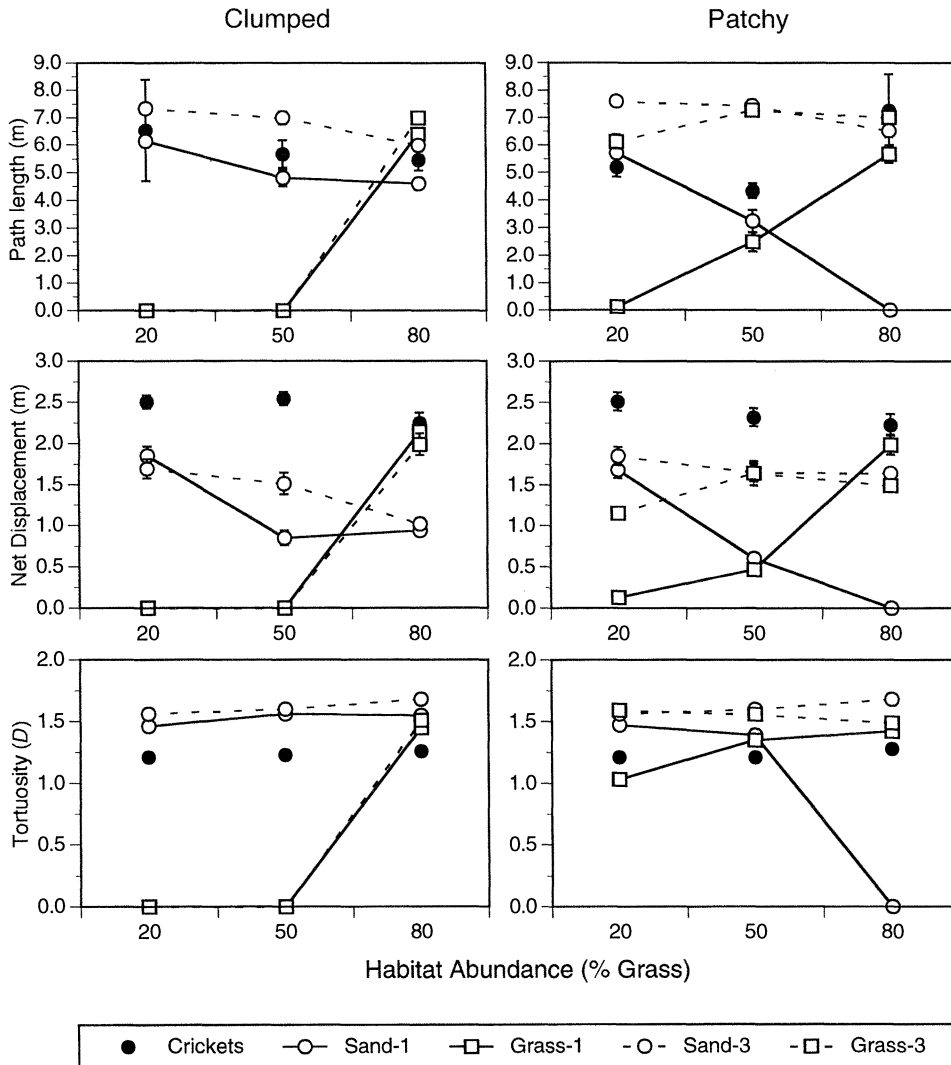


FIG. 4. Effect of patch structure (clumped [$H = 0.9$] patchy [$H = 0.1$]) on the movement responses of cybercrickets and real crickets ("Crickets") in fractal landscapes. Movement was simulated as a percolation process for cybercrickets at two scales (Rule 1 or Rule 3) and in different percolating media (grass vs. sand). Thus, "Sand-1" refers to sand cybercrickets moving as a nearest-neighbor process (Rule 1).

2]. Consequently, larger crickets exhibited slightly more linear patterns of movement than small crickets (tortuosity: large, $D = 1.21 \pm 0.21$; small, $D = 1.24 \pm 0.11$; Table 2). Nevertheless, small crickets made just as many cell transitions on average as did large crickets (small: 31 ± 16.9 cell transitions, range = 5–128 cells; large: 33 ± 16.5 cells, range = 6–122 cells; $P = 0.06$, t test).

Effect of habitat abundance on movement.—Habitat abundance generally had the greatest effect on the movement responses of crickets (Tables 1 and 2). Crickets moved faster and produced more linear pathways (tortuosity, $D \rightarrow 1$) in the control plot (Fig. 5). Cricket pathways were most tortuous in the 80% grass plots, and movement rates were significantly reduced in the 50% and 80% grass plots (Fig. 5). Grass was

either a more viscous habitat that impeded movement, or it was preferred for cover; both explanations appeared to be important in explaining cricket movement responses. Crickets scurried rapidly across sand with few detours until a grass cell was encountered. Crickets were then observed to struggle through "forests" of grass blades before burrowing down beneath the canopy and remaining motionless (observations were terminated if crickets stopped moving for ≥ 5 min). There was a significant interaction between body size and habitat abundance for net displacement (Tables 1 and 2). The interaction effect occurred because small and large crickets moved similar distances in the 50% grass plots, but differed significantly in net displacement within the control and other grass plots (Fig. 6). Large crickets were little affected by the amount of habitat

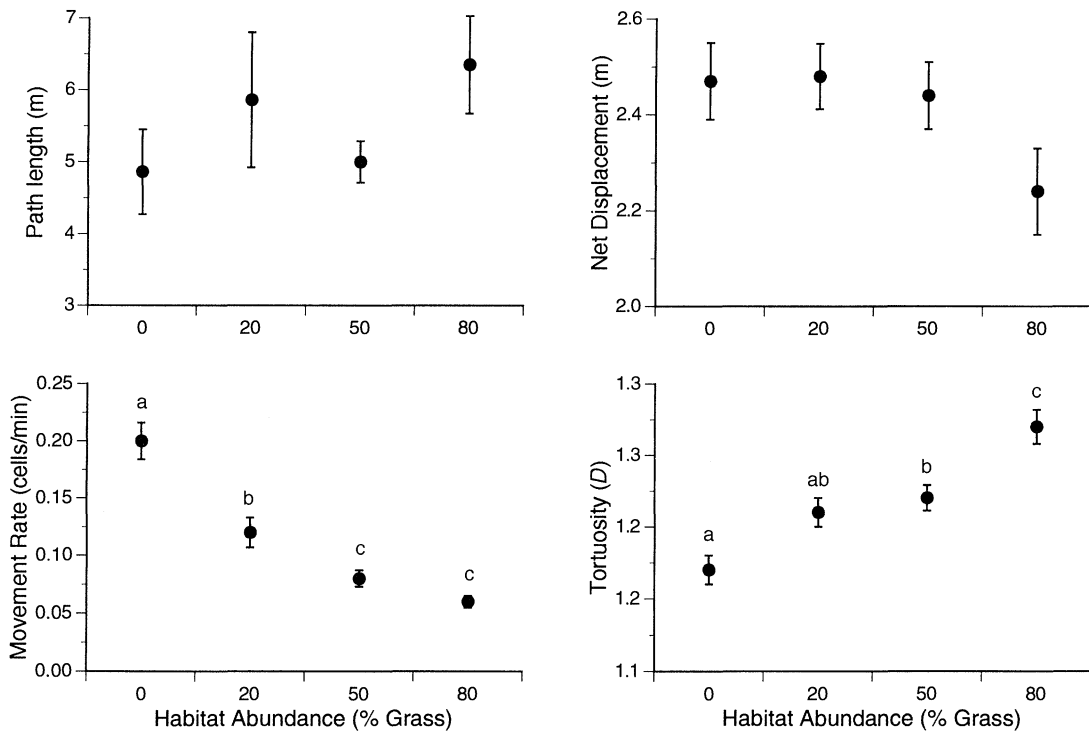


FIG. 5. Effect of habitat abundance (percentage grass cells) on various movement parameters of crickets traversing experimental fractal microlandscapes. Sample sizes are: 0% grass ($n = 44$ crickets), 20% grass ($n = 86$ crickets), 40% grass ($n = 85$ crickets), and 80% grass ($n = 83$ crickets). Means (± 1 SE) with the same letter are not significantly different at the $\alpha = 0.05$ level (Tukey test of significant ANOVA results).

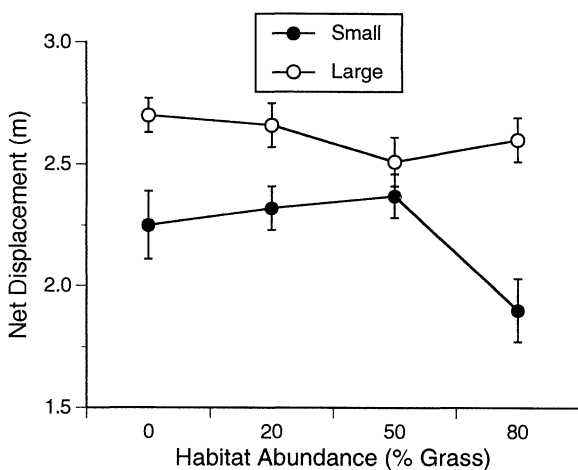


FIG. 6. Net displacement (mean ± 1 SE) in small and large crickets as a function of habitat abundance in fractal microlandscapes. Sample sizes are: small = 0% grass ($n = 22$ crickets), 20% grass (44 crickets), 50% grass (43 crickets), 80% grass (42 crickets); large = 0% grass (22 crickets), 20% grass (42 crickets), 50% grass (42 crickets), 80% grass (41 crickets).

on the microlandscape, but small crickets exhibited an abrupt decline in net displacement between 50% and 80% grass cover.

The effect of habitat abundance on movement responses thus appeared to be essentially linear (tortuosity) or curvilinear (movement rate) rather than a threshold, although net displacement came closest to exhibiting threshold behavior between 50% and 80% grass, at least for small crickets (Fig. 6). Movement by small crickets is facilitated by vast areas of bare ground (>50%), and is significantly reduced when grass dominates the landscape.

Effect of habitat fragmentation on movement.—Habitat fragmentation, the degree of clumping of grass cells, only affected habitat use by crickets (Table 2). The use of habitat was proportional to its abundance in all but the 20% grass plot, where crickets used grass cells significantly more ($28.5 \pm 19.35\%$, $n = 86$ crickets) than expected (Fig. 7A). Crickets spent 73% more time on grass cells in the 20% patchy fractal microlandscape than expected, whereas use of habitat in the 20% clumped plot (and in all other microlandscapes) was not significantly different than predicted (Table 2, Fig. 7B). Crickets in the 20% patchy plot either were encountering grass cells more often than crickets in the 20% clumped plot, or were reluctant to leave grass cells once they did encounter them. Note that a cricket re-

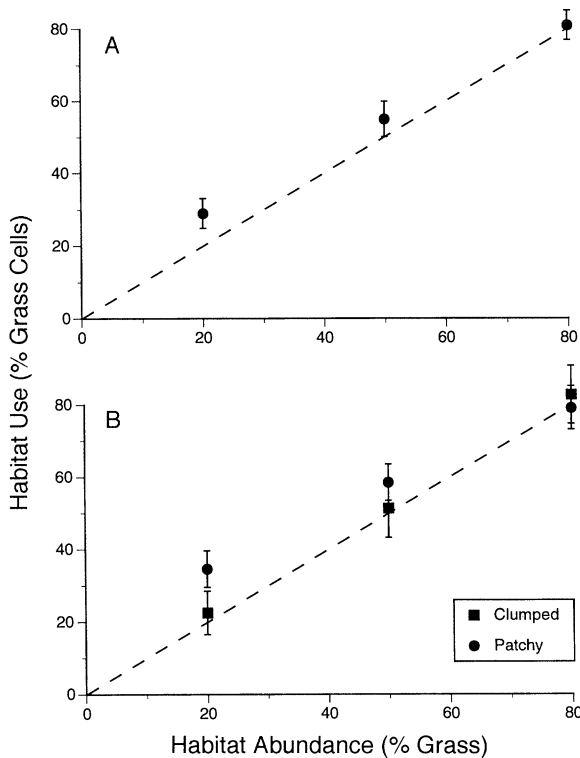


FIG. 7. Habitat use (percentage of grass cells traversed [mean \pm 2 SE]) by crickets moving across experimental fractal microlandscapes (A) and relative habitat use in clumped ($H = 0.9$) and patchy ($H = 0.1$) fractal microlandscapes (B). The dashed line is the predicted use of habitat if random. Sample sizes for A: 20% grass ($n = 86$ crickets), 50% grass (85 crickets), 80% grass (83 crickets). Sample sizes for B: Clumped = 20% grass ($n = 43$ crickets), 50% grass (42 crickets), 80% grass (42 crickets); Patchy = 20% grass (43 crickets), 50% grass (43 crickets), 80% grass (41 crickets).

leased in the center of the 20% patchy microlandscape should have a higher probability of encountering a grass cell when traversing the landscape than in the 20% clumped landscape, where the habitat occurred in a few large patches (Fig. 1). Once a grass cell was found, however, crickets were obviously reluctant to leave an isolated cell and were observed to walk around the periphery of the cell repeatedly before racing across the landscape in search of more substantial cover.

Comparison between simulated and real movement pathways

Real crickets move most readily on sand, and because they can traverse both cover types in these plots (i.e., they have gap-crossing abilities), their expected movement response to patch structure is perhaps best modeled by sand cybercrickets with gap-crossing abilities (Sand-3, Figs. 3 and 4). Note that sand cybercrickets with gap-crossing abilities are predicted to be little affected by habitat abundance; no thresholds are evident (Sand-3, Figs. 3 and 4). Likewise, the movement distances of real crickets was not affected by

habitat abundance in the field experiment (Fig. 5). Real crickets generally had path lengths comparable to sand cybercrickets in the clumped landscapes, but path lengths for sand cybercrickets were significantly longer than real crickets in 20% and 50% patchy landscapes (Sand-3, Fig. 4). Regardless of the underlying patch structure, real crickets moved farther (net displacement) and produced more linear patterns of movement ($D \rightarrow 1$, tortuosity) than cybercrickets. Cybercrickets were simulated to move with random directionality between steps, whereas real crickets maintained a directional bias over a number of steps.

DISCUSSION

Neutral landscape models have been presented as a theoretical tool for defining landscape connectivity, for identifying how different species perceive landscape structure, and for evaluating how spatial complexity affects ecological processes such as dispersal (Gardner et al. 1993, With and Crist 1995, Pearson et al. 1996, With 1997, With and King 1997). Because habitat fragmentation may have threshold effects that result in the abrupt decline and sudden extinction of species (Lande 1987, With and King 1999a), it can be difficult to predict the consequences of habitat fragmentation until after the threshold has been crossed (Pulliam and Dunning 1994), at which point it may be too late (and costly) to implement recovery efforts. At the very least, habitat loss and fragmentation (the pattern of loss) should disrupt movement processes across the landscape. Disruption of dispersal leads to the isolation of populations and enhances extinction risk of metapopulations (e.g., Opdam 1990). A first step toward predicting the potential threshold effects of habitat fragmentation is thus to demonstrate a disruption of movement across the landscape.

The realization of neutral landscape patterns in the field have provided the first experimental tests of percolation theory in terms of how habitat loss and fragmentation affect movement behavior. Wiens et al. (1997) were able to document strong threshold effects in a number of movement parameters (mean step length, net displacement and vector length) for tenebrionid beetles in random landscapes. This threshold occurred between 0% and 20% habitat, at lower levels than predicted by measures of patch connectivity ($p_{crit} = 0.59$ on random landscapes, using Rule 1). Note, however, that beetles also traverse both grass and sand, which suggests that a rule incorporating gap-crossing abilities (e.g., Rule 3) provides a more appropriate scale at which to assess landscape connectivity. In random landscapes, $p_{crit} = 0.29$ if patch connectivity is defined by Rule 3 (Plotnick and Gardner 1993). Thus, thresholds in beetle movement responses still occur below the level at which patch structure is expected to become disrupted.

Thresholds in movement responses are generally not expected in fractal landscapes, as evidenced by our

simulation experiment, and organisms operating at broader spatial scales or capable of crossing gaps (e.g., Rule 3) are expected to be insensitive to patch structure (Fig. 4). This may explain the lack of response observed in crickets to the experimental fractal patterns in the field. Although significant differences in movement responses did occur among levels of habitat abundance, threshold effects were not evident for any of the movement parameters we measured (Fig. 5). An exception is the net displacement of small crickets, which exhibited an abrupt decline in movement between 50% and 80% grass landscapes (Fig. 6). Because cricket movement was facilitated by sand, the threshold can be viewed as occurring when sand cover is limiting on the landscape (e.g., 20%). The threshold thus occurs between 20% and 50% sand cover, which is still at a higher level of habitat abundance than the threshold observed for tenebrionid beetles. In any case, a threshold in net displacement was not expected; only a threshold in tortuosity was observed in the simulation experiment (Fig. 3).

The rate at which organisms move across the landscape affects whether they are able to perceive the patch structure that occurs at a particular scale (With 1994a, b). Movement defines the spatial grain and extent at which organisms are able to interact with landscape structure, which is a function of the perceptual resolution of the organism (Kotliar and Wiens 1990). A large grasshopper species (*Xanthippus corallipes* [Orthoptera: Acrididae]) moved 6 times faster across microlandscapes in a grassland mosaic than did two smaller species (*Psoloessa delicatula*, *Opeia obscura*; With 1994a). Consequently, the large species was not affected by fine-scale heterogeneity that influenced the movement responses of the smaller species, as evidenced by their more tortuous pathways (higher D of movement patterns). While small organisms are expected to have a perceptual resolution that is shifted to finer scales than that of large organisms (With 1994a, b), we had hoped that by quantifying the grain of movement on the basis of cell transitions, which is equivalent to the grain of the landscape pattern in our plots, that we could at least control for differences in how large and small crickets might be perceiving heterogeneity within cells. Nevertheless, it is apparent that large crickets were little affected by differences in habitat abundance (Fig. 6), which suggests that they were not as sensitive to the microlandscape patterns to which we subjected them in the field. This may be because they were moving more rapidly across the microlandscapes and thus were operating at a greater spatial extent than imposed by the dimensions of our plot. Future studies should explore the effect of grain (cell) size and spatial extent (plot dimensions) on movement responses to patch structure.

One of the advantages of fractal neutral landscape models is that they afford a means of systematic control over both the abundance, as well as the spatial con-

tagion, of habitat distributions. This enabled us to assess the relative effects of habitat loss and patch structure (fragmentation) on animal movement. The only effect of fragmentation, however, was on habitat use by crickets. Crickets used habitat significantly more often than expected in the 20% patchy ($H = 0.1$) landscape (Fig. 7B). Crickets were obviously reluctant to leave isolated grass cells once they were encountered. The tenebrionid beetle *Eleodes obsoleta* also spent significantly more time (three times greater than expected) on grass cells in a 20% random microlandscape and beetles appeared to stop more frequently on grass cells in this plot (shorter step lengths; Wiens et al. 1997). Simulation of dispersal as a random walk on fractal landscapes revealed abrupt thresholds in dispersal success (probability of encountering a habitat cell) at $p < 0.1$, which corresponds to thresholds in the gap structure (lacunarity; Plotnick et al. 1993) between habitat patches of the landscape (With and King 1999b). The finding of thresholds in movement or dispersal behavior far below the critical threshold in landscape connectivity (e.g., Wiens et al. 1997), coupled with observations that individuals are obviously reluctant to cross gaps of a certain size, suggests that it may be the gap structure rather than the patch structure that ultimately influences movement responses to landscape structure.

Individual movement behavior has important implications for population-level responses to habitat fragmentation (Turchin 1991, Johnson et al. 1992b, Wiens et al. 1993, Crist and Wiens 1995, With and Crist 1996). The differential rates of movement by individuals through a landscape mosaic affect the spatial structure and dynamics of a population, and can produce dissimilar patterns of dispersion among species; that is, not all species will be affected similarly by fragmentation. For example, if movement is modeled as a percolation process, then the fine-scale movement responses of the grasshopper *X. corallipes* within grass cells that differed in forage abundance and heterogeneity suggested that this species should be retained within a third of the landscape (movement was reduced in habitat types comprising 35% of the landscape), resulting in an overall clumped distribution. The individual movement responses of the sympatric *P. delicatula* were similar across habitat types comprising the majority of the landscape, such that this species was expected to be randomly distributed. Although it was not possible to reproduce the exact levels of aggregation attained by either species in a simulation model that applied individual-based movement responses within different microhabitats (With and Crist 1996), it was possible to predict the different types of population distributions (clumped vs. random) that were expected to emerge in a given landscape (With and Crist 1995). Empirical distributions of the two grasshopper species thus matched the predictions of the percolation model based

on the relative rates of movement in a spatially complex and heterogeneous landscape.

In summary, the application of percolation theory to ecological applications requires further evaluation. The value of the neutral landscape approach is that it provides quantitative predictions as to when landscape connectivity is disrupted and thus when fragmentation effects are likely to occur. Few studies have attempted to examine how the underlying assumptions of percolation theory limit its application to the study of ecological flows in spatially complex landscapes and whether thresholds in landscape connectivity correspond to shifts in flow dynamics, such as dispersal or movement behavior. The lack of correspondence between thresholds in movement behavior and predicted thresholds in patch structure should not be viewed as a condemnation of neutral landscape models, or of percolation theory upon which they are based, however (e.g., Schumaker 1996). While experimentation at the landscape-scale is intractable or impossible, neutral landscape models have provided a useful null model for initial testing of the consequences of landscape connectivity for ecological processes (With and King 1997).

ACKNOWLEDGMENTS

This work was made possible by a Major Grant from the Faculty Research Committee at Bowling Green State University and a Conservation and Restoration Biology grant from the National Science Foundation (DEB-9532079) to K. A. With. We are grateful to Tony King for the use of the "cybercricket" model and to Bob Gardner for the use of RULE, the FORTRAN model used to generate and analyze the fractal landscape maps. We thank Philip Dixon, Eric Gustafson, and Alan Johnson for their thoughtful comments on this manuscript. This is publication no. 101 of the Ecology Research Station at Bowling Green State University.

LITERATURE CITED

- Anderson, R. V., C. R. Tracy, and Z. Abramsky. 1979. Habitat selection in two species of short-horned grasshoppers. *Oecologia* **38**:359–374.
- Andr n, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355–366.
- Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* **6**:535–544.
- Crist, T. O., and J. A. Wiens. 1995. Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). *Journal of Animal Ecology* **64**:733–746.
- Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. *Conservation Biology* **8**:1027–1036.
- Dicke, M., and P. A. Burrough. 1988. Using fractal dimensions for characterizing the tortuosity of animal trails. *Physiological Entomology* **13**:393–398.
- Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* **1**:19–28.
- Gardner, R. H., and R. V. O'Neill. 1991. Pattern, process, and predictability: the use of neutral landscape models for landscape analysis. Pages 289–307 in M. G. Turner and R. H. Gardner, editors. *Quantitative methods in landscape ecology*. Springer-Verlag, New York, New York, USA.
- Gardner, R. H., R. V. O'Neill, and M. G. Turner. 1993. Ecological implications of landscape fragmentation. Pages 208–226 in S. T. A. Pickett and M. G. McDonnell, editors. *Humans as components of ecosystems: subtle human effects and ecology of populated areas*. Springer-Verlag, New York, New York, USA.
- Hansson, L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society* **42**:89–103.
- Johnson, A. R., B. T. Milne, and J. A. Wiens. 1992a. Diffusion in fractal landscapes: simulations and experimental studies of Tenebrionid beetle movements. *Ecology* **73**:1968–1983.
- Johnson, A. R., B. T. Milne, J. A. Wiens, and T. O. Crist. 1992b. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* **7**:63–75.
- Keitt, T. H., and Johnson, A. R. 1995. Spatial heterogeneity and anomalous kinetics: emergent patterns in diffusion-limited predator-prey interaction. *Journal of Theoretical Biology* **172**:127–139.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**:253–260.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**:624–635.
- Mann, C. C., and M. L. Plummer. 1995. Are wildlife corridors the right path? *Science* **270**:1428–1430.
- Opdam, P. 1990. Dispersal in fragmented populations: the key to survival. Pages 3–17 in R. G. H. Bunce and D. C. Howard, editors. *Species dispersal in agricultural habitats*. Belhaven, New York, New York, USA.
- Pearson, S. M., M. G. Turner, R. H. Gardner, and R. V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. Pages 77–95 in R. C. Szaro and D. W. Johnston, editors. *Biodiversity in managed landscapes: theory and practice*. Oxford University Press, Oxford, UK.
- Plotnick, R. E., and R. H. Gardner. 1993. Lattices and landscapes. Pages 207–224 in R. H. Gardner, editor. *Lectures on mathematics in the life sciences: predicting spatial effects in ecological systems*. Volume 23. American Mathematical Society, Providence, Rhode Island, USA.
- Plotnick, R. E., R. H. Gardner, and R. V. O'Neill. 1993. Lacunarity indices as measures of landscape texture. *Landscape Ecology* **8**:201–211.
- Pulliam, H. R., and J. B. Dunning, Jr. 1994. Demographic processes: population dynamics on heterogeneous landscapes. Pages 179–205 in G. K. Meffe, C. R. Carroll, and contributors. *Principles of conservation biology*. Sinauer, Sunderland, Massachusetts, USA.
- Saupe, D. 1988. Algorithms for random fractals. Pages 71–136 in H.-O. Petigen and D. Saupe, editors. *The science of fractal images*. Springer, New York, New York, USA.
- Schumaker, N. 1996. Using landscape indices to predict habitat connectivity. *Ecology* **77**:1210–1225.
- Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* **68**:571–573.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**:1253–1266.
- . 1996. Fractal analysis of animal movement: a critique. *Ecology* **77**:2086–2090.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385–397.
- Wiens, J. A., T. O. Crist, K. A. With, and B. T. Milne. 1995.

- Fractal patterns of insect movement in microlandscape mosaics. *Ecology* **76**:663–666.
- Wiens, J. A., and B. T. Milne. 1989. Scaling of “landscapes” in landscape ecology, or landscape ecology from a beetle’s perspective. *Landscape Ecology* **3**:87–96.
- Wiens, J. A., R. L. Schooley, and R. D. Weeks, Jr. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* **78**:257–264.
- Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* **66**:369–380.
- With, K. A., 1994a. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* **9**:25–36.
- . 1994b. Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. *Functional Ecology* **8**:477–485.
- . 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* **11**:1069–1080.
- With, K. A., and T. O. Crist. 1995. Critical thresholds in species’ responses to landscape structure. *Ecology* **76**:2446–2459.
- With, K. A., and T. O. Crist. 1996. Translating across scales: simulating species distributions as the aggregate responses of individuals to heterogeneity. *Ecological Modelling* **93**:125–137.
- With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**:151–169.
- With, K. A., and A. W. King. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* **79**:219–229.
- With, K. A., and A. W. King. 1999a. Extinction thresholds for species in fractal landscapes. *Conservation Biology* **13**, *in press*.
- With, K. A., and A. W. King. 1999b. Dispersal success in fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* **14**, *in press*.