HOW DOES HABITAT PATCH SIZE AFFECT ANIMAL MOVEMENT?
AN EXPERIMENT WITH DARKLING BEETLES

NANCY E. McINTYRE1 AND JOHN A. WIENS

Department of Biology and Graduate Degree Program in Ecology, Colorado State University,
Fort Collins, Colorado 80523-1878 USA

Abstract. We used an experimental model system consisting of darkling beetles (Coleoptera: Tenebrionidae, Eleodes obsoleta Say) in a microlandscape to assess the effects of habitat patch size on the movement patterns of animals. The ratio of habitat area to nonhabitat in a 25-m² “microlandscape” was held constant while the grain of patchiness (patch size) was varied in four treatments. Beetle movement pathways were electronically surveyed, and seven pathway metrics were used to quantify movement characteristics. ANOVA and Fisher’s Protected Least Significant Difference post hoc comparisons revealed that both the presence and the grain of spatial heterogeneity influenced how animals moved through landscapes. Intermediate patch sizes elicited the strongest behavioral responses, whereas movements were similar between finely patchy landscapes with small habitat patches and coarsely patchy landscapes with larger habitat patches. These results indicate that organisms may use landscapes that possess different configurations of habitat in similar ways. Predicting how organisms respond to spatial heterogeneity therefore requires an assessment of how organisms use landscapes, in addition to an assessment of the structural characteristics of landscapes, such as grain size.

Key words: animal movement; darkling beetles; Eleodes obsoleta; landscape ecology; microlandscape; patch size; scale; spatial heterogeneity.

INTRODUCTION

Environments are heterogeneous in space and time. The patterning of this heterogeneity affects the abundance and distribution of organisms and the array of population, community, and ecosystem patterns that follow from distribution and abundance (Robinson et al. 1992). In a sense, these two statements embody a major focus of landscape ecology (Turner 1989, Ims 1995, Pickett and Cadenasso 1995, Wiens 1995).

A “landscape” may be both an ecological entity and a human construct (Pickett and Cadenasso 1995), viewed in one of (at least) three ways: (1) as a large stretch of land that could potentially contain several local populations of an organism (the traditional definition; Forman and Godron 1986, Forman 1995); (2) as a level in a hierarchy of ecological organization between ecosystem and biosphere (Lidicker 1988, Allen and Hoekstra 1992); and (3) as a template of any size upon which heterogeneity exists. Here, we adopt a “size doesn’t matter” stance (With 1994, Burke 1997) and follow the third view of landscape.

Within any landscape, the behaviors of organisms will be influenced by both the heterogeneity or spatial patterning of the mosaic and the scale on which landscape pattern is perceived (Kotliar and Wiens 1990, With 1994, Bissonnette et al. 1997). The finest resolution of scale that is perceived by an organism (“grain”) is contrasted with the broadest perceptual resolution of scale (“extent”) (Turner 1989). Because spatial patterns change with changes in scale, issues of scale are central to ecology and landscape ecology (Meentemeyer and Box 1987, Wiens 1989, Levin 1992, 1993, Dale et al. 1994, Bissonette 1997). Understanding how landscape pattern affects the abundance and distribution of organisms therefore requires an understanding of scale dependency. Given the complexity of organism-environment interactions, achieving such an understanding will require integrating information from both theoretical and empirical studies (Weiner 1995). Because we do not yet have anything resembling a “theory of scaling” (Meentemeyer and Box 1987), however, we must rely on empirical studies to provide baseline information about scaling effects in ecology (Wiens 1995, Bowers 1997, Steinberg and Kareiva 1997).

McCauley 1995, Cresswell 1997), the spread of diseases and parasites (Holmes 1993), or energy flow and nutrient transfer (Elmes 1991). Thus, understanding how structural features of the landscape influence animal movements may be a key component in comprehending population, community, and ecosystem composition and functioning (Forman 1995, Wiens 1995, 1996). For these reasons, developing an empirical understanding of how animal movement patterns are affected by landscape pattern has been promoted as a research priority for landscape ecology (Wiens 1989, 1990, Kareiva 1990, Ims 1995).

Empirical studies of the relationship between movement and the scale of landscape pattern, however, are scarce. Here, we report the results of an experimental study that was explicitly designed to assess the effects of the grain of landscape pattern on animal movements. We used an experimental model system (EMS; Wiens and Milne 1989, Ims et al. 1993, Wiens et al. 1993b) consisting of darkling beetles (Coleoptera: Tenebrionidae, Eleodes obsoleta Say) moving in microlandsapes in which the proportion of different landscape elements was held constant, but the grain of the pattern was varied. Using an EMS design permits manipulation that would be logistically unfeasible at larger scales. Other studies, particularly in agroecosystems, have documented the relationships between insect movement and patch use or landscape structure (e.g., Kareiva 1985, 1987, Wallin and Ekbom 1988, Watten and Thomas 1990, Bell 1991, Vermuelen 1994, Riecken and Raths 1996). In this study, however, we have manipulated the grain of habitat patchiness (patch size) while keeping the overall amount of habitat constant, and have examined how these factors influence individual behaviors.

As the scale of patchiness becomes broader (i.e., as patches become larger), the ratio of patch perimeter to patch area decreases, resulting in fewer patch boundary zones. Because beetle movements differ in landscapes containing different habitat types (e.g., grass and sand; Wiens et al. 1985, Wiens and Milne 1989, Crist et al. 1992, Wiens et al. 1997), they are likely to be affected by patch boundaries. From this, we predict that movements should be more constrained and localized in fine-grained landscapes. This is because the frequent boundaries between patches will interrupt the flow of movements in a particular habitat type and cause repeated transitions among movement patterns. In a fine-grained mosaic, an individual’s movement behavior must be continually readjusted. Percolation models also predict a nonlinear relationship between habitat patch size and movement patterns (Wiens et al. 1997, With et al. 1997, Wirth and King 1997). Because our experimental design incorporated patches of preferred beetle habitat (grass) embedded in a matrix of less suitable habitat (sand), the results also bear on the issue of how the scale of habitat fragmentation might affect animal movements, compared to the null hypothesis that movements in heterogeneous mosaics are identical to those in homogeneous landscapes (Merriam 1995).

**METHODS**

**Study site**

We conducted our research from May through September 1996 at the Central Plains Experimental Range (CPER) in Weld County, Colorado, USA. Located ~120 km northeast of Denver, the CPER is the National Science Foundation Shortgrass Steppe Long-Term Ecological Research site. The site is characterized by low-stature vegetation, consisting of a heterogeneous mosaic of shortgrasses (primarily Bouteloua gracilis [H.B.K.] Lag. and Buchloe dactyloides [Nutt.] Engelm.), bare-ground areas, cactus (Opuntia polyacantha Haw.), and low shrubs (primarily Artemisia frigida Willd., Atriplex canescens [Pursh.] Nutt., Chrysothamnus nauseosus [Pall.] Britt., and Gutierrezia sarothrae [Pursh.] Britt. and Rusby) (Lauenroth and Milchunas 1991, Crist et al. 1992).

**Experimental model system**

Experiments provide a way to identify the mechanisms underlying the patterns that we observe in nature, and conducting experimental manipulations allows subtle features of these mechanisms to be discerned (Diamond 1986). Experimental model systems (EMS’s) are used when such manipulations need to be conducted at more tractable scales than are possible in natural settings, because an EMS’s smaller size allows for a greater degree of control over potentially confounding variables (Ims et al. 1993). As a “model system,” an EMS serves as a small-scale example of a more general situation. An EMS in a field setting, in effect, serves as a compromise between the natural features of a field study and the more controlled atmosphere of a laboratory study. We used a field EMS to manipulate landscape characteristics that would be impractical (if not impossible) to vary by other means (Wiens et al. 1997).

We used darkling beetles as model organisms in our experiments. Eleodes obsoleta is a generalist detritivore, feeding primarily on grasses and forbs (Yount 1971, Rogers et al. 1988); it is abundant at the CPER (Whicker and Tracy 1987). Their small size (average live mass 173 mg, Crist et al. 1992), diurnal habits, and flightlessness have made darkling beetles ideal subjects for empirical analyses of movement (e.g., Wiens and Milne 1989, Crist et al. 1992, Johnson et al. 1992, Wiens et al. 1993a). For our study, we used beetles captured in shortgrass habitat within a few kilometers of the experimental arena. Beetles were kept in a 2-m² field enclosure under natural conditions prior to use in experiments. All beetles were released in the vicinity of capture upon completion of the experiments.

An experimental landscape was created in a 25-m² area of bare sand surrounded by a 12 cm high wooden fence, following the design of Wiens et al. (1997). We
Wiens et al. (1997) showed that movement patterns of habitat patches in a sand (nonhabitat) matrix. Buffalo-grass (Buchloë dactyloides) sod to make 0.5 m grass patches, (c) 0.25 X 0.25 m grass patches, and (d) 0.125 X 0.125 m grass patches.

Fig. 1. Experimental model system. The overall ratio of grass (dark patches) to sand (light areas) was held constant at 20:80, except for a control of 100% sand (not shown). Treatment levels are: (a) 1 X 1 m grass patches, (b) 0.5 X 0.5 m grass patches, (c) 0.25 X 0.25 m grass patches, and (d) 0.125 X 0.125 m grass patches.

used buffalograss (Buchloë dactyloides) sod to make habitat patches in a sand (nonhabitat) matrix. Buffalo-grass is a natural component of the darkling beetles’ grassland environment (Lauenroth and Milchunas 1991) and provides food and shelter that bare sand areas do not.

We maintained a constant coverage of grass patches (20%) and bare sand areas (80%) in all experimental treatments. These proportions were chosen because Wiens et al. (1997) showed that movement patterns of darkling beetles did not change significantly as grass coverage increased from 20% to 80%, but differed strongly when no grass was present (100% sand). Four treatments, representing four habitat patch sizes, were created (Fig. 1). To create the grass and sand configurations within each of these treatments, each landscape was divided into squares (0.125 X 0.125 m, 0.25 X 0.25 m, 0.5 X 0.5 m, 1 X 1 m; hereafter, the “treatments”). A random-number generator was then used to determine whether a square was to be planted with grass or left as sand. A homogeneous sand landscape (0% grass coverage) was used as a reference (hereafter, “control”) to assess how beetles moved independently of landscape pattern.

In some cases, the random placement of grass patches resulted in patch clustering, which may have an effect on movement patterns in addition to the effect of patch size per se. We calculated the mean patch size for each of our treatments by considering any grass squares that touched each other to be a single patch.

Because beetles can move in any direction, including a diagonal, but cannot “leapfrog” or fly over squares (Wiens et al. 1997), they are presumably most affected by a square’s eight adjacent neighbor squares. Animals with different movement capabilities would be affected by the same landscape structure in different ways, i.e., the same spatial structure might prove less of a hindrance to more mobile animals (With 1994, Pearson et al. 1996). Although all of our treatments possess sand corridors that can potentially allow unimpeded movement across the entire arena, we tried to determine if the presence of wide sand corridors affected movement by comparing the average number of beetles that reached the boundary fence among the treatments, using ANOVA.

To determine to what degree our experimental grass-patch sizes mimicked the natural distribution of grass-patch sizes at the CPER, we measured the size and spacing of grass clusters along four 25-m line transects in July 1996. These transects were randomly situated ~1 km from our experimental arena and were separated from one another by ~1 km. Both of the dominant shortgrass species (Bouteloua gracilis and Buchloë dactyloides) present at the CPER are sod-forming grasses that grow into distinct clumps, although ramets may send out tillers into adjacent clumps, forming large clusters of several genetically distinct individuals. Clusters separated by ≥2.5 cm of bare soil were considered distinct patches. The size of these grass patches was averaged across the four transects. A 99% ci around this measure provided a way for us to compare the grass-patch sizes we used in our treatments to a more natural situation faced by darkling beetles.

Because our treatments aimed to represent levels of patch size while keeping percent cover constant, the number of grass patches varied among treatments. It is difficult to keep edge constant when patch number varies; to assess the effects of differing edge amounts among our treatments, we calculated the total grass-patch perimeter length for each treatment and used this perimeter length as a covariate in our analyses. We tried to ameliorate edge effects by sinking the sod patches into the sand, softening boundaries and facilitating sand–grass transitions.

In our design, the four grass–sand landscape configurations represented treatments, whereas our homogeneous sand landscape represented a control. Within each of these, individual movement pathways (see Movement analyses section) were replicates. We used only one landscape permutation per treatment because our primary focus in this research was on how animals respond to different scales of spatial heterogeneity (other things being equal), not with how variability in pattern at a particular scale may affect animal movements (which is what multiple replicates of a particular treatment would represent). Having such replicated permutations would have lowered the within-treatment variance, decreasing the likelihood of making a Type
I (α) statistical error. Even with a single-treatment pattern design such as ours, there are ways of countering the likelihood of making a Type I error; we did so by lowering the α level of significance to 0.01 for all analyses (including confidence intervals), obtained by dividing the traditional (and arbitrary) value of 0.05 by the five landscape permutations that we used (Sokal and Rohlf 1981).

Movement analyses

Because we wanted to use movement data for the 0.25 × 0.25 m treatment that had been obtained in 1994 by Wiens et al. (1997), we were careful to match the experimental protocol used by Wiens et al. (1997). We used the same sandbox arena, the same species of beetle and grass sod (both of which we obtained from the same sources as did Wiens and his colleagues), and the same surveying equipment. We followed the same sod-laying procedure, used the same beetle-handling protocol, and performed our movement and statistical analyses in an identical fashion. We obtained advice and field assistance from the coauthors of Wiens et al. (1997) to ensure that we were faithfully recreating their experimental design. As a final precaution against between-year effects, we performed a multivariate analysis of variance (MANOVA) on the 1994 data from Wiens et al. (1997) and the data we collected in 1996.

Movement analyses followed the protocol of Wiens et al. (1993a) and Wiens et al. (1997). Movement trials were conducted when unshaded soil surface temperatures were 18°–29°C (mean 22°C), which corresponds to temperatures when darkling beetles are active at the CPER (Whicker and Tracy 1987). Soil temperature was used as a covariate in all movement analyses to ensure that there were no significant temperature effects. Movement data for the 0.25 × 0.25 m treatment had a sample size of N = 10 movement paths. We conducted 20 trials for each of the three other treatments and the control (N = 80 paths). Beetles were released in the center of the arena and their locations were marked at 5-s intervals with sequentially numbered flags. Beetles were followed for 100 such time steps (N = 6 paths) or until they reached the boundary fence (N = 84 paths), which usually occurred between 25 and 50 time steps (mean 39 time steps). A 5-s time interval was chosen as the smallest interval in which locational data could be collected without disturbing the beetle with the placement of the flags. A 5-s time interval has also been used successfully in beetle—microlandscape studies by Crist et al. (1992) and Wiens et al. (1997), who verified that a 5-s interval provides an accurate representation of pathway characteristics. This 5-s interval allowed enough time to pass between placement of successive flags for a beetle to have moved away, although we also took the additional precaution of waiting a few time steps if a beetle was stationary. At no time was a beetle “herded” by an observer.

We took considerable pains to ensure that our beetles behaved as naturally as possible during the experimental trials. Being nomadic (Calkins and Kirk 1973, Doyen and Tschinkel 1974, Crist et al. 1992), darkling beetles routinely encounter unfamiliar territory during movement. Accordingly, we did not familiarize our beetles with the experimental arena, and each individual was tested only once. The experimental arena was swept clean after every trial to remove footprints or potential odor cues. Beetles were handled as little as possible. Our beetles apparently behaved normally and did not exhibit the stereotypical tenebrionid raised-abdomen defense posture (Alsopp 1980, Borrer et al. 1989), indicating that we were not disturbing them. Some beetles actually paused to eat in grass patches, providing further anecdotal evidence that their behaviors in the sandbox arena were normal.

The angles and distances between successive 5-s locations in the beetle movement pathways were surveyed electronically with a Pentax PTS-IIIa (Tokyo, Japan) surveying station. Angle and distance data were downloaded into a Corvallis Microtechnology CMT MC-II field microcomputer (Corvallis, Oregon, USA) and were translated into Cartesian coordinates with computer software designed by the Maptech Corporation (Loveland, Colorado, USA). Surveyed movement pathways were described by seven path metrics: (1) the habitat type (grass or sand) where a beetle was located for each 5-s time step, (2) the total number of time steps taken, (3) the number of stops (pauses in successive time intervals without spatial displacement), (4) net linear displacement to quantify the distance covered by a beetle, (5) displacement rate to quantify a beetle’s velocity, (6) average movement distance (step length) per 5-s interval, and (7) fractal dimension to quantify path tortuosity (using the dividers protocol; Dicke and Burrough 1988). Fractal geometry was developed for the express purpose of measuring non-Euclidian objects (Mandelbrot 1983). Being neither perfectly straight lines nor completely random walks, movement pathways are non-Euclidian, and fractal geometry therefore provides a useful measure of path tortuosity (Wiens and Milne 1989, Milne 1991, Wiens et al. 1995). The fractal dimension of a movement pathway ranges from 1 to 2, with a value of 1 indicating a straight-line path and a value of 2 indicating a completely random path (Mandelbrot 1983). The fractal dimension was assumed to be independent of scale over the extent of our experimental design (Turchin 1996). In addition to comparing path tortuosity among our treatments, we also compared the fractal dimension of the movement pathways to the fractal dimension of the landscape treatment patterns, using the square perimeter—area formula of Gardner et al. (1987) as applied by Milne (1991), where \( D = \log(\text{area covered by grass patches})/\log(\text{perimeter of grass patches}) \times \text{four sides to a square patch} \). This value ranges between 1 (perfect square) and 2 (highly irregular shape) (Milne 1991). We also performed a regression of path-
way fractal dimension on average nearest neighbor grass-patch distance to determine if patch clustering affected beetle movements (either by attraction, which would be indicated by a positive association, or repulsion, indicated by a negative relationship). Nearest neighbor distances were calculated by measuring the straight-line distances between each grass patch and its five nearest grass-patch neighbors (two nearest neighbors for the 1 × 1 m treatment, as there were only three patches total). These distances were averaged across all grass patches within a treatment to give a single value for each treatment. A best fit regression line was used.

Because animal movement pathways are, by definition, collections of spatially autocorrelated points, we based our statistical analyses of pathway values on the replicate pathways within a treatment rather than on characteristics of individual pathways. A multivariate analysis of covariance (MANCOVA) was used to detect significant differences in movement path metrics with changes in habitat patch size over all treatments, with grass-patch size as a fixed main effect and soil surface temperature and grass-patch perimeter length as covariates. If significant overall effects were found, the model was reduced to a separate analysis of covariance (ANCOVA) for each of the seven pathway variables, with grass-patch size as a fixed main effect. If soil surface temperature and perimeter length were not significant covariates, models were further simplified as simple ANOVAs. Variables with significant ANCOVA or ANOVA models were then subjected to Fisher’s protected least significant difference (LSD) comparisons among treatment means (Sokal and Rohlf 1981) to detect significant differences in path metrics among treatments.

**RESULTS**

The actual patch sizes of our four treatments were slightly larger than the stated treatment sizes (0.125 × 0.125, 0.25 × 0.25, 0.50 × 0.50, and 1 × 1 m) because of patch clustering (Table 1). The grass-patch sizes that we used in our experimental treatments fell within the range of variation (which was considerable) of natural grass-patch sizes found at our study site (mean 0.022 m, with a 99% CI of 12.0 cm).

**TABLE 1.** Grass-patch sizes (mean ± 1 sd) actually used in our treatments are larger than the treatment patch sizes, due to patch clustering from random placement of grass patches. See Methods: Experimental model system for methodology used to calculate patch sizes.

<table>
<thead>
<tr>
<th>Treatment patch size</th>
<th>Actual patch size (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.125 × 0.125 m = 0.016 m²</td>
<td>0.189 ± 0.133</td>
</tr>
<tr>
<td>0.25 × 0.25 m = 0.062 m²</td>
<td>0.63 ± 0.60</td>
</tr>
<tr>
<td>0.50 × 0.50 m = 0.25 m²</td>
<td>1.25 ± 1.16</td>
</tr>
<tr>
<td>1 × 1 m = 1 m²</td>
<td>1.67 ± 1.15</td>
</tr>
</tbody>
</table>

MANCOVA revealed that the movement path data that we collected in 1996 were not significantly different from the 0.25 × 0.25 m treatment data collected in 1994 by Wiens et al. (1997) ($F_{6,33} = 1.3076, P = 0.3205$). Accordingly, we combined the data sets for further analyses and considered significant differences between the 0.25 × 0.25 m treatment and the other treatments as actual treatment effects rather than temporal artifacts.

There were significant effects of grass-patch size on the movement behaviors that we quantified (MANCOVA: $F = 5.3626; df = 53, 445; P = 0.0001$). Separate ANCOVA models revealed significant effects for all seven pathway metrics (model $P < 0.01$ for all cases). Soil surface temperature and grass-patch perimeter length were not significant covariates for any model ($P > 0.20$ for all cases).

Movement patterns in the control area, which lacked vegetation, differed significantly from those in all other treatments (Figs. 2 and 3). This indicates a heterogeneity effect. For example, significantly more beetles reached the EMS boundary fence in the homogeneous sand control than in the heterogeneous grass–sand treatments (ANOVA, control vs. treatments: $F = 7.60; df = 4, 6; P = 0.0001$), but there were no significant differences among the four treatments in the average number of beetle pathways that reached a boundary fence (ANOVA, comparison among treatments: $F = 0.40; df = 3, 6; P = 0.7534$).

Habitat patch size significantly affected the mechanics of beetle movement. Beetles in landscapes with larger habitat patches generally moved in a more linear fashion and paused more often than did those in more finely patchy landscapes with 0.125 × 0.125 m habitat patches. Heterogeneous landscapes elicited shorter pathways than did the homogeneous control (Fig. 2a). Beetles also moved more slowly in patchy landscapes than in the homogeneous control (Fig. 2b, c). Beetles spent more time in movement (taking more timesteps) in heterogeneous landscapes (Fig. 2d). This response is also reflected in the amount of time that they spent in habitat patches. Intermediate patch sizes elicited longer patch residency times (Fig. 2e), probably because beetles paused more often in such microlandscapes (Fig. 2f). Heterogeneous landscapes also induced beetles to move in a less linear fashion (Fig. 3).

Beetles clearly responded to changes in patch size in the microlandscapes (Figs. 2 and 3). Many of the strongest responses were associated with intermediate patch sizes (0.25 × 0.25 m and 0.5 × 0.5 m grass patches). Movement responses for most variables were similar in smaller (0.125 × 0.125 m) and larger (1 × 1 m) grass patches (Fig. 2), although the smallest grass patches evoked the most convoluted pathways (Fig. 3).

**DISCUSSION**

Both the existence of heterogeneity and the scale (grain) of heterogeneity had important effects on animal movement patterns. There were significant differences between the homogeneous sand control and the
four heterogeneous grass–sand treatments, in terms of the number of beetles that traversed the extent of the EMS. There were also significant differences between the control and treatments and among the four treatments for various movement characteristics (Fig. 2), demonstrating that the presence of spatial heterogeneity affects animal behaviors. Furthermore, the significant differences among the treatments in Fig. 2 (manifested as peaked distributions in Fig. 2d, e, and f) demonstrate that animals respond differently to different grains of heterogeneity. The similarity of responses to 0.125-m and 1-m treatments illustrates that landscapes may be structurally dissimilar and yet functionally equivalent, at least for movement at these scales. Beetles concentrated their time in movement on sand, taking fewer time steps on grass, which resulted in more linear pathways in landscapes with no grass patches or a few large patches than when there were numerous small patches.

These peaked distributions may be interpreted relative to how beetles may perceive patches of different sizes as having different ecological functions. Small grass patches may have been perceived simply as obstacles because they contain insufficient resources, whereas larger patches may have been viewed as colonizable habitat. This would explain the increase in response to patch size observed for most variables between the 0.125-m and 0.25-m treatments. When a habitat patch’s area is quite large, however, a beetle may use habitat in a lesser proportion than predicted by the
beetles seem to respond most strongly to patches when grains and extents to which beetles respond. That is, movement responses to habitat patch size, correspondingly (Gardner et al. 1992, Wiens 1992), this aspect is important effects upon animal dispersal and patch colonization. Three patch sizes were statistically indistinguishable (0.125 X 0.125, 0.50 X 0.50, and 1 X 1 m), but were separated by an intermediate size (0.25 X 0.25 m), suggesting that there may have been a trade-off between attraction to grass as habitat and avoidance of grass because it is more difficult to move through than is sand. The greater viscosity of grass compared to sand (Crist et al. 1992, Wiens et al. 1997) probably accounted for the more convoluted and localized beetle movements in the more finely patterned landscapes, where the numerous grass patches interrupted the flow of movement. This response to grass may also explain why fewer beetles reached the boundary of the EMS compared to the control. Because patch boundary presence and type are thought to have important effects upon animal dispersal and patch colonization (Gardner et al. 1992, Wiens 1992), this aspect of landscape patchiness merits further research.

FIG. 3. Mean (+1 se) fractal dimension of movement pathways by treatment. The abscissa indicates treatment levels as in Fig. 1. Means denoted with the same letter do not differ significantly (Fisher’s protected LSD test, P > 0.05).

habitats’ size. This would explain why landscapes with large and small patches have pathway fractal dimensions statistically indistinguishable from one another (Fig. 3), and yet these landscapes with large patches evoke different responses than do landscapes with patches of intermediate size (Fig. 2). Thus, different mechanisms or constraints may be acting at different spatial scales to create such peaked responses.

Both the landscapes with the smallest grass patches and the landscapes with the largest patches evoked the most convoluted movement paths (Fig. 3), once again suggesting that patches of different sizes may have assumed different roles to beetles. However, the nonlinear response that we observed in movement pathways was more complex than a simple reaction to patch aggregation. Three patch sizes were statistically indistinguishable (0.125 X 0.125, 0.50 X 0.50, and 1 X 1 m), but were separated by an intermediate size (0.25 X 0.25 m), suggesting that there may have been a trade-off between attraction to grass as habitat and avoidance of grass because it is more difficult to move through than is sand. The greater viscosity of grass compared to sand (Crist et al. 1992, Wiens et al. 1997) probably accounted for the more convoluted and localized beetle movements in the more finely patterned landscapes, where the numerous grass patches interrupted the flow of movement. This response to grass may also explain why fewer beetles reached the boundary of the EMS compared to the control. Because patch boundary presence and type are thought to have important effects upon animal dispersal and patch colonization (Gardner et al. 1992, Wiens 1992), this aspect of landscape patchiness merits further research.

Thus, there may be a characteristic scale of beetle movement responses to habitat patch size, corresponding to an intermediate grain size (0.25 X 0.25 m). The existence of such a scale indicates the boundaries of “domains of scale” (Wiens 1989) that characterize the grains and extents to which beetles respond. That is, beetles seem to respond most strongly to patches when they are 0.25 X 0.25 m in area. Smaller and larger patches are treated differently, because smaller patches appear to fall below a threshold of grain below which they cannot be distinguished from the landscape matrix (i.e., they are too small to be noticed), whereas larger patches may exceed a threshold of extent above which they, too, cannot be distinguished from the matrix (i.e., they are so large that they appear to be the matrix) (Wiens et al. 1997). Detection of characteristic scales of response is a critical step in understanding how landscape patterns influence ecological processes (Wiens 1995, Wu and Loucks 1995).

These individual movement responses to spatial structure may have consequences for the distribution of darkling beetle populations. Based upon our results, for example, E. obsoleta darkling beetles should occur most often in heterogeneous landscapes (particularly those that possess discrete patches of vegetation ~0.25 X 0.25 m in size). Such spatial structure would better deter linear movements that would direct a beetle out of the area, thereby eliciting longer local residency times (Crist and Wiens 1995), than would homogeneous grasslands or areas with larger or smaller habitat patches. Although prior studies of darkling beetle–habitat relationships in the region where our study was conducted did not measure patch size explicitly, E. obsoleta and other darkling beetle species are more common in heterogeneous areas than in relatively homogeneous regions of the shortgrass steppe (Whicker 1983, Crist et al. 1992, Stapp 1997). Thus, not only the total amount of habitat, but also the sizes of habitat patches, may affect habitat suitability (Johnson 1980).

Although we cannot be completely certain that unmeasured aspects of landscape structure had an effect on beetle movements, darkling beetles exhibited patterns of landscape use that did not correspond exactly to landscape habitat patterns, and landscape use also varied with habitat patch size. Therefore, predicting how organisms respond to spatial heterogeneity requires an assessment of the functional role of landscape pattern in addition to its structural characteristics. Such nonlinear effects of landscape pattern emphasize the need for a multiscaled, landscape ecology approach to understand organism–environment interactions (Fahrig and Merriam 1994, Wiens 1996).

Our study represents one of the few field experiments to examine how manipulating landscape pattern alters movement parameters. Our experimental design is representative of situations potentially faced by all mobile animals in patchy environments, but animals with different movement strategies (e.g., learning, territoriality) might have responded differently to our experimental design, and the nonlinear scale responses that we observed have implications about how effectively our results can be extrapolated to the abundance, distribution, and behavior of animals at other scales. Generally speaking, the problem of realism in extrapolation occurs in all ecological studies (particularly experi-
ments) and is not unique to experimental model systems such as ours (With 1997b). The true value of ecological experiments often lies primarily in their heuristic uses. Although our design may not be directly applicable to other scales, animals, or systems, our research can serve as a model for understanding pattern–process relationships. Our study, for example, asks the rhetorical question, “If all landscapes were nonrandom, would one still expect the same results?” This question is sometimes left unaddressed in ecological studies and highlights the need for a landscape ecology approach in ecology in general. Given the infeasibility of conducting studies on all possible organisms at all possible scales, studies such as ours provide ways of thinking about patterns and processes at a variety of scales (Ims et al. 1993, Burke 1997, With 1997a), despite potential difficulties in translating patterns and processes across scales (Levin 1992, McIntyre 1997). Most studies of landscape effects have been conducted at a fixed scale. Our results show, however, that a more realistic way of considering landscapes must allow for the detection of scale-dependent effects. Experimentation may provide one useful (and underutilized) way to determine the presence and nature of scale-dependent effects. An experimental approach is often infeasible in landscape ecology, however, where manipulation and replication may be difficult, if not impossible, to achieve because of the trade-offs between control and realism, particularly at large spatial scales (Diamond 1986), and an experimental model system may not be suitable for all questions or systems. In these cases, natural history observations mapped onto landscape patterns, coupled with spatially explicit simulation modeling, may provide the best means of understanding how environmental features affect organisms (Kareiva 1990, Levin 1994). A pluralistic approach in landscape ecology (and in ecology, in general) is therefore likely to produce the greatest understanding of how spatial pattern affects ecological processes.

ACKNOWLEDGMENTS

We thank Jeff Cordulack, Alisha Holloway, Dan Hopkins, and Ron Weeks for field assistance. Ron Weeks also collected the vegetation data. Comments from Bill Baker, Jim Miller, Bob Schooley, and three anonymous reviewers improved manuscript drafts. Funding was provided by the National Science Foundation Shortgrass Steppe Long-Term Ecological Research Project (BSR-911659, Principal Investigators L.C. Burke and W. K. Lauenroth, Colorado State University). The Central Plains Experimental Range is administered by the High Plains Grasslands Research Unit of the United States Department of Agriculture’s Agricultural Research Service.

LITERATURE CITED


269 in O. L. Lange, H. A. Mooney, and H. Remmert, editors. Landscape boundaries. Springer-Verlag, New York, New York, USA.


— 1995. Landscape mosaics and ecological theory.


