Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns

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Abstract

To examine how resource distributions affect the movement behaviors of fed and food-deprived *Eleodes extricata* Say darkling beetles (Coleoptera: Tenebrionidae), we experimentally manipulated the dispersion of food to create clumped, random, and uniform distributions in an otherwise homogeneous 25-m^2 experimental field landscape. Quantitative measures of the tortuosity, net linear displacement, overall path length, and velocity of beetle movement pathways showed that food-deprived beetles generally moved more slowly and over shorter distances than did fed beetles. This effect was mediated by the spatial distribution of food, however; food distributed randomly over the landscape evoked more tortuous paths over larger overall distances. The foraging movements of food-deprived beetles were most different from those of fed individuals in treatments with randomly distributed food resources. These results show that the influence of spatial structure on individuals depends not only on the arrangement of pattern but also on the function that the structure plays. Thus, 'spatial structure' is defined not only by physical characteristics of the landscape but also by how that structure is used by animals.

Introduction

Theory (De Roos et al. 1991; Wiens et al. 1993b), models (Turchin 1991; Gustafson and Gardner 1996), and empirical observations (Levin et al. 1971; Kareiva 1985; Crist et al. 1992; Cartar and Real 1997) indicate that the movements of organisms are influenced by the structure of the landscapes they occupy and that variations in movement patterns can have profound effects on the structure and dynamics of populations, communities, and ecosystems. Understanding how and why individuals move through a heterogeneous landscape is therefore an essential component in developing a mechanistic foundation for landscape ecology (Merriam 1988; Ims 1995; Wiens 1995).

Determination of the mechanisms accounting for movement patterns, however, has proven elusive (Wiens et al. 1995; Cartar and Real 1997). A lack of detailed information about landscape factors that influence movements may arise from inherent difficulties in manipulating landscapes. Experimental model systems (EMS) have proven to be useful tools for elucidating movement-landscape relationships by permitting testing of hypotheses about the ecological consequences of landscape structure at tractable scales with empirical rigor (Ims et al. 1993; Wiens et al. 1993b, 1997). By studying fine-scale systems, such as the responses of voles (Ims et al. 1993) or beetles (Wiens and Milne 1989; Wiens et al. 1997) to spatial heterogeneity in structurally simple environments, the details of movement patterns can be quantified and related to 'microlandscapes' in which the mosaic pattern is experimentally manipulated. In addition to providing information about the spatial ecology of voles or

beetles, such studies can provide insights that may help direct our thinking about ecological dynamics in broader-scale landscapes, where experimentation is far more difficult. For example, research on *Microtus oeconomus* in experimentally fragmented landscapes has indicated how the spatial pattern of a landscape may influence home-range size (Ims et al. 1993) and how variations in corridor width and connectivity can influence dispersal rates (Andreassen et al. 1996a, b). Similar experimental work on *Eleodes* beetles has shown that microlandscape heterogeneity, connectivity, and the scale of patchiness influence beetle movements (Wiens and Milne 1989; Johnson et al. 1992; Crist et al. 1992; Wiens et al. 1997). Investigations of beetles (*Eleodes*) and grasshoppers (*Psoloessa* and *Xanthippus*) have shown that nonlinear effects of landscape patterns on individual movements may produce distributional patchiness of populations of organisms that may not relate closely to a spatial mapping of habitat patches in the landscape (Wiens et al. 1997; With 1994; With and Crist 1995).

These studies have focused on how the fine-scale movement patterns of individuals reflect the spatial properties of mosaics. Landscape mosaics possess several features that may affect the behavior of organisms; one obvious factor is food. The distribution of food resources should be expected to influence movements (Arditi and Dacorogna 1988; Bernstein et al. 1988; Cartar and Real 1997), and we might therefore expect a hungry animal to respond differently to food distributions than would a satiated one (Bell 1991). Optimal foraging theory, for example, has provided some insights into how animal behaviors may differ depending on hunger, the availability and distribution of food, and food quality (Pyke 1984). Optimal foraging theory also assumes that animals are acting optimally (i.e., maximizing food gains while minimizing costs). This assumption (as well as the broader assertion of optimal foraging theory as a useful paradigm in animal behavior) has been criticized (Maynard Smith 1978; Ollason 1980; Jander 1982). Rather than asking whether animals respond to landscape structure in a manner that facilitates resource-gathering while also minimizing the costs of foraging, then, it may be more appropriate to ask the question of how landscape structure interacts with the state of an organism to determine movement pathways, free of the constraints imposed by optimization.

Here, we report the results of experiments designed to test the effects of resource (food) distribution and animal motivational state (food-deprived versus fed

individuals) on movement patterns of *Eleodes* beetles when other characteristics of the underlying landscape are held constant. Patch-foraging theory (Hassell and Southwood 1978; Kareiva 1985; Fromm and Bell 1987; Bell 1990, 1991; Cartar and Real 1997; Cresswell 1997) and studies on area-restricted searching (Tinbergen et al. 1967) have shown that although many animals may initiate foraging in a random direction, foraging success tends to canalize movement trajectories. When food resources are distributed in a uniform pattern, this behavior is highly successful and results in strongly directional movements. In an area with aggregated food resources, however, animals may travel great distances between clumps but small distances within each clump. Variability in the rewards per unit of travel time means that when a clump is encountered, it would be in an animal's best interests to deplete it, given the uncertainty as to when another clump will be discovered. These behaviors would lead to variable overall movement patterns. Randomly distributed resources would elicit movement behaviors intermediate between these two extremes. Therefore, we predict that:

(1) movements by foraging beetles in areas with aggregated food resources will be longer, slower, and less linear than in areas where food resources are randomly or uniformly dispersed; and

(2) these effects will be more pronounced in food-deprived than in fed individuals, whose motivation to find food will be less intense.

In testing these predictions, we assume that the primary motivation to move in starved beetles is to find food. *Eleodes* beetles are naturally very active and mobile, although the proximal causes of the near-constant movement in this genus are unknown (Calkins and Kirk 1973; Doyen and Tschinkel 1974; Crist et al. 1992). Therefore, we also assume that fed individuals will move as well (but for unknown reasons). Because beetles probably have a limited search radius, owing to their small size, we may predict that food-deprived individuals would follow a more convoluted pathway and cover shorter distances per time interval than would satiated individuals because of more intense searching behavior. We do not know the search radius of the beetles we used in our studies, although wind-tunnel experiments (McIntyre and Vaughn 1997) suggest that beetles may orient to food by means of olfaction over distances of at least 80 cm.

Methods

Experimental model system

To examine the relationships between resource distribution, satiation level, and movement patterns, we used an EMS consisting of darkling beetles (Coleoptera: Tenebrionidae, *Eleodes extricata* Say) moving through 25-m² experimental microlandscapes in which food was provided in different spatial configurations. Darking beetles are good experimental subjects for studies such as these because they are common in semi-arid ecosystems of North America (Crawford 1981; Whicker and Tracy 1987), small (average length = 12.0 ± 0.6 mm, N = 25; average live mass = 96.8 ± 17.5 mg, N = 15; Crist et al. 1992), flightless yet very active and highly vagile (Calkins and Kirk 1973; Doyen and Tschinkel 1974; Crist et al. 1992), and diurnal on the shortgrass steppe (Whicker and Tracy 1987). They are generalist detritivores, feeding primarily on plant matter, especially grasses and forbs (Yount 1971; Rogers et al. 1988). Darkling beetles have been used in numerous ecological studies of movement (e.g. Wiens and Milne 1989; Crist et al. 1992; Johnson et al. 1992; Wiens et al. 1993a, 1997).

We conducted research from May through August 1995 and 1996 in a shortgrass steppe ecosystem at the Central Plains Experimental Range (CPER) in northeastern Colorado, U.S.A. All vegetation in an enclosed 5 × 5-m area was removed, a 12-cm high wooden fence was placed around the perimeter, and the area was filled to a level depth of 4 cm with sand, following the design in Wiens et al. (1997). A 25-m² study extent was used to allow direct comparison with previous darkling beetle movement research (Wiens et al. 1997). This sandbox arena mimicked an extensive bare-ground area similar to areas of soil that beetles would encounter when foraging in their natural grassland environment.

Although some studies of darkling beetle movements have been performed in natural field settings (Calkins and Kirk 1973; Crist et al. 1992; Wiens et al. 1993a; Crist and Wiens 1995), many others have used EMS designs like ours in order to discern the mechanisms responsible for variations in movement patterns with spatial pattern (Wiens and Milne 1989; Johnson et al. 1992; Wiens et al. 1997). In these studies, 5 × 5 m arenas were constructed in which various habitat factors could be examined, such as the presence of spatial heterogeneity in the form of grass patches

(Johnson et al. 1992, who also compared movement responses at this scale to those in arenas that were 20 × 20 m in size), the fractal structure of such heterogeneity (Wiens and Milne 1989), and the ratio of grass habitat patches to sand (Wiens et al. 1997). Our EMS design was modeled after the 5 × 5 m arenas used in these studies. Like Wiens et al. (1997), we manipulated spatial features of the arena, creating different resource distributions.

Resource distributions

In the shortgrass steppe, darkling beetles forage in a heterogeneous mosaic consisting primarily of grass and bare ground areas (created by erosion, harvester ants [*Pogonomyrmex occidentalis*], rodents such as prairie dogs [*Cynomys ludovicianus*], and wallowing cattle [*Bos taurus*] or bison [*Bison bison*]) (Crist et al. 1992). Because they are generalist detritivores, they probably have almost unlimited access to food, although no data exist to assess this claim. To determine how food resources are distributed in this mosaic at a scale relevant to beetle movements (Wiens and Milne 1989), we recorded the vegetation type at 30-cm intervals along 12 5.1-m line transects. The transect length was chosen to represent the length of our sandbox arena's diagonal, which made the scale of the vegetation data directly comparable to that of our experiments. The transects were randomly located in the area surrounding our experimental sandbox arena and were spaced 0.5 to 6 km apart. Vegetation was categorized as potential darkling beetle food (grass or forb) versus non-food (bare ground, cactus, or shrub) (based upon darkling beetle dietary information from Yount 1971; Rogers et al. 1988). The distribution of food sources was then determined using an index of dispersion (variance:mean ratio), which was tested against a random (Poisson) distribution using a chi-square test (Ludwig and Reynolds 1988).

We created three treatments ('random', 'uniform', and 'clumped'; Figure 1) to assess the effects of food distribution on movement patterns in the microlandscape arena. These treatments were categorized by the range and variance in interpatch distance (with random>clumped>uniform). The treatments were presented in a random sequence so as to minimize any possible order effect. Beetles were randomly assigned to treatments, and each individual was used only once. In each treatment, we used piles of commercial gerbil food (ground alfalfa pellets; Amazon Smythe Superior Nutrition Guinea Pig Food®, Chilton, Wisconsin,
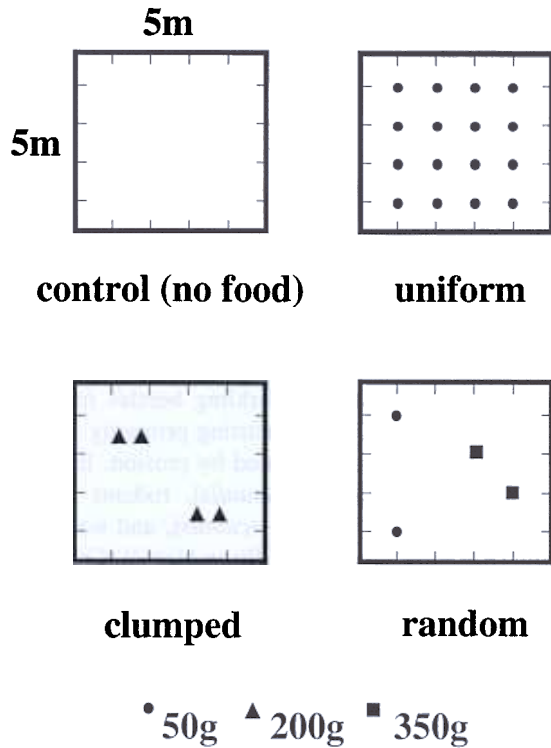
5m

Figure 1. Experimental model system (sandbox arena) used. Small hash marks along arena border mark 1-m increments. Amount of food was held constant at 800 g across treatments. All food piles covered the same area (7-cm diameter circle), differing only in volume (height).

USA) to create patches of food. This food was used because it was readily eaten by captive beetles and because the pellets were uniform in color and size, which standardized the sensory stimuli received by beetles in different treatments. The amount of food present in the microlandscape was held constant at 800 g across all treatments. In the 'random' treatment, 800 g of food was placed in four randomly located locations, two of which had single piles of 50 g of food while the other two locations each had 350 g (seven 50-g piles combined to form one larger pile). Pile locations were determined by gridding the arena into 1 × 1-m squares, numbering the corners of each square, and using a random number generator to determine the four point locations. In the 'uniform' treatment, 800 g of food was placed in 16 50-g piles. In the "clumped" treatment, 800 g of food was placed at four locations, each with 200 g. At each of these four locations, the 200 g of food was divided into two 100-g piles, and these piles were clustered into groups of two, with the pair within each group separated by 10 cm. In

addition, a control was used in which no food was present in the enclosure. All piles covered the same horizontal area (a 7-cm-diameter circle), varying only in volume (height). While taller food piles may have been slightly more prominent, the tallest piles were no more than 2 cm higher than the smallest ones, minimizing potential differences in visual attractiveness with pile height.

Several aspects of this design bear comment. Our primary objective was to assess the effects of food-patch dispersion on movement patterns. We therefore used a design that minimized interactions between patch quality (i.e., grams of food in patches) and patch distribution. We standardized the total amount of food present in the experimental arena across all treatments (800 g) and used food piles that contained much more food than an individual could consume immediately, a biologically feasible situation for small generalist detritivores like darkling beetles. The food piles thus did not vary in their foraging value relative to one another, as all piles in all treatments consisted of larger amounts of food than could be consumed immediately. This means that having food piles of different volumes among treatments is unlikely to confound effects from resource abundance with those from overall landscape 'quality' since all food piles in all treatments represented bonanza resources. Note that the random and clumped treatments can be considered variations on the uniform treatment's basic design of 16 50-g piles of food: both the random and the clumped treatments combined some of these small piles to form larger ones, but the total amount of food present in the sandbox arena was the same for all three treatments. The total horizontal area of the sandbox arena covered by food was identical between the random and clumped treatments (4 piles $\times \pi r^2 = 616\,cm^2$) but less than that of the uniform treatment (16 piles $\times \pi r^2 = 2464\,cm^2$), even though there were more food piles in the uniform treatment. We were concerned, however, that our design might bias the number and horizontal area of the food piles with their dispersion, so we decided to test for the presence of this potential bias in our results. We predicted that if different resource distributions affect animal movement patterns differently, there should be significant differences between the random and clumped treatments. If, however, the abundance of resources (i.e., number of food piles) is more important than their spatial arrangement, then the magnitude of responses should be equal between the random and clumped treatments but differ from

that in the uniform treatment (see also design of Cartar and Real 1997).

Each of our four treatments used a single layout of the food piles (i.e., there was only one pattern used per treatment; Figure 1). Having replicate designs of each treatment would have lowered the within-treatment variance, thereby decreasing the likelihood of committing a Type I (α) statistical error. However, this approach would also have possibly introduced some bias from differences in pattern *within* a treatment. Therefore, we used a conservative statistical approach to deal with this aspect of our experimental design. We minimized the likelihood of committing a Type I error by lowering the α level of significance (Triola 1995). We accepted significance at $\alpha = 0.0125$, obtained by dividing the traditional value of $\alpha = 0.05$ by the number of treatments (4). This is also a workable solution when dealing with natural landscapes that may not be good replicates of one another.

Food deprivation

Beetles were collected by pitfall trapping within a few km of the experimental plot in late May 1995 and 1996 and were maintained in 50 × 25 × 30 cm terraria with an 8-cm soil base and maintained at ca. 23 °C, 37% relative humidity, and natural lighting conditions. Beetles were randomly assigned to one of two groups. 'Fed' beetles ($N = 28$) were provided with water (in saturated cotton wadding) and food *ad libitum*. The food consisted of commercial gerbil food, commercial fish food (TetraMin Flake Food®, Blacksburg, Virginia, USA), and natural vegetation. 'Food-deprived' beetles ($N = 28$) were starved for 30 d but were provided with water *ad libitum*. A 30-d starvation period was used because preliminary trials indicated that *E. extricata* could survive without food for 2 wk with no changes in field behavior (NEM unpublished data). A 30-d starvation period incurred less than 15% mortality but was evidently at the upper range of starvation tolerance, as 100% of a trial set of beetles died after 40 d of starvation. Darkling beetles only feed during favorable environmental conditions (Yount 1971; NEM personal observation). Therefore, they probably encounter natural starvation periods of various lengths, depending on extremes in temperature and precipitation and on season. The weather of the shortgrass steppe encompasses great daily and seasonal extremes (Lauenroth and Milchunas 1991), so a 30-d starvation period is probably not outside the natural range of starvation experienced by beetles in the wild.

Movement analyses

Movement trials were conducted between 0700 and 1100 MDT when unshaded soil-surface temperatures were 16–30 °C, representing times and temperatures when darkling beetles are normally most active on the shortgrass steppe (Whicker and Tracy 1987). Because both the type and the availability of different resources may vary throughout the day, beetle movement patterns may differ accordingly at different times of day. For example, even hungry beetles may search for favorable microclimates at dawn, midday, and dusk instead of for food because they are exothermic animals. As we were interested in how beetles respond to food and not to other factors, we tried to hold such factors constant by conducting trials during a consistent thermal window at consistent times of day.

To initiate a trial, an individual beetle was placed under an inverted plastic cup in the center of the arena for 2 min, after which the cup was removed and the trial started. The beetle's location was marked at 15-s intervals and its path electronically surveyed, following the protocol of Wiens et al. (1993a). Beetles were followed until they reached the perimeter of the arena ($N = 35$ beetles) or until they remained stationary for 10 successive time-steps (which occurred only when they ate from a food pile; $N = 21$). Foraging movement patterns may be affected by contact with resources (Jander 1975; Mols 1979; Carter and Dixon 1982), but as we were interested in movements to find food initially, we excluded movements made after the beetles contacted food.

Because darkling beetles are nomadic, possessing no true home ranges (Calkins and Kirk 1973; Doyen and Tschinkel 1974; Crist et al. 1992), we tried to ensure that our experimental subjects were similarly naïve about the experimental surroundings. Therefore, we did not familiarize the beetles with the experimental arena, and each individual was tested only once. To minimize disturbance to the beetles, only one observer (NEM) handled the beetles and was present in the sandbox arena during movement trials. The beetles were handled as little as possible and were given a 2-min rest period between handling (during placement in the arena) and the commencement of a movement trial. The observer crouched at least 0.5 m away from the beetle at all times and ensured that her shadow did not fall upon the beetle or its trajectory at any time.

Placement of the numbered flags was delayed for ca. 1 s to prevent herding the beetle. A 15-s time interval was used to minimize pursuit of the beetles. Because none of the beetles displayed the characteristic raised-abdomen defensive posture that is assumed by this species when disturbed (Parmenter and MacMahon 1988), we are reassured that our beetles were not moving in order to escape during our experimental trials. We also observed beetles feeding during the movement trials, another anecdotal indication that our beetles were behaving 'normally' and not in an evasive fashion. This protocol has been used for nearly a decade in the study of insect movement patterns (Wiens and Milne 1989; Crist et al. 1992; Johnson et al. 1992; Wiens et al. 1993a; With 1994; Crist and Wiens 1995; Wiens et al. 1995, 1997).

The movement pathways of food-deprived and fed beetles were compared in each of the four resource distributions (random, uniform, clumped, and control). We measured seven replicate pathways per hunger treatment per resource distribution treatment ($N = 56$ paths; 16 paths in 1995, 40 in 1996). For each pathway, we calculated: (1) total path length to assess total time spent in travel; (2) net linear displacement to assess distance covered; (3) step length per 15-s interval to assess velocity (Crist et al. 1992); and (4) fractal dimension (using the dividers method; Dicke and Burrough 1988) to assess path tortuosity. We also recorded whether a beetle contacted and ate from a food pile. The first three path metrics quantify slightly different aspects of the general movement behavior, length of movement, whereas the fourth metric quantifies movement complexity (Crist et al. 1992). The fractal dimension theoretically ranges from 1 to 2, with values near 1 indicating a linear, directional path and values near 2 denoting a completely random path (Hastings and Sugihara 1993). These theoretical values are derived from simulated random-walk pathways that are thousands of steps long. Such paths are 'recurrent' (i.e., they eventually return to their starting point, thereby filling a plane and generating a fractal dimension of 2; Mandelbrot 1983). In practice, however, real movement pathways are usually much shorter, which means that the upper theoretical limit of 2 is usually not reached in even a random path.

All statistical analyses were performed using SAS software (SAS Institute Inc. 1996). We used analysis of covariance (ANCOVA) to assess significant differences in the four pathway metrics with level of food deprivation and with food distribution. Each of the four pathway metrics was tested with a sepa-rate ANCOVA model, with soil-surface temperature as a covariate and food-deprivation treatment and resource-distribution treatment as fixed main effects. If soil-surface temperature was not a significant covariate, then the model was simplified to an analysis of variance (ANOVA). Variables with significant ANCOVA or ANOVA models were then compared among the four treatments with Fisher's Protected Least Significant Difference (LSD) test for simultaneous comparisons among means (Sokal and Rohlf 1981). The frequency of contacting a food pile as affected by hunger and resource distribution was assessed with Yates' continuity-corrected chi-square test (Sokal and Rohlf 1981).

Movement trials were initially conducted in 1995; the entire experiment was replicated in 1996. Multivariate analysis of variance (MANOVA) was used to detect any between-year differences in the data to determine whether data from the two years could be pooled for further analysis.

Results

Because no differences were found in response variables with year (MANOVA: $F_{4,50} = 7.55$, $P = 0.1779$), data from both years were pooled for analysis.

Natural resource distributions

The dispersion of the grasses and forbs usually fed on by darkling beetles did not differ significantly from a Poisson (random) distribution in the beetles' natural environment (mean $= 14.66$, variance $= 16.02$; $\chi^2 = 14.30$, df $= 11$, P $= 0.48$). Thus, food is randomly distributed rather than being clumped or homogeneously distributed at a beetle's scale of resolution.

Food deprivation

There was a significant effect of food deprivation on beetle movements ($\chi^2 = 9.143$, df $= 1$, P $= 0.002$). Food-deprived beetles contacted food piles significantly more often (12 of 21 non-control trials) than did fed ones (0 of 21). Of these contacts with food, 4 came in the random treatment, 3 in the clumped treatment, and 5 in the uniform treatment. All of the hungry beetles that contacted food piles paused to eat from them. Food-deprived beetles also moved more slowly than did fed ones, covering less ground in 15-s intervals than did fed beetles (Figure 2a). As a consequence,
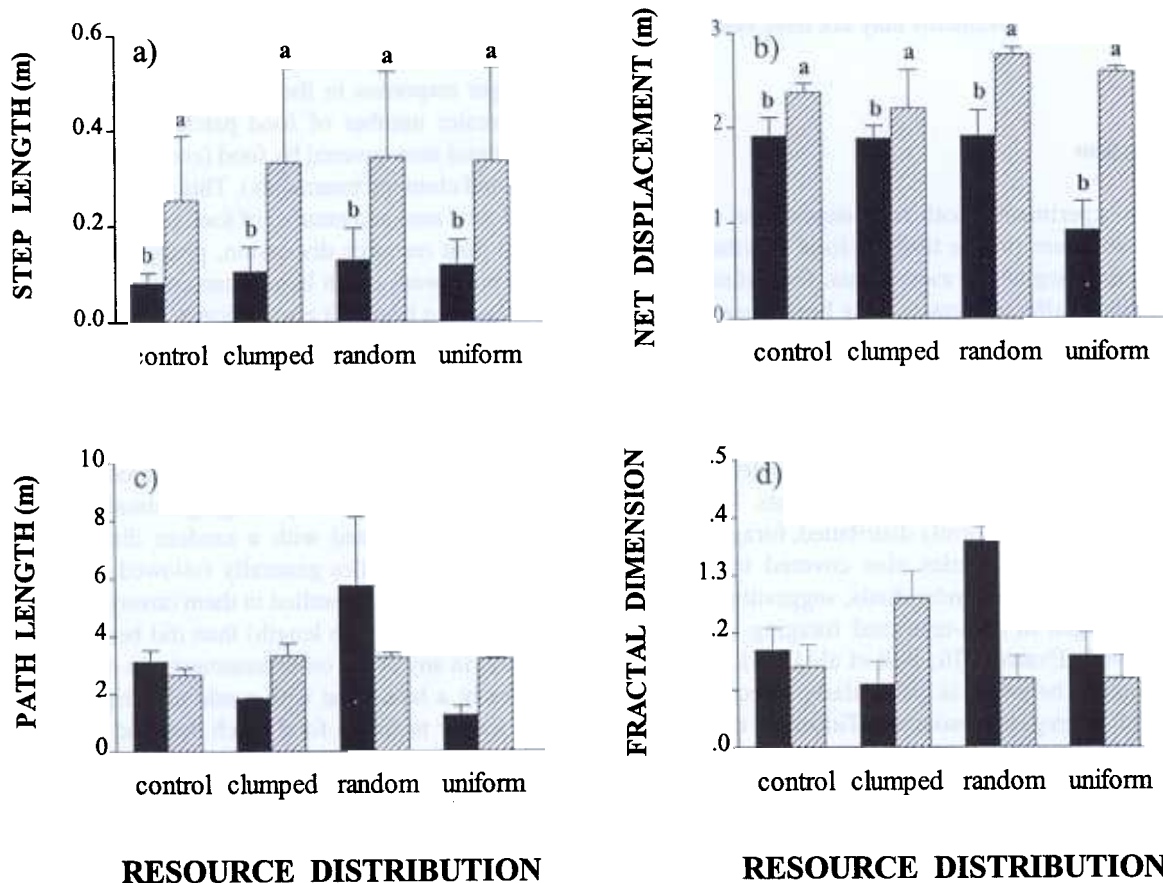
Figure 2. Mean (± SE) path metrics for food-deprived (solid bars) and fed (hatched bars) *E. extricata* in areas with no food resources (control) and resources in clumped, random, and uniform distributions. (a) length of 15-s steps, (b) net linear displacement, (c) total path length, (d) fractal dimension. Means denoted with different letters are significantly different (P < 0.0125, Fisher's Protected LSD). Fisher's post-hoc comparisons were only performed on length of 15-s steps and net linear displacement because total path length and fractal dimension had non-significant overall ANOVA models.

food-deprived beetles covered a smaller overall area in a given time period (smaller net displacement, Figure 2b). Again, this difference was consistent across all of the food-dispersion treatments.

Experimental resource distributions

Soil-surface temperature was not a significant covariate in any of the four pathway-metric ANCOVA models. Two pathway metrics varied significantly with food deprivation and resource distribution (net displacement: $F = 4.17$, df $= 9$, $P = 0.0006$; step length: $F = 6.79$, df $= 9$, $P = 0.0001$). The two other variables did not differ significantly among the treatments under our conservative approach (recall that $\alpha = 0.0125$; path length: $F = 2.29$, df $= 9$, $P = 0.0325$; fractal dimension: $F = 2.17$, df $= 9$, $P = 0.0426$); even so,

Figure 2 illustrates some trends with hunger and across treatments for these variables. For example, food-deprived beetles exhibited the greatest overall path length and the highest fractal dimensions in treatments with randomly distributed food patches (Figures 2c, 2d). In contrast, hungry beetles had somewhat shorter overall path lengths (but not fractal dimensions) in treatments with clumped and with uniformly distributed resources (Figures 2c, 2d). Not surprisingly, the average time taken to reach food was greatest in treatments with randomly distributed resources (39 s), intermediate in the clumped treatment (31 s), and least in the uniform treatment (19 s). The average fractal dimension (Figure 2d) for pathways of all beetles in all treatments was < 1.50 (the theoretical midpoint value of the two-dimensional fractal value range), suggest-

ing that beetle movements may not have been random walks.

Discussion

In our experiments, both food deprivation and landscape structure (in the form of food distribution) affected darkling beetle movements. Food distributions particularly affected how quickly beetles moved (step length) and how beetles encountered food patches (net displacement), but they did not have as strong an effect on overall wandering (total path length) or path complexity (fractal dimension). Food-deprived beetles moved more slowly and over shorter distances than did fed beetles across all treatments. When food was clumped or uniformly distributed, foraging movements of hungry beetles also covered less ground than did those of fed individuals, suggesting that they were engaged in area-restricted foraging (Tinbergen et al. 1967; Evans 1976; Bell et al. 1985). This type of foraging behavior is particularly effective in areas with aggregated resources (Tinbergen et al. 1967; Evans 1976; Baars 1979; Duvall et al. 1994), although its effectiveness may depend on the scale of aggregation (i.e., interpatch distances) relative to the patch-detection distance of foragers (Fahrig and Paloheimo 1988). In the laboratory, *E. extricata* uses both olfaction and vision equally well and with approximately equal frequency in foraging, and it is likely that foraging in the field involves both vision and olfaction as well. All food piles in our experiment were within the potential sensory range of this species ($\leq$ 80 cm, McIntyre and Vaughn 1997) from their release point in the center of the arena. During the trials we observed six food-deprived beetles raising their antennae from their customary drooping posture when directly downwind of food. McIntyre and Vaughn (1997) demonstrated that this behavior ('antennal waving') is associated with the use of olfaction in foraging in the laboratory. Olfactory cues on the shortgrass steppe may be strongly directional, depending on wind speed and direction. Considering that the beetles had no prior knowledge about the spatial array of food in the experimental arena, use of both vision and olfaction may have been a more prudent strategy than using either singly.

Beetles did not encounter large food piles more often than small ones in the random treatment, so food-pile volume was less important than food-pile dispersion to beetles in our experiments. This may be due to the fact that beetles have a limited sensory range. Similarly, beetles did not show significantly stronger responses in the uniform treatment, despite the greater number of food patches and amount of horizontal area covered by food (compared to the random and clumped treatments). This indicates that total horizontal area and number of food piles are less influential than resource dispersion, probably because all food piles were much larger than could be consumed in a day by a beetle. It also indicates that any potential bias from the confounding effects of number, area, and dispersion of food resources in our experimental design was minimal. As natural landscapes display these effects in a blended fashion rather than a compartmentalized one, our experimental design modeled a very realistic scenario faced by foraging animals.

When confronted with a random distribution of food patches, beetles generally followed a more tortuous pathway that resulted in them covering a greater overall distance (path length) than did beetles (fed or hungry) in any of the other treatments; in other words, beetles in a landscape with randomly dispersed food took longer to find a food patch than did the hungry beetles in other treatments. Thus, although a random distribution of food resources appears to characterize the beetles' natural grassland environment (at least at fine scales), their movements in an experimental arena with this particular food-dispersion pattern are less effective in locating food patches than when food is distributed in different patterns. Thus, beetles appear to be more effective in locating food resources when the food is clumped or uniformly distributed than when it is randomly arrayed (see Cartar and Real 1997 and Cresswell 1997 for similar responses in foraging bumblebees).

Contrary to our initial predictions, the strongest movement responses were not elicited in areas with aggregated food patches. Knowing now how food patches are naturally distributed in the beetles' grassland environment, however, makes this response biologically logical. As predicted, movement responses were more pronounced in food-deprived than in fed individuals, whose motivation to find food was presumably less intense. In general, food-deprived individuals had more convoluted pathways and covered shorter distances per time interval than did satiated individuals, presumably because of the more intense searching behavior of hungry animals.

Our results are consistent with those of other studies that have shown that the distribution of resources (e.g. Mitchell 1963; Tortorici et al. 1986; Mols 1987;

Fromm and Bell 1987; Vail 1993; Edwards et al. 1994) and food deprivation (e.g. Holling 1966; Jander 1975; Hassell and Southwood 1978; Mols 1979, 1987; Carter and Dixon 1982; McIntyre and Vaughn 1997) interact to affect the behavior of a variety of organisms under field, laboratory, and simulation conditions. Exactly what sort of movement pattern might be best under differing resource distributions, however, is open to debate. Some workers (e.g. Jander 1975; Dusenbery 1989) have argued that when animals have no information about the spatial location of resources, a linear path may be the most energetically effective movement strategy. Indeed, the relatively low fractal dimensions of beetle movements in all treatments (Figure 2d) suggest that *E. extricata* may be following this strategy, at least in part. In a landscape that is heterogeneous at broader scales, however, linear movement ultimately results in progression of an animal out of favorable habitat. Under these conditions, it may be more prudent to move in a more convoluted fashion, even when the distribution of resources is unknown (Bell and Kramer 1979; Fromm and Bell 1987; Duvall et al. 1994). Beetles also appear to employ this strategy, especially when resources are randomly distributed (and thus spatially unpredictable). Ultimately, gauging the effectiveness of the observed movement pathways in each of the resource-dispersion arrays requires that they be compared with expected outcomes based on some null model (Gardner et al. 1989; Johnson et al. 1992; Milne et al. 1992). This is probably best accomplished by coupling experiments such as ours with spatially explicit simulation models, in which the consequences of various movement algorithms under specified resource-distribution patterns can be assessed. The relationship between movement pathways and food dispersion will also vary with scale (of both the landscape pattern and the organism's perceptual range; Wiens 1989; Kotliar and Wiens 1990). Such scaling relationships could also be explored through a combination of field observations (e.g., McIntyre 1997), EMS experiments (e.g., Ims et al. 1993), and simulation models (e.g., Gardner et al. 1989, 1991). The interaction between food deprivation and landscape structure (in the form of food distributions) affected darkling beetle movement behaviors more so than did either of these two factors acting alone. This nonlinear relationship between the spatial structure of a landscape and its use by organisms demonstrates how difficult it may be to predict how animals may respond to landscape changes.

Our results illustrate how the effects of spatial structure depend not only on the pattern of that structure but also on how the structure is used (see also With and King 1997). Therefore, 'spatial structure' can be defined not only on the basis of its physical characteristics (e.g. distance between patches of food) but also on how that structure is used by animals for activities such as foraging. The organism-environment relationship that is the focus of ecology results from the coupling of an individual's condition with the spatial distribution of resources on the landscape.

Because ecological processes and patterns are scale-dependent and because different kinds of organisms differ in the ways and scales of responding to landscape patterns such as the distribution of resources (Rose and Leggett 1990; Edwards et al. 1994), it is difficult to generalize in detail from studies of EMS such as beetles in sandbox arenas (With 1997). Nonetheless, our experiments have revealed some of the behavioral mechanisms that may underlie variations in how organisms move through heterogeneous landscape mosaics at any scale (Ims 1995; Burke 1997). Although our experimental setup may provide some insights into how manipulated landscape pattern can influence animal behaviors, certainly additional studies are needed in more natural settings to provide a more complete picture of this relationship. By conducting such studies over a range of organisms representing different suites of life-history traits, it may be possible to generate an empirical foundation for the development of general, predictive theory in landscape ecology (Wiens et al. 1993b; Wiens 1995).

Acknowledgements

References

Andreassen, H.P., Halle, S. and Ims., R.A. 1996a. Optimal width of movement corridors for root voles: not too narrow and not too wide. J. Appl. Ecol. 33: 63–70.

Andreassen, H.P., Ims, R.A. and Steinset, O.K. 1996b. Discontinuous habitat corridors: effects on male root vole movements. J. Appl. Ecol. 33: 555–560.

Arditi, R. and Dacorogna, B. 1988. Optimal foraging on arbitrary food distribution and the definition of habitat patches. Am. Nat. 131: 837–846.

Baars, M.A. 1979. Patterns of movement of radioactive carabid beetles. Oecologia 44: 125–140.

Bell, W.J. 1990. Searching behavior patterns in insects. Annu. Rev. Entomol. 35: 447–467.

Bell, W.J. 1991. Searching Behaviour: The Behavioural Ecology of Finding Resources. Chapman and Hall, London.

Bell, W.J. and Kramer, E. 1979. Search and anemotactic orientation of cockroaches. J. Insect Physiol. 25: 631–640.

Bell, W.J., Tortorici, C., Roggero, R.J., Kipp, L.R. and Tobin, T.R. 1985. Sucrose-stimulated searching behaviour of Drosophila melanogaster in a uniform habitat: modulation by period of deprivation. Anim. Behav. 33: 436–448.

Bernstein, C., Kacelnik, A. and Krebs, J.R. 1988. Individual decisions and the distribution of predators in a patchy environment. J. Anim. Ecol. 57: 1007–1026.

Burke, V.J. 1997. The value of descriptive studies in landscape ecology. US-IALE Newsletter 13(2): 6–8.

Calkins, C.O. and Kirk, V.M. 1973. Distribution and movement of adult false wireworms in a wheat field. Ann. Entomol. Soc. Am. 66: 527–532.

Cartar, R.V. and Real, L.A. 1997. Habitat structure and animal movement: the behaviour of bumble bees in uniform and random spatial resource distributions. Oecologia 112: 430–434.

Carter, M.C. and Dixon, A.F.G. 1982. Habitat quality and the foraging behaviour of coccinellid larvae. J. Anim. Ecol. 51: 865–878.

Crawford, C.S. 1981. Biology of Desert Invertebrates. Springer-Verlag, New York, NY.

Cresswell, J.E. 1997. Spatial heterogeneity, pollinator behaviour and pollinator-mediated gene flow: bumblebee movements in variously aggregated rows of oil-seed rape. Oikos 78: 546–556.

Crist, T.O., Guertin, D.S., Wiens, J.A. and Milne, B.T. 1992. Animal movement in heterogeneous landscapes: an experiment with Eleodes beetles in shortgrass prairie. Funct. Ecol. 6: 536–544.

Crist, T.O. and Wiens, J.A. 1995. Individual movement and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). J. Anim. Ecol. 64: 733–746.

De Roos, A.M., McCauley, E. and Wilson, W.G. 1991. Mobility versus density-limited predator-prey dynamics on different spatial scales. Proc. R. Soc. London B246: 117–122.

Dicke, M. and Burrough, P.A. 1988. Using fractal dimensions for characterizing tortuosity of animal trails. Physiol. Entomol. 13: 393–398.

Doyen, J.T. and Tschinkel, W.F. 1974. Population size, microgeographic distribution, and habitat separation in some tenebrionid beetles. Ann. Entomol. Soc. Am. 67: 617–626.

Dusenbery, D.B. 1989. Ranging strategies. J. Theoret. Biol. 136: 309–316.

Duvall, D., Chiszar, D. and Mintzer, R.A. 1994. Plane geometry for naïve searchers: some results of the simulation Rattlesnake® . Am. Zool. 34: 78A.

Edwards, G.R., Newman, J.A., Parsons, A.J. and Krebs, J.R. 1994. Effects of the scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep. J. Anim. Ecol. 63: 816–826.

Evans, H.F. 1976. The searching behaviour of Anthocoris confusus (Reuter) in relation to prey density and plant surface topography. Ecol. Entomol. 1: 163–169.

Fromm, J.E. and Bell, W.J. 1987. Search orientation of Musca domestica in patches of sucrose drops. Physiol. Entomol. 12: 297–307.

Gardner, R.H., O'Neill, R.V., Turner, M.G. and Dale, V.H. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. Landscape Ecol. 3: 217–227.

Gardner, R.H., Turner, M.G., O'Neill, R.V. and Lavorel, S. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. In Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments. pp. 76–89. Edited by M.M. Holland, P.G. Risser and R.J. Naiman. Chapman and Hall, New York, NY.

Gustafson, E.J. and Gardner, R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94–107.

Hassell, M.P. and Southwood, T.R.E. 1978. Foraging strategies of insects. Annu. Rev. Ecol. Syst. 9: 75–98.

Hastings, H.M. and Sugihara, G. 1993. Fractals: A User's Guide for the Natural Sciences. Oxford University Press, Oxford.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. No. 48.

Ims, R.A. 1995. Movement patterns related to spatial structures. In Mosaic Landscapes and Ecological Processes. pp. 85–109. Edited by L. Hansson, L. Fahrig and G. Merriam. Chapman and Hall, London.

Ims, R.A., Rolstad, J. and Wegge, P. 1993. Predicting space use responses to habitat fragmentation: can voles Microtus oeconomus serve as an experimental model system (EMS) for capercaillie grouse in boreal forest? Biol. Conserv. 63: 261–268.

Jander, R. 1975. Ecological aspects of spatial orientation. Annu. Rev. Ecol. Syst. 6: 171–188.

Jander, R. 1982. Random and systematic search in foraging insects. In The Biology of Social Insects. pp. 28–31. Edited by M.D. Breed, C.D. Michener and H.E. Evans. Westview Press, Boulder, CO.

Johnson, A.R., Milne, B.T. and Wiens, J.A. 1992. Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements. Ecology 73: 1968–1983.

Kareiva, P.M. 1985. Finding and losing host plants by Phyllotreta: patch size and surrounding habitat. Ecology 66: 1809–1816.

Kotliar, N.B. and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253–260.

Lauenroth W.K. and Milchunas, D.G. 1991. Short-grass steppe. In Ecosystems of the World 8A: Natural Grasslands. pp. 183–226. Edited by R.T. Coupland. Elsevier, Amsterdam.

Levin, D.A., Kerster, H.W. and Niedzlek, M. 1971. Pollinator flight directionality and its effect on pollen flow. Evolution 25: 113–118.

Ludwig, J.A. and Reynolds, J.F. 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley and Sons, New York, NY.

Mandelbrot, B.B. 1983. The Fractal Geometry of Nature. W.H. Freeman, New York, NY.

Maynard Smith, J. 1978. Optimization theory in evolution. Ann. Rev. Ecol. Syst. 9: 31–56.

McIntyre, N.E. 1997. Scale-dependent habitat selection by the darkling beetle Eleodes hispilabris (Coleoptera: Tenebrionidae). Am. Midl. Nat. 138: 230–235.

McIntyre, N.E. and Vaughn, T.T. 1997. Effects of food deprivation and olfactory and visual cues on the movement patterns of two *Eleodes* species (Coleoptera: Tenebrionidae) in a wind tunnel. Ann. Entomol. Soc. Am. 90: 260–265.

Merriam, G. 1988. Landscape dynamics in farmland. Trends Ecol. Evol. 19: 16–20.

Milne, B.T., Turner, M.J., Wiens, J.A. and Johnson, A.R. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theor. Pop. Biol. 41: 337–353.

Mitchell, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank): I. Life cycles and feeding behaviour. J. Anim. Ecol. 32: 289–299.

Mols, P.J.M. 1979. Motivation and walking behaviour of the carabid beetle *Pterostichus coerulescens* L. at different densities and distributions of the prey: a preliminary report. Misc. Papers 18 Ag. Univ., Wageningen, The Netherlands. Edited by P.J. Den-Boer, H.U. Thiele and F. Weber. H. Veenman and Zonen B.V., Publishers, Wageningen.

Mols, P.J.M. 1987. Hunger in relation to searching behaviour, predation and egg production of the carabid beetle *Pterostichus coerulescens* L.: results of simulation. Acta Phytopath. Entomol. Hung. 22: 187–205.

Ollason, J.G. 1980. Learning to forage-optimally? Theor. Popul. Biol. 18: 44–56.

Parmenter, R.R. and MacMahon, J.A. 1988. Factors limiting populations of arid-land darkling beetles (Coleoptera: Tenebrionidae): predation by rodents. Environ. Entomol. 17: 280–286.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15: 523–575.

Rogers, L.E., Woodley, N.E., Sheldon, J.K. and Beedlow, P.A. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within a shrub-steppe ecosystem. Ann. Entomol. Soc. Am. 81: 782–791.

Rose, G. and Leggett, W. 1990. The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. Ecology 71: 33–43.

SAS Institute Inc. 1996. SAS/STAT® Software: Changes and Enhancements through Release 6.11. SAS Institute, Inc., Cary, NC.

Sokal, R.R. and Rohlf, F.J. 1981. Biometry (2nd ed.). W.H. Freeman, New York, NY.

Tinbergen, N., Impekoven, M. and Franck, D. 1967. An experiment on spacing-out as a defence against predation. Behaviour 28: 307–321.

Tortorici, C., Brody, A. and Bell, W.J. 1986. Influence of spatial patterning of resources on search orientation of adult *Drosophila melanogaster*. Anim. Behav. 34: 1568–1570.

Triola, M.F. 1995. Elementary Statistics, 6th ed. Addison-Wesley, Reading, MA.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72: 1253–1266.

Vail, S.G. 1993. Scale-dependent responses to resource spatial pattern in simple models of consumer movement. Am. Nat. 141: 199–216.

Whicker, A.D. and Tracy, C.R. 1987. Tenebrionid beetles in the shortgrass prairie: daily and seasonal patterns of activity and temperature. Ecol. Entomol. 12: 97–108.

Wiens, J.A. 1989. Spatial scaling in ecology. Funct. Ecol. 3: 385–397.

Wiens, J.A. 1995. Landscape mosaics and ecological theory. *In* Mosaic Landscapes and Ecological Processes. pp. 1–26. Edited by L. Hansson, L. Fahrig and G. Merriam. Chapman and Hall, London.

Wiens, J.A., Crist, T.O. and Milne, B.T. 1993a. On quantifying insect movements. Environ. Entomol. 22: 709–715.

Wiens, J.A., Crist, T.O., With, K.A. and Milne, B.T. 1995. Fractal patterns of insect movement in microlandscape mosaics. Ecology 76: 663–666.

Wiens, J.A. and Milne, B.T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecol. 3: 87–96.

Wiens, J.A., Schooley, R.L. and Weeks, R.D. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78: 257–264.

Wiens, J.A., Stenseth, N.C., Van Horne, B. and Ims, R.A. 1993b. Ecological mechanisms and landscape ecology. Oikos 66: 369–380.

With, K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecol. 9: 25–36.

With, K.A. 1997. Microlandscape studies in landscape ecology: experimental rigor or experimental *rigor mortis*? US-IALE Newsletter 13(1): 13–16.

With, K.A. and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446–2459.

With, K.A. and King, A.W. 1997. The use and misuse of neutral landscape models in ecology. Oikos 79: 219–229.

Yount, V.A. 1971. Diets of selected insects in a grassland ecosystem. M.S. Thesis, Colorado State University, Fort Collins, CO.