

DISSERTATION

LANDSCAPE HETEROGENEITY AT MULTIPLE SCALES:
EFFECTS ON MOVEMENT PATTERNS AND HABITAT SELECTION
OF ELEODID BEETLES

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED
UNDER OUR SUPERVISION BY NANCY E. McINTYRE ENTITLED LANDSCAPE
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ABSTRACT OF DISSERTATION

LANDSCAPE HETEROGENEITY AT MULTIPLE SCALES: EFFECTS ON MOVEMENT PATTERNS AND HABITAT SELECTION OF ELEODID BEETLES

I combined observational studies with field experiments to investigate how landscape heterogeneity influences habitat selection in eleodid beetles of the shortgrass prairie of Colorado. I examined correlations in spatio-temporal patterns of habitat occupancy, population density, and community structure in eleodids with spatial and abiotic features of the landscape; I then explored how variations in spatial structure could affect how animals move through a landscape, accounting for the observed patterns of habitat occupancy. I combined these observations with experimental manipulations of several landscape features that affect the movement behaviors of beetles. The results from these experiments show how interactions among animal behavior, landscape composition and configuration, and the scale of spatial structure determine where animals occur in a heterogeneous environment.

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Writing my dissertation has been like performing alchemy--I have had to take an enormous amount of data and from it distill a "truth serum." This process was made possible through the assistance of numerous people, far too many to be thanked properly in this format. I will, however, acknowledge the contributions of the principals here while being mindful of the legion of other players to whom I owe a debt of gratitude.

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"Behold the fruit of pensive nights and laborious days... "

Sherlock Holmes (A.C. Doyle)

"His Last Bow" in *His Last Bow* (1917)

Hodder and Stoughton, Toronto, ON

CHAPTER I

OVERVIEW

Most landscapes are composed of areas of habitat and non-habitat, preferred areas and avoided areas, with a gradient of preferability in between. Animals must assess the differences among these areas to select and occupy preferred ones. To do so, animals must view their surroundings as a heterogeneous mosaic of components that differ in size, configuration, and context with other components. Such comparisons must also integrate heterogeneity at different spatial scales, from broad-scale differences among landscape components to fine details within these components. At the heart of understanding organism-environment relationships, then, is understanding how animals perceive heterogeneity and how they navigate heterogeneous landscapes.

For my dissertation work, I examined how spatial heterogeneity influences patterns of habitat selection and habitat occupancy in animals. My primary research interest is in how landscape pattern affects the abundance and distribution of animals. To elucidate this organism-environment interaction, I conducted both observational studies and field experiments that examined where animals occur (habitat occupancy) and animal movement (the process by which animals come to occupy habitat). These studies focused on darkling beetles (*Eleodes* spp., Coleoptera: Tenebrionidae) of the shortgrass prairie of northern Colorado. Although my results are specific to these beetles, the questions, methods, and implications may be extended to situations faced by animals in general.

My dissertation is arranged in a deductive fashion, proceeding from large-scale interactions between spatial heterogeneity and patterns of habitat occupancy to small-scale field experiments that explored how specific landscape features influence beetle movement

patterns and how movement behaviors determine patterns of habitat occupancy. Chapter II describes the results of a 4-year field study on landscape and climatological factors that affect darkling beetle community structure; this chapter also describes my dissertation study site in detail. Chapter III explores how patterns of habitat preference at one spatial scale cannot be translated into accurate predictions of habitat preference at another scale if different mechanisms of habitat selection are acting at different scales. Chapters IV-VI discuss field experiments that manipulated several environmental features (Chapter IV: distribution of food; Chapter V: scale of landscape patchiness; Chapter VI: habitat amount and configuration) to investigate various mechanisms by which spatial heterogeneity modifies movement patterns. Chapter VII synthesizes overall conclusions.

These chapters explore how animals respond to landscape heterogeneity. I have combined observations on the ecology of darkling beetles with field experiments that manipulated spatial patterns to determine some of the mechanisms accounting for variations in the abundance and distribution of animals. Although the small-scale experimental systems I used are seemingly far removed from broader-scaled landscapes, these systems were designed to examine features common to heterogeneous landscapes at any scale, such as habitat patch size.

"At first, I believed my study...would be simple. How naïve! I never realized how many personalities, problems, and blind alleys would be encountered."

David Costello

The Prairie World (1969)

University of Minnesota Press, Minneapolis, MN

CHAPTER II

COMMUNITY STRUCTURE OF *ELEODES* BEETLES (COLEOPTERA: TENEBRIONIDAE) IN THE SHORTGRASS PRAIRIE: SCALE-DEPENDENT PERCEPTIONS OF HETEROGENEITY

ABSTRACT

Patterns in the community structure of darkling beetle (*Eleodes* spp., Coleoptera: Tenebrionidae) assemblages in the shortgrass prairie of north-central Colorado were monitored by live pitfall trapping for four summers. The beetle community changed as much in composition within a year as among years. There were significant correlations between weather (temperature and precipitation) and species richness and the number of individuals per species captured; effects from weather conditions also displayed 1-month and 1-year delayed effects. Population densities of a subset of the eleodid community were monitored by mark-recapture methods. Densities of darkling beetles varied relatively little among years and sites, although eleodid density was correlated with temperature and precipitation. Abiotic influences on both density and richness differed between macrohabitats. Affinities with cactus and shrub microhabitats (and an avoidance of bare soil) were evident. Because these results do not conform well to previous explanations of why darkling beetle assemblages are spatially and temporally heterogeneous, an alternative mechanism concerning scale-dependent perceptions of heterogeneity and mobility is proposed to account for eleodid community patterns.

Key words: Coleoptera, darkling beetle, *Eleodes*, population density, precipitation, richness, shortgrass prairie, temperature, Tenebrionidae, DISTANCE

INTRODUCTION

The shortgrass prairie of the western United States (Fig. 2.1) is one of the least-studied ecosystems in North America. Disparagingly called "the Great American Desert" by early explorers and homesteaders because of its apparent monotony and harsh climate, this biome is in fact a spatio-temporally dynamic ecosystem (Knopf and Samson 1997). The long-standing and persistent misperception of the shortgrass prairie as homogeneous may stem from the coarse perceptual scale of the observers. Many of its other occupants, however, may more readily perceive the heterogeneous nature of the shortgrass prairie, owing to differences in body size and mobility. In this chapter I examine evidence for scale-dependent perceptions of heterogeneity in various species of darkling beetle (*Eleodes* spp., Coleoptera: Tenebrionidae) of the northern shortgrass prairie of Colorado.

Darkling beetles (eleodids) are among the most abundant macroarthropods of the shortgrass prairie, with as many as nine sympatric species (Bell 1971, Kumar et al. 1976), although very little is known about the basic biology of most shortgrass-prairie species. In general, eleodids live most of their lives as soil-inhabiting larvae that feed on roots and detritus. Upon eclosion, they may live for 2 years as adults (Allsopp 1980). Adults are detritivorous, feeding mainly on grasses and forbs, and there is a high degree of dietary overlap among species (Yount 1971, Doyen and Tschinkel 1974, Slobodchikoff 1978, Rogers et al. 1988). Although flightless, the beetles are highly mobile and wander over great distances (Kramm and Kramm 1972, Calkins and Kirk 1973, Doyen and Tschinkel 1974). Individuals are active when temperatures permit. On the southern shortgrass prairie and desert, activity is usually crepuscular and nocturnal from spring through autumn; on the northern shortgrass and mixed-grass prairies and shrub-steppe desert, darkling beetles are mostly diurnal from late spring through early autumn, with peaks of activity in the early morning and early evening (Kramm and Kramm 1972, Wise 1981b, Kenagy and Stevenson 1982, Richman et al. 1982, Whicker 1983, Marino 1986, Whicker and Tracy 1987, Stapp 1997a). More detailed information on darkling beetle ecology may

be found in Doyen and Tschinkel (1974), Allsopp (1980), Parmenter and MacMahon (1984), Sheldon and Rogers (1984), Whicker and Tracy (1987), Rogers et al. (1988), and Parmenter et al. (1989b).

The similarity of life history, diet, range, and behavior among species prompts the question of how the darkling beetle community is structured in space and time. The factors that account for the spatio-temporal patterns of darkling beetle community composition have been subject to much speculation by past researchers. The presence of a high degree of niche overlap suggests that environmental factors may play more important roles in structuring eleodid assemblages and populations than do biotic factors such as competition and predation (Wiens and Rotenberry 1979, Wise 1981a; but see Abrams 1980), which may play only minor roles in determining the abundance and distribution of darkling beetles (Wise 1981a, Wise 1985, Parmenter and MacMahon 1988). Therefore, an examination of habitat-specific patterns should provide some insights into darkling beetle ecology.

Previous studies have demonstrated that darkling beetle activity and occurrence are influenced by various environmental factors, including soil texture (Calkins and Kirk 1975; Krasnov and Shenbrot 1996, 1997; Stapp 1997a), shrub cover (Parmenter et al. 1989b, Stapp 1997a), and thermoregulatory resources (Rickard 1971, Slobodchikoff 1983, Whicker 1983, Whicker and Tracy 1987, Parmenter et al. 1989c). However, none of these studies examined the interaction between abiotic (weather) and habitat factors in influencing eleodid communities and populations. In this study, I investigated multiscaled habitat preferences and spatio-temporal variations in eleodid density and diversity over a 4-year period. In particular, I focused on how eleodids respond to temperature, precipitation, and the presence of shrubs (which encompassed several covariates and indirect effects, discussed below and in Chapter III).

Some eleodid species are more abundant in and move to areas with greater shrub cover (Parmenter and MacMahon 1988), possibly because shrubs provide protection from

vertebrate predators (Parmenter and MacMahon 1988, Stapp 1997b) and shade. I investigated both of these factors.

Hypotheses

First, I tested the hypothesis (A1) that eleodids prefer shrub-dominated areas because of the thermoregulatory resources that shrubs provide. This hypothesis was addressed by comparing pitfall-trap captures among naturally shaded, artificially shaded, and unshaded traps. I then tested two pairs of alternative hypotheses regarding the relationship between predation risk, body size, and shrub cover. Although eleodids can produce unpalatable quinones when threatened with predation (Tschinkel 1975), they are sometimes preyed upon by birds and rodents (Wiens et al. 1974, Wiens and Rotenberry 1974, Stapp 1997b). If eleodids partition habitat according to risk of predation, then that partitioning may take one of two forms as related to body size:

- B1) Larger species, being more obvious to predators, should be more abundant in areas with greater shrub coverage because shrubs serve as refugia from predators; smaller eleodids, being less vulnerable to predation because of their more inconspicuous size, should be widespread. (Parmenter and MacMahon 1988)

- B2) Smaller species should be more abundant in areas with numerous refugia from predators (i.e., areas with finely textured soils with cracks that serve as refugia; such soils do not support high densities of shrubs); larger species, being less vulnerable to predation because of their size (being unmanageably large for a predatory rodent or bird), should be widespread. (Stapp 1997a, 1997b)

To test these hypotheses, I compared the presence and abundance of eleodids that differ in body size in areas differing in the amount of shrub cover.

Eleodid species exhibit different preferences in ambient temperatures in which they are active, perhaps reflecting species-specific differences in ability to conserve water (Kramm and Kramm 1972, Campbell and Smith 1975, Slobodchikoff 1983, Whicker 1983, Whicker and Tracy 1987, Parmenter et al. 1989c). I therefore examined two hypotheses of how eleodid richness and abundance might vary with temperature and precipitation:

- C1) If eleodids are heat-sensitive, they should vary negatively with temperature and positively with precipitation.
- C2) If eleodids are cold-sensitive, they should vary positively with temperature and negatively with precipitation.

Because the shortgrass prairie is in the cool-temperate zone, I assumed that temperature and precipitation should have a negative relationship with species richness and abundance.

Because shrubs can provide both cooler- and warmer-than-ambient microclimates at different times of day (Stapp 1997a), however, hypotheses B1 and B2 were modified to generate the following hypothesis, which was tested against the null hypothesis that eleodids are indifferent to temperature:

- D1) Eleodids in areas with lower shrub coverage should exhibit a greater number of strong correlations with weather variables than beetles in areas with greater shrub coverage.

Results from these tests are discussed with respect to interactions between darkling beetle presence and abundance, body size, and movement capacity and mobility, producing new insights into how spatio-temporal variations in eleodid community structure may be an expression of how different species interact with the same spatial structure in different ways.

METHODS

Study site

Research was conducted during May-August 1994-1997 at the 6280-ha Central Plains Experimental Range (CPER) on the Pawnee National Grassland, Colorado (Fig. 2.1). Characterized by gently rolling topography, the site possesses primarily sandy loam and loamy sand soils. Approximately 1630 m in elevation ASL, the area receives 322 mm average annual precipitation, primarily in the form of spring rains and summer convective thunderstorms. The climate is semi-arid, with mild summers and cold, dry winters. Perennial warm-season C₄ shortgrasses (primarily *Bouteloua gracilis* and *Buchloë dactyloides*) comprise most of the vegetative biomass (Lauenroth and Milchunas 1991). Forbs (particularly *Aster tanacetifolia*, *Astragalus* spp., *Gaura coccinea*, *Helianthus petiolaris*, *Leucocrinum montanum*, *Lomatium cous*, *Oenothera albicaulis*, *Oxytropis* spp., *Plantago patagonica*, *Sphaeralcea coccinea*, and *Thelesperma filifolium*) account for most of the vegetative diversity of the ecosystem. There are also low shrubs (primarily *Artemisia frigida*, *Atriplex canescens*, *Chrysothamnus nauseosus*, *Eriogonum effusum*, and *Gutierrezia sarothrae*), particularly in floodplains associated with ephemeral creek channels. Soapweed (*Yucca glauca*) is abundant on rocky hilltops. Prickly-pear cactus (*Opuntia polyacantha*) is found throughout the region and is especially abundant in upland areas with finely textured soils. There are also numerous small areas of bare ground and vegetative detritus. There is little free-standing permanent water, with the few stream channels present containing water only sporadically in most locations. The topography, soils, climate, and biota of the shortgrass prairie have been described in more detail by Lauenroth and Milchunas (1991).

Visually, the shortgrass prairie appears to be composed of two large-scale habitat types that extend for dozens of square kilometers: upland areas dominated by shortgrasses with few shrubs and lowland floodplains with numerous shrubs. To determine whether

this macrohabitat categorization was valid, six circular 638-m² sites were chosen for study (Table 2.1). Three of these sites were located in each of the two putative macrohabitat types (sites 1-3 of Table 2.1 in upland, sites 4-6 in floodplain). Within a macrohabitat, sites were separated by 1-3 km; a 4-km separation existed between sites differing in macrohabitat type. Vegetational composition (proportion of grass/forb, shrub, bare soil, cactus, and vegetative detritus) was measured at each site in July of each year by determining percent horizontal coverage along two randomly located 29.25-m line transects. A hierarchical cluster analysis (using average-neighbor distances and pooled covariance matrices) was then performed on the arcsine/square-root transformed percentages, with clustering distance correlations > 0.50 accepted as clusters. The cluster analysis provided a means of quantifying similarities and differences in the six sites rather than relying on subjective categorization (Johnson and Wichern 1992).

Assessing community richness

Darkling beetles were live-trapped in 480 pitfall traps in six 638-m² trapping webs of 80 unbaited traps each. One trapping web was situated in each of the six study locations. Each pitfall trap was a 500 ml Barber-style trap (Weeks and McIntyre 1997). Traps were spaced 1.5 m apart in 8 lines along the 8 primary cardinal directions to create 10 concentric rings of traps (McIntyre 1995). Traps were checked once daily for 7 consecutive days (6 nights) during the third week of each month from May through August 1994 - 1997 (46,080 total trap-nights). Changes in community composition with month and year were noted by assessing eleodid species richness each month from May through August of each year for each trapping web.

Weather data have been collected daily at the CPER since 1961, and the data from 1961-1990 have been compiled to give 29-year averages in precipitation and temperature (Internet URL: <http://lternet.edu/im/climate/climdes/sgs/sgsclim.htm>, http://sgs.cnr.colostate.edu/data/data_cat/climateindex.html). Weather data collected during

the weeks I trapped were compared to these 29-year averages (Table 2.2). A Spearman correlation was used to detect a significant relationship among species richness, daily minimum and maximum air temperatures, and daily amount of precipitation averaged over each trapping week. Correlations were also performed on temperature and precipitation data with 1-month and 1-year time lags to determine whether eleodids exhibit a delayed response to weather.

Monitoring population densities

Eleodes extricata and *E. hispilabris* individuals that were captured in the pitfall trapping array were marked on the elytra with colored enamel paint to distinguish recaptured individuals from new captures. These two species were chosen for population monitoring because they are among the most widespread and abundant eleodids at the CPER (Bell 1971, Whicker 1983). The computer package DISTANCE was used to estimate the population densities of these species (Buckland et al. 1993). DISTANCE uses distance-sampling theory, whereby the spacing between captures is used to derive significantly fitted models of detection probabilities to estimate population density (Wilson and Anderson 1985, Laake et al. 1994). Only new captures are used in fitting these models so as to minimize bias from "trap-happy" individuals. Although DISTANCE may not perform well for highly mobile organisms such as darkling beetles (Parmenter et al. 1989a), producing inflated density estimates, it has been used in a variety of field studies (Anderson et al. 1983, Parmenter et al. 1989a, McIntyre 1995) and performs well when capture rates are not extremely low (< 15 individuals). Low capture rates necessitate calculating density as number of animals trapped per area (which may give inflated density estimates; Anderson et al. 1983) or pooling data among dates or sites and calculating density for coarser spatio-temporal scales.

Numbers of *E. extricata* and *E. hispilabris* were tallied each month from May through August of each year for each trapping web. Preliminary analyses revealed that

capture rates were highly variable. Variation in capture rates can bias density estimations made with DISTANCE, but this can be corrected by pooling data across time (Buckland et al. 1993, Laake et al. 1994). Therefore, data were pooled across months and density calculated for each year for each trapping web; simple abundances of species are reported by month for descriptive purposes only (Appendix 2.2). Ninety-five percent confidence intervals (95% CI) were constructed around the mean estimated density of individuals per square meter. Densities in trapping webs where < 15 beetles were captured were estimated as number of beetles caught per trapping web area (638 m²) and have no confidence intervals associated with them. A Spearman correlation was used to detect significant relationships among beetle densities, daily minimum and maximum air temperatures, and daily amount of precipitation. Correlations were also performed on temperature and precipitation data with 1-month and 1-year time lags.

Multiscaled habitat analyses

Macrohabitat preferences of eleodids were assessed with analysis of variance (ANOVA), using clusters from the hierarchical cluster analysis based on vegetation as blocks of variance. Species richness and population density were compared among blocks. Significant factors in ANOVA models were then compared among blocks with Tukey's Studentized Range (HSD) test for post-hoc comparisons.

To assess the microhabitat preferences of eleodids, a 25-cm diameter circle centered around each pitfall trap was characterized by the following microhabitat types: grass, bare ground (unvegetated areas at least as large as the opening of a pitfall trap), cactus, vegetative detritus, and shrub. Each trap was then categorized as having caught either at least as many as or fewer than the average number of eleodid individuals (obtained by taking the total number of individuals captured in a trapping web during a given year and dividing by the 80 traps present in a web). Trap "success" was therefore a binary quantity comprised of two mutually exclusive categories. Representing trap success as a binary

quantity in this manner rather than as a continuous response variable circumvents the assumption that the data assume a Poisson distribution, which is not present in this case (mean and variance differed significantly, $\chi^2 = 960.65$, $P = 0.0001$). Binomial logistic regression was used to correlate a trap's success with the microhabitats surrounding it. Data were pooled by site and year; pooling is justified because calculating trap success in the manner described above accounts for any among-site and -year variation and allows for general trends to emerge. If eleodids are attracted to certain microhabitat types, then traps surrounded by those microhabitats should capture more beetles (as determined by a Wald χ^2 analysis; SAS Institute Inc. 1996).

Effects of shade on eleodid captures

One of the three shrub-floodplain sites (site 4 of Table 2.1) was selected at random for experimental manipulation of the effects of shade on eleodid captures. Each of the 80 pitfall traps present was classified as being naturally shaded by shrubs or unshaded (following the criterion of Rickhard and Haverfield 1965). A random subset of the unshaded traps was provided with artificial shade in the form of paper "parasols" (25-cm diameter circles supported atop 20-cm-high nails placed adjacent to a trap). To provide a balanced design, equal numbers of naturally shaded, artificially shaded, and unshaded traps were selected at random for analysis ($N = 26$ traps per three treatments). These traps were open for 6 consecutive days in July 1994, with eleodid captures in each trap type tallied each day. Average eleodid captures were then compared among trap type using a Kruskal-Wallis test.

RESULTS

General community patterns

Nine darkling beetle species were captured (Appendix 2.1). These species were readily distinguishable in the field (Bell 1971). The beetle community changed as much in

composition among months within a year as during the same month across years (Appendix 2.2). Analysis of variance revealed that there were significant differences in species richness among months within 1995 ($F = 6.03$, $df = 3$, $P = 0.0043$), although not within 1994, ($F = 2.43$, $df = 3$, $P = 0.0956$), 1996 ($F = 0.55$, $df = 3$, $P = 0.6571$), or 1997 ($F = 0.69$, $df = 3$, $P = 0.5709$). In 1995, the highest diversity of species was trapped in August; trapping in May, June, and July captured similar numbers of species ($HSD = 2.09$, $df = 20$, $P < 0.05$). Significantly more species were trapped in each of the six trapping sites in 1997 than in the other three years, which did not significantly differ from one another ($HSD = 1.99$, $df = 92$, $P < 0.05$).

For abundance (individuals within species; Appendix 2.2), significant differences among months were found in 1994 ($F = 13.96$, $df = 3$, $P = 0.0001$), 1995 ($F = 4.32$, $df = 3$, $P = 0.0167$), and 1997 ($F = 3.35$, $df = 3$, $P = 0.0395$). In 1994, the greatest number of eleodid individuals was trapped in May, with the remaining three months not significantly different from one another ($HSD = 3.96$, $df = 20$, $P < 0.05$). In 1995, the reverse was true, with significantly more individuals per species being captured in June, July, and August than in May ($HSD = 3.96$, $df = 20$, $P < 0.05$). In 1997, the most individuals were captured in July, the least in June ($HSD = 3.96$, $df = 20$, $P < 0.05$). Significantly more individuals for each of the nine species were trapped in 1994 than in the other years, and the least number of eleodids was captured in 1995 ($HSD = 1.99$, $df = 92$, $P < 0.05$).

Of the nine eleodids captured, most were found throughout the four-month trapping period (Appendix 2.2). Certain species, however, were more abundant early in the season (*E. extricata* and *E. fusiformis*), whereas others were more common in late summer (*E. longicollis* and *E. obsoleta*). *E. suturalis* and *E. tricostata* were most abundant in mid-summer (Figs. 2.2, 2.3).

Results from multiscaled habitat analyses

Cluster analysis quantitatively supported the visual separation of two macrohabitat types within the shortgrass prairie, based upon percent horizontal vegetation coverage (basal branching of sites 1-3: normalized root mean squared correlation = 0.61; basal branching of sites 4-6: normalized root mean squared correlation = 0.77). Three trapping webs were located within upland shortgrass areas (sites 1-3 of Table 2.1), which were characterized by extensive grass coverage, few shrubs, and moderate amounts of bare ground. The other three trapping areas were located within shrub floodplains (sites 4-6 of Table 2.1), which possessed higher amounts of shrubs, vegetative detritus, and bare ground but less extensive grass coverage. Significant correlates with eleodid species richness among the six trapping areas were macrohabitat type ($F = 203.86$, $df = 1$, $P = 0.0001$) as well as year ($F = 7.79$, $df = 3$, $P = 0.0020$) and month ($F = 5.34$, $df = 3$, $P = 0.0024$).

More eleodid species were trapped in the floodplains than in the uplands (Figs. 2.3, 2.4; $F = 203.86$, $df = 1$, $P = 0.0001$; HSD: 2.825, $df = 64$, $P < 0.05$). The densities of *E. extricata* and *E. hispilabris*, however, did not differ significantly between the two macrohabitats (Fig. 2.5; *E. extricata*: $F = 0.98$, $df = 7$, $P = 0.4778$; *E. hispilabris*: $F = 1.12$, $df = 7$, $P = 0.3972$) or among years (Fig. 2.5; *E. extricata*: $F = 1.78$, $df = 3$, $P = 0.1921$; *E. hispilabris*: $F = 1.17$, $df = 3$, $P = 0.3520$), probably because of the high variance associated with the density estimates.

Some significant microhabitat affinities were revealed. Traps located near cactus caught more eleodids than did traps where cactus was absent ($\chi^2 = 12.2047$, $P = 0.0005$). A similar relationship was noted for traps near shrubs ($\chi^2 = 11.8918$, $P = 0.0006$). Conversely, traps located near areas of bare ground caught fewer beetles ($\chi^2 = 5.3276$, $P = 0.0210$). No significant relationships were noted for the presence of grass or vegetative detritus.

Shade preferences

No significant differences were found in eleodid captures among naturally shaded, artificially shaded, and unshaded pitfall traps ($\chi^2 = 0.44015$, $df = 2$, $P = 0.8025$).

Shrub cover, predation risk, and body size

Although most species were widespread, certain species attained higher numbers in one or the other macrohabitat type (Appendix 2.2). The largest species (*E. hispilabris*, *E. longicollis*, *E. obscura*, and *E. suturalis*) were more abundant in the shrub floodplains (body size information from Whicker 1983 and Crist et al. 1992), and two of these species (*E. longicollis* and *E. opaca*) occurred only in the shrub-floodplain sites. The smallest species (*E. extricata*) was more common in the shortgrass uplands, but it overlaps considerably in size with other species (*E. fusiformis*, *E. opaca*, and *E. tricostata*) that were more abundant in the floodplain sites or were equally abundant in both macrohabitat types (*E. obsoleta*). Five eleodid species (*E. extricata*, *E. fusiformis*, *E. hispilabris*, *E. obscura*, and *E. obsoleta*) were found each month of each year in all of the six trapping areas.

Weather

Precipitation was highly variable in timing and amount during the 4-year study period (Table 2.2). While 1994 was drier than the 29-year average, 1995-1997 were wetter. There was also variation among the months within each year, with May receiving the most precipitation in most years (except 1997, when August received the most precipitation). The years of my study were also cooler than the 29-year average (Table 2.2). Although maximum daily air temperatures in 1994 and 1995 fell within the 29-year range, 1996 and 1997 were consistently cooler by 2-3°C. There was variation among months within each year, with July and August being the hottest months.

Some weather variables were significantly correlated with richness during some months and years in certain trapping sites. For example, precipitation levels were significantly negatively correlated with eleodid species richness at trapping sites 2 and 5 in

1995 ($r^2 = -0.97, P = 0.0003$; $r^2 = -0.99, P = 0.0001$). The number of species trapped at sites 1, 2, and 6 in 1995 were positively correlated with maximum air temperature ($r^2 = 0.96, P = 0.0005$; $r^2 = 0.97, P = 0.0003$; $r^2 = 0.97, P = 0.0003$) and negatively correlated with minimum air temperatures ($r^2 = -0.97, P = 0.0010$; $r^2 = -0.98, P = 0.0002$; $r^2 = -0.97, P = 0.0003$) and daily air temperatures ($r^2 = -0.99, P = 0.0001$; $r^2 = -0.97, P = 0.0003$; $r^2 = -0.97, P = 0.0003$).

There were also some significant effects on eleodid richness from weather conditions of the previous year or month, but these were mediated by site. Temperatures in 1994 were significantly correlated with richness at trapping site 1 in 1995, for example ($r^2 = 0.83, P = 0.0026$), and temperatures in the summer of 1995 significantly affected richness at site 4 in 1996 ($r^2 = 0.86, P = 0.0028$). Precipitation in 1996 negatively affected richness in site 5 in 1997 ($r^2 = -0.90, P = 0.0019$). Precipitation levels in May 1994 affected the number of eleodid species trapped at sites 2, 3, and 5 ($r^2 = -0.97, P = 0.0003$; $r^2 = -0.97, P = 0.0010$; $r^2 = -0.97, P = 0.0003$); and maximum air temperatures in June 1996 were negatively correlated with the number of species trapped at site 3 in July ($r^2 = -0.90, P = 0.0019$).

The density of *E. extricata* and *E. hispilabris* populations were affected by some weather variables. *E. extricata* densities were primarily affected by the weather conditions of the previous year, and this effect was mediated by site. For example, at trapping sites 1, 3, and 5, density was significantly correlated with daily mean temperature of the previous year ($r^2 = 0.99, P = 0.0001$ for all sites). At sites 2, 4, and 6, densities responded to precipitation levels and temperature maxima (for all cases, precipitation: $r^2 = -0.99, P = 0.0001$; maximum air temperature: $r^2 = -0.97, P = 0.0003$). *E. hispilabris* numbers were significantly correlated with weather variables of the current and previous years, depending on site. For instance, density was significantly correlated with the current year's minimum and daily mean air temperatures at site 1 (minimum air temperature: $r^2 = -0.90, P = 0.0031$; daily air temperature: $r^2 = 0.97, P = 0.0003$) and precipitation and maximum air

temperature at site 6 (precipitation: $r^2 = -0.99$, $P = 0.0001$; maximum air temperature: $r^2 = 0.99$, $P = 0.0001$). Densities at sites 3 and 4 were affected by both current (site 3, precipitation: $r^2 = -0.99$, $P = 0.0001$; site 4, maximum air temperature: $r^2 = -0.96$, $P = 0.0005$) and prior (site 3, minimum air temperature: $r^2 = -0.99$, $P = 0.0001$; site 4, precipitation: $r^2 = -0.99$, $P = 0.0001$) weather conditions.

DISCUSSION

A recap of the patterns observed

Eleodid community composition of the northern shortgrass prairie possessed as much variation among months within a year as among years. Some eleodid species experienced irregular increases and declines in abundance in response to weather (primarily precipitation and minimum air temperatures), although population densities of the two focal species remained relatively stable across years and sites.

Most of the nine eleodid species present at the CPER were widespread, occurring in both macrohabitat types (shortgrass uplands and shrub floodplains), although certain species were more abundant in one or the other macrohabitat (Figs. 2.2, 2.3). The four largest species (*E. hispilabris*, *E. longicollis*, *E. obscura*, and *E. suturalis*) were more abundant in the shrub floodplains. Most of the smaller species were more abundant in the floodplain sites (*E. fusiformis*, *E. opaca*, and *E. tricostata*), although one species (*E. obsoleta*) was equally abundant in both macrohabitat types. The smallest species (*E. extricata*) was more common in the shortgrass uplands. Beetles were captured more often in traps located near cactus and shrub microhabitats in both macrohabitats, and significantly lower capture rates were noted for traps associated with the presence of bare soil (see also Stapp 1997a).

Most of the eleodids were widespread over time, being present throughout most of the summer, although there was some phenological turnover in species abundance and

community composition (Figs. 2.2, 2.3). In addition, most species were present every year (Appendix 2.2), suggesting that I sampled the entire local eleodid species pool (see also Kumar et al. 1976).

Shrubs and shade

No significant shrub-shade effects (hypothesis A1) were found, probably because beetles were captured during a thermally favorable "window" of time (Whicker 1983), a daily period when beetles can be active (and, thus, pitfall trapped). During most of this window, beetles do not need to seek out thermoregulatory sites associated with shrubs. Therefore, it is not surprising that beetle captures were similar between shaded and unshaded traps. Parmenter and MacMahon (1984) reported similar negative results from a shrub-removal experiment, which suggests that shade is not an important resource provided by shrubs when eleodids are active (although it may be important during other portions of the day or at night; Stapp 1997a).

Shrubs, predation risk, and body size

Regarding the hypotheses about body-size differences in predation risk by macrohabitat/degree of shrub cover, my data do not completely support either alternative. With alternative B1, for example, although some of the smaller eleodid species were more abundant in upland sites (Appendix 2.2), others were more abundant in shrub floodplains with coarsely textured soils that do not provide refugia, and larger species were not widespread. With alternative B2, smaller species were not widespread, with some being more abundant in the uplands and others achieving higher numbers in the floodplains (Figs. 2.2, 2.3). In other words, neither explanation accounts for why there were fewer individuals of only some of the smaller eleodid species in the shrub floodplains and simultaneously why there were lower numbers of the larger species in the uplands. Given these results as well as the paucity of empirical data on differential rates of species-specific eleodid predation, these hypotheses of why eleodid communities are structured as they are

must be viewed with skepticism. Instead, eleodids may prefer areas with shrubs because of resources that shrubs provide or because of environmental (particularly edaphic) factors that are correlated with but independent of shrub presence (Parmenter and MacMahon 1984, Parmenter et al. 1989b, Stapp 1997a).

Shrubs and weather

Species-specific differences in physiological tolerance of weather variables may account for the phenological turnovers in species richness and abundance I observed each year (Whicker 1983, Whicker and Tracy 1987). However, physiological differences do not account for the high degree of overlap that I observed in community composition and population density among weather conditions and years (Appendix 2.2; Figs. 2.2, 2.3).

Instead, species-specific physiological differences may be compromised by habitat effects. For example, the avoidance of bare-soil microhabitats may reflect an avoidance of areas in which thermoregulation is difficult (cf. McIntyre in review) or where food resources are absent. In addition, insectivorous rodents create areas of bare soil during burrow excavations (Stapp 1997b), so eleodids may also be more exposed to predation in bare-ground areas and thereby avoid such areas. This microhabitat avoidance was not reflected in macrohabitat occupation, however, because the shrub-floodplain sites possessed more bare soil (Table 2.1). Different mechanisms of habitat selection may be operating at different scales, creating this apparent paradox of habitat preference. This topic will be explored further in Chapter III.

Hypothesis D1 received only partial support, suggesting that the eleodid community is somewhat insensitive to weather. Because darkling beetles are ectotherms, it comes as no surprise that they responded to some weather variables (see also Hinds and Rickard 1973) but is surprising that they did not respond more strongly and consistently to weather variables. This weak relationship may be artefactual, however, because the test of hypotheses C1 and C2 included a hidden bias. Pitfall trapping is influenced by both insect

abundance (with more abundant species exhibiting higher capture rates) and insect activity (with more mobile species being captured more often than sedentary species) (Southwood 1966). Eleodids are active only during a thermally favorable window of time each day (Whicker 1983). Beetles are pitfall trapped only when they are active, with the daily timing and duration of their activity window determined by the weather. Therefore, beetles may in fact respond strongly to temperature and precipitation, insofar as these variables affect when beetles can be active (and thus be pitfall-trapped), but not density or diversity.

An alternative explanation for the patterns observed

Various forms of habitat partitioning seem to offer only partial explanations for the spatio-temporal characteristics of the eleodid community of the shortgrass prairie. Can other mechanisms provide a more comprehensive explanation of the abundance and distribution of eleodids on the shortgrass prairie?

Because all of the eleodid species are highly vagile, they are presumably not excluded from one or another macrohabitat type because of an inability to reach it. The presence of at least a few individuals of nearly all species in both macrohabitat types indicates that this is true, and the macrohabitats themselves are interspersed throughout the shortgrass prairie, being separated by no more than a few kilometers. Because macrohabitats are defined by differences in vegetative structure (e.g. presence vs. absence of shrubs), differences in this structure may be driving the eleodid community patterns by acting as a filter to movement, the process by which animals achieve habitat selection. This idea was first hinted at by Roughgarden (1974) with respect to how different scales of environmental heterogeneity affect population dynamics by affecting dispersal distances, and was further modified by Wiens and Milne (1989), Crist et al. (1992), Crist and Wiens (1995), Keitt et al. (1997), and Wiens et al. (1997).

Different macrohabitats, by virtue of their differences in physiognomic structure, possess different "viscosities." Species that differ in their movement behaviors (*capacity*

and *mobility*, defined below) would therefore respond differently to different portions of a landscape (Roughgarden 1974, Rolstad 1991). Overall movement *capacity* (distance travelled in a given time period) is affected by body size, with larger species able to cover greater distances than smaller species (With 1994, Keitt et al. 1997). An animal's *mobility* (flexibility or ease of movement) is also affected by its body size because animals interact with environmental features according to the scale (*grain* and *extent*; Kotliar and Wiens 1990) of those features. *Grain* represents the finest resolution of scale (the finest details able to be perceived; details at a smaller scale than this grain are perceived as being homogeneous); *extent* represents the coarsest resolution (details at a larger scale are considered homogeneous). For example, large, mobile animals are able to disregard fine-grained features such as small variations in topography or vegetative physiognomy. Small species, on the other hand, are affected by these small features, which are (relative to themselves) not small at all. Large eleodids do indeed move over features that smaller eleodids circumambulate (Crist et al. 1992, NEM personal observation). Thus, large, mobile species perceive landscapes as more connected because they interact with spatial features at a broader (coarser) scale (Levins 1968, Kotliar and Wiens 1990). That is, if a structure is very large relative to the size of an animal, the structure in its entirety may be disregarded and interactions made only with its component parts (see Rolstad 1991 for treatment of a similar relationship between an animal's home range size and its perception of spatial heterogeneity).

To a large eleodid beetle, then, shortgrass poses no obstructions to movement; to a small beetle, however, shortgrass may represent a veritable thicket. Large beetles would be forced to interact with shrubs, however, but small beetles may be able simply to move through small gaps in the above-ground roots and leaf litter. Therefore, larger species should accumulate in areas with coarse physical structure (i.e., shrub macrohabitats), whereas smaller species should be found more often in areas with finer-textured vegetation

that is sufficiently large enough to detain them (i.e., shortgrass uplands). This scale-dependent mobility explains why there were more individuals of the large eleodid species in the shrub floodplains, why some small species were more abundant in the shrub floodplains than in the shortgrass uplands, and why the smallest species was most abundant in the uplands. Scale-dependent perceptions of heterogeneity also explain how an individualistic behavior such as movement can translate into population- and community-scale patterns (Crist and Wiens 1995). Scale-dependent effects of heterogeneity on habitat selection will be the focus of Chapter III, and testing how various aspects of spatial structure affect eleodid movements will be the focus of Chapters IV-VI.

The shortgrass prairie has an abundant, diverse, and understudied arthropod fauna. Its darkling beetle community possesses some spatio-temporal dynamics that resist straightforward explanations. Continued long-term monitoring of eleodids and weather in both shortgrass-upland and shrub-floodplain macrohabitat types may reveal how abiotic and environmental factors interact to influence darkling beetle community structure. Particular attention should be paid to how environmental heterogeneity may be perceived at different scales to create dynamic community patterns.

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LITERATURE CITED

- Abrams, P. 1980. Some comments on measuring niche overlap. *Ecology* 61:44-49.
- Allsopp, P.G. 1980. The biology of false wireworms and their adults (soil-inhabiting Tenebrionidae) (Coleoptera): A review. *Bulletin of Entomological Research* 70:343-379.
- Anderson, D.R., K.P. Burnham, G.C. White, and D.L. Otis. 1983. Density estimation of small-mammal populations using a trapping web and distance sampling methods. *Ecology* 64:647-680.
- Bell, R.T. 1971. Identifying Tenebrionidae (darkling beetles). U.S. International Biological Program Grasslands Biome Technical Report 58, Fort Collins, CO.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993. Distance sampling: Estimating abundance of biological populations. Chapman and Hall, London.
- Calkins, C.O., and V.M. Kirk. 1973. Temporal and spatial distribution of *Pasimachus elongatus* (Coleoptera: Carabidae), a predator of false wireworms. *Annals of the Entomological Society of America* 67:913-914.
- Calkins, C.O., and V.M. Kirk. 1975. Distribution of false wireworms (Coleoptera: Tenebrionidae) in relation to soil texture. *Environmental Entomology* 4:373-374.
- Campbell, G.D., and E.N. Smith. 1975. Temperature preferences of two species of *Eleodes* beetles (Tenebrionidae). *Pan-Pacific Entomologist* 51:327-329.
- Crist, T.O., D.S. Guertin, J.A. Wiens, and B.T. Milne. 1992. Animal movements in heterogeneous landscapes: An experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6:536-544.
- 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.
- Doyen, J.T., and W.F. Tschinkel. 1974. Population size, microgeographic distribution and habitat separation in some Tenebrionid beetles (Coleoptera). *Annals of the Entomological Society of America* 67:617-626.

- Hinds, W.T., and W.H. Rickard. 1973. Correlations between climatological fluctuations and a population of *Philolithus densicollis* (Horn) (Coleoptera: Tenebrionidae). *Journal of Animal Ecology* 42:341-351.
- Johnson, R.A., and D.W. Wichern. 1992. *Applied Multivariate Statistical Analysis*, 3rd ed. Prentice Hall, Englewood Cliffs, NJ.
- Keitt, T.H., D.L. Urban, and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* [online] 1:4. Internet URL: <http://www.consecol.org/vol1/iss1/art4>
- Kenagy, G.J., and R.D. Stevenson. 1982. Role of body temperature in the seasonality of daily activity in tenebrionid beetles of eastern Washington. *Ecology* 63:1491-1503.
- Knopf, F.L., and F.B. Samson. 1997. *Ecology and Conservation of Great Plains Vertebrates*. Springer, New York, NY.
- Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* 59:321-324.
- Kramm, R.A., and K.R. Kramm. 1972. Activities of certain species of *Eleodes* in relation to season, temperature, and time of day at Joshua Tree National Monument (Coleoptera: Tenebrionidae). *Southwestern Naturalist* 16:341-355.
- Krasnov, B., and G. Shenbrot. 1996. Spatial structure of community of darkling beetles (Coleoptera: Tenebrionidae) in the Negev Highlands, Israel. *Ecography* 19:139-152.
- Krasnov, B., and G. Shenbrot. 1997. Seasonal variation in spatial organization of a darkling beetle (Coleoptera: Tenebrionidae) community. *Environmental Entomology* 26:178-190.
- Kumar, R., R.J. Lavigne, J.E. Lloyd, and R.E. Pfadt. 1976. *Insects of the Central Plains Experimental Range, Pawnee National Grassland*. University of Wyoming Agricultural Experiment Station, Laramie, WY.
- Laake, J.L., S.T. Buckland, D.R. Anderson, and K.P. Burnham. 1994. *DISTANCE User's Guide V2.1*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.
- Lauenroth, W.K., and D.G. Milchunas. 1991. Short-grass steppe. Pp. 183-226 in: *Ecosystems of the World 8A: Natural Grasslands* (R.T. Coupland, ed.). Elsevier, Amsterdam.

- Levins, R. 1968. *Evolution in Changing Environments*. Princeton University Press, Princeton, NJ.
- Marino, P.C. 1986. Activity patterns and microhabitat selection in a desert tenebrionid beetle (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America* 79:468-471.
- McIntyre, N.E. In review. Use of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae) nest-sites by tenebrionid beetles (Coleoptera: Tenebrionidae) for oviposition and thermoregulation in a temperate grassland. *Southwestern Naturalist*.
- McIntyre, N.E. 1995. Methamidophos application effects on *Pasimachus elongatus* (Coleoptera: Carabidae): An update. *Environmental Entomology* 24:559-563.
- Parmenter, R.R., and J.A. MacMahon. 1984. Factors influencing the distribution and abundance of ground-dwelling beetles (Coleoptera) in a shrub-steppe ecosystem: The role of shrub architecture. *Pedobiologia* 26:21-34.
- Parmenter, R.R., and J.A. MacMahon. 1988. Factors limiting populations of arid-land darkling beetles (Coleoptera: Tenebrionidae): Predation by rodents. *Environmental Entomology* 17:280-286.
- Parmenter, R.R., J.A. MacMahon, and D.R. Anderson. 1989a. Animal density estimation using a trapping web design: Field validation experiments. *Ecology* 70:169-179.
- Parmenter, R.R., C.A. Parmenter, and C.D. Cheney. 1989b. Factors influencing microhabitat partitioning among coexisting species of arid-land darkling beetles (Tenebrionidae): Behavioral responses to vegetation architecture. *Southwestern Naturalist* 34:319-329.
- Parmenter, R.R., C.A. Parmenter, and C.D. Cheney. 1989c. Factors influencing microhabitat partitioning in arid-land darkling beetles (Tenebrionidae): Temperature and water conservation. *Journal of Arid Environments* 17:57-67.
- Richman, D.B., E.W. Huddleston, and M. Ortiz. 1982. Seasonal activity of tenebrionid beetles in New Mexico mesquite dunes. *Southwestern Naturalist* 27:305-308.
- Rickard, W.H. 1971. Observations on the distribution of *Eleodes hispilabris* (Say) (Coleoptera: Tenebrionidae) in relation to elevation and temperature in the Rattlesnake Hills. *American Midland Naturalist* 85:521-526.

- Rickhard, W.H., and L.E. Haverfield. 1965. A pitfall trapping survey of darkling beetles in desert steppe vegetation. *Ecology* 46:873-875.
- Rogers, L.E., N.E. Woodley, J.K. Sheldon, and P.A. Beedlow. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within in shrub-steppe ecosystem. *Annals of the Entomological Society of America* 81:782-791.
- Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: Conceptual issues and the evidence. *Biological Journal of the Linnean Society* 42:149-163.
- Roughgarden, J. 1974. Population dynamics in a spatially varying environment: How population size "tracks" spatial variation in carrying capacity. *American Naturalist* 108:649-664.
- SAS Institute Inc. 1996. SAS/STAT Software: Changes and Enhancements through Release 6.11. SAS Institute, Inc., Cary, NC.
- Sheldon, J.K., and L.E. Rogers. 1984. Seasonal and habitat distribution of tenebrionid beetles in shrub-steppe communities of the Hanford site in eastern Washington. *Environmental Entomology* 13:214-220.
- Slobodchikoff, C.N. 1978. Habitat use by mimetic coastal tenebrionid beetles. *American Midland Naturalist* 99:45-57.
- Slobodchikoff, C.N. 1983. Water balance and temperature preferences, and their role in regulating activity times of tenebrionid beetles. *Oikos* 40:113-119.
- Southwood, T.R.E. 1966. *Ecological Methods*. Methuen, London.
- Stapp, P. 1997a. Microhabitat use and community structure of darkling beetles (Coleoptera: Tenebrionidae) in shortgrass prairie: Effects of season, shrub cover and soil type. *American Midland Naturalist* 137:298-311.
- Stapp, P. 1997b. Small mammal predation on darkling beetles (Coleoptera: Tenebrionidae) in pitfall traps. *Southwestern Naturalist* 42:352-355.
- Tschinkel, W.R. 1975. A comparative study of the chemical defensive system of tenebrionid beetles: Chemistry of the secretions. *Journal of Insect Physiology* 21:753-783.

- Weeks, R.D., and N.E. McIntyre. 1997. A comparison of live versus kill pitfall trapping techniques using various killing agents. *Entomologia Experimentalis et Applicata* 82:267-273.
- Whicker, A.D. 1983. Spatial and temporal distributions of tenebrionid beetles, genus *Eleodes*, in a grassland community. Ph.D. Dissertation, Colorado State University, Fort Collins, CO.
- Whicker, A.D., and C.R. Tracy. 1987. Tenebrionid beetles in the shortgrass prairie: Daily and seasonal patterns of activity and temperature. *Ecological Entomology* 12:97-108.
- 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. 1997. Patchy landscapes and animal movements: Do beetles percolate? *Oikos* 78:257-264.
- Wiens, J.A., J.F. Ward, and J.T. Rotenberry. 1974. Dietary composition and relationships among breeding bird populations as US/IBP Grassland Biome sites, 1970. U.S. International Biological Program Grasslands Biome Technical Report 262, Fort Collins, CO.
- Wiens, J.A., J.F. Ward, and J.T. Rotenberry. 1979. Diet niche relationships among North American grassland and shrubsteppe birds. *Oecologia* 42:253-292.
- Wilson, K.R., and D.R. Anderson. 1985. Evaluation of a density estimator based on a trapping web and distance sampling theory. *Ecology* 66:1185-1194.
- Wise, D.H. 1981a. A removal experiment with darkling beetles: Lack of evidence for interspecific competition. *Ecology* 62:727-738.
- Wise, D.H. 1981b. Seasonal and yearly patterns in the densities of darkling beetles (Coleoptera: Tenebrionidae) in a montane community. *Environmental Entomology* 10:350-358.
- Wise, D.H. 1985. Negative correlation between numbers of a darkling beetle and a carabid predator. *Southwestern Naturalist* 30:148-150.
- With, K.A. 1994. Ontogenetic shifts in how grasshoppers interact with landscape structure: An analysis of movement patterns. *Functional Ecology* 8:477-485.

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

Table 2.1 Descriptions of the six trapping areas at the Central Plains Experimental Range. Percent horizontal vegetation cover was assessed from two replicate 29.25-m transects averaged over measurements taken each July, 1994 - 1997. Percentages may not sum to unity because of rounding error. Vegetation types: grass = grass and forb, litter = vegetative detritus, shrub = woody shrub, bare soil = unvegetated areas, cactus = *Opuntia polyacantha*.

Site	Elevation (m)	Primary soil type(s)	% grass	% litter	% shrub	% bare soil	% cactus
1	1636	Ulm Fine Sandy Loam	74.18	1.75	1.94	15.14	1.58
2	1642	Ulm Fine Sandy Loam	89.19	1.80	1.81	5.15	0.60
3	1651	Ulm Fine Sandy Loam, Ulm-Renohill Complex	96.04	0.09	0.83	1.11	0.57
4	1625	Remmit Loamy Sand	68.88	4.98	10.85	10.84	2.02
5	1628	Edgar Loam, Remmit Loamy Sand	54.75	8.84	21.42	11.81	1.03
6	1611	Edgar Loam, Olney Fine Sandy Loam	58.31	1.54	11.72	27.74	0.19

Table 2.2. Weather data from the Central Plains Experimental Region from 1994 - 1997, compared to historical data collected from 1961-1990. PPT = precipitation (mm), AIRMAX = maximum daily air temperature (°C), AIRMIN = minimum daily air temperature (°C), TEMP = average daily air temperature (°C). A dash (-) indicates no data.

Year	PPT	AIRMAX	AIRMIN	TEMP
Historic	282.7	17.28	1.13	9.27
1994				
Year	135.0	17.81	-0.45	8.63
May	11.8	28.96	7.88	19.19
June	0	31.38	10.36	21.31
July	0	34.05	11.01	22.85
August	1.0	32.15	14.76	22.66
1995				
Year	302.9	17.37	-0.97	7.66
May	4.31	13.69	-6.83	7.69
June	-	-	-	-
July	0	26.13	11.03	17.89
August	0	29.58	12.13	23.65
1996				
Year	423.4	16.89	-0.66	7.99
May	0.25	15.98	5.81	7.48
June	1.02	26.86	11.84	20.12
July	0.25	29.42	12.14	20.12
August	0	30.46	10.44	20.22
1997				
Year	408.8	15.36	-1.02	7.07
May	-	-	-	-
June	4.32	27.02	10.83	17.99
July	0	31.56	11.71	22.44
August	13.72	29.02	13.91	20.93

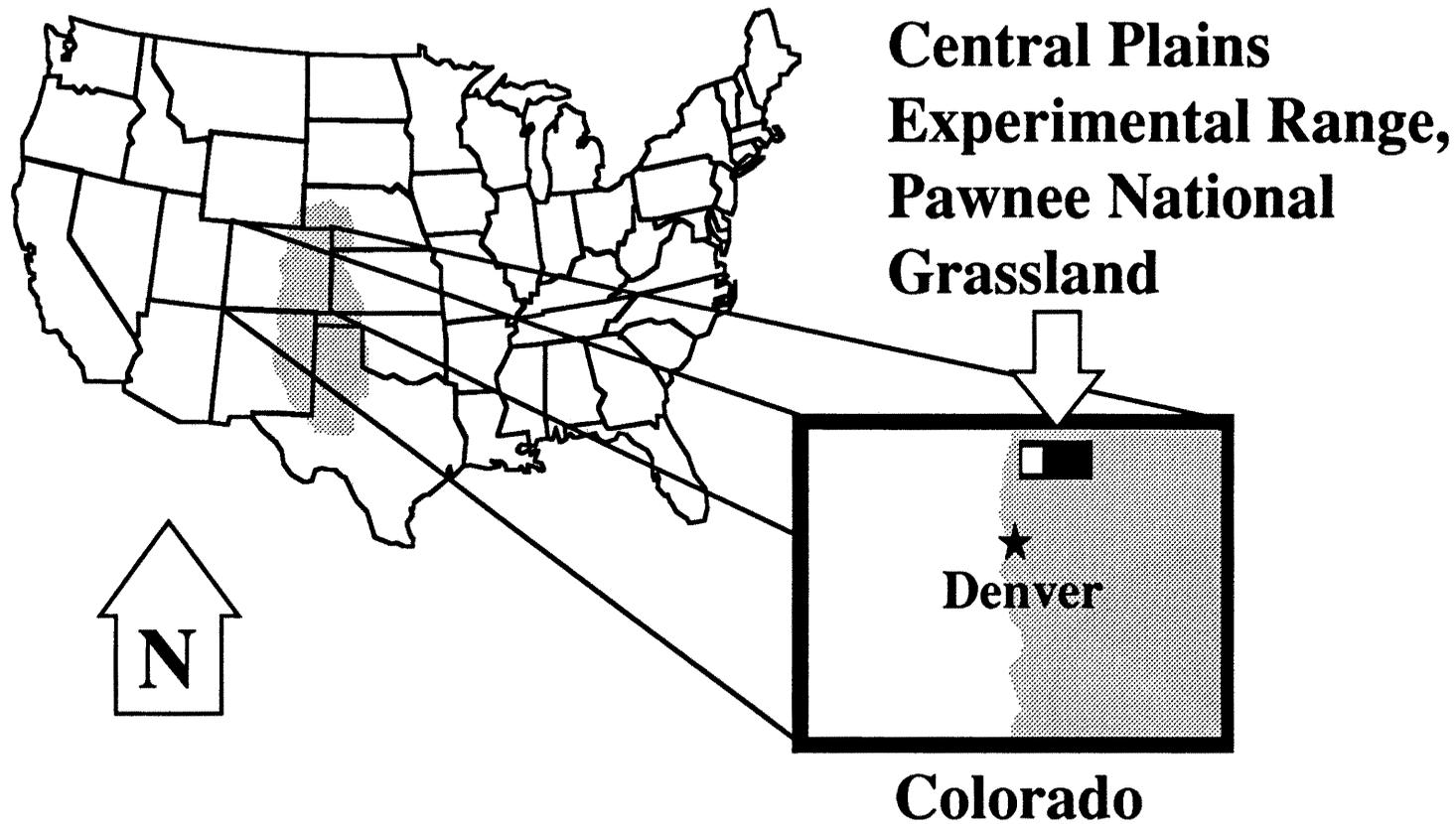


Fig. 2.1. Map of the extent of the shortgrass steppe (shaded area) within the United States (after Lauenroth and Milchunas 1991, Fig. 11.2). Inset: location of the study site within the state of Colorado. Study site represented as white rectangle on western edge of Pawnee National Grassland (black rectangle).

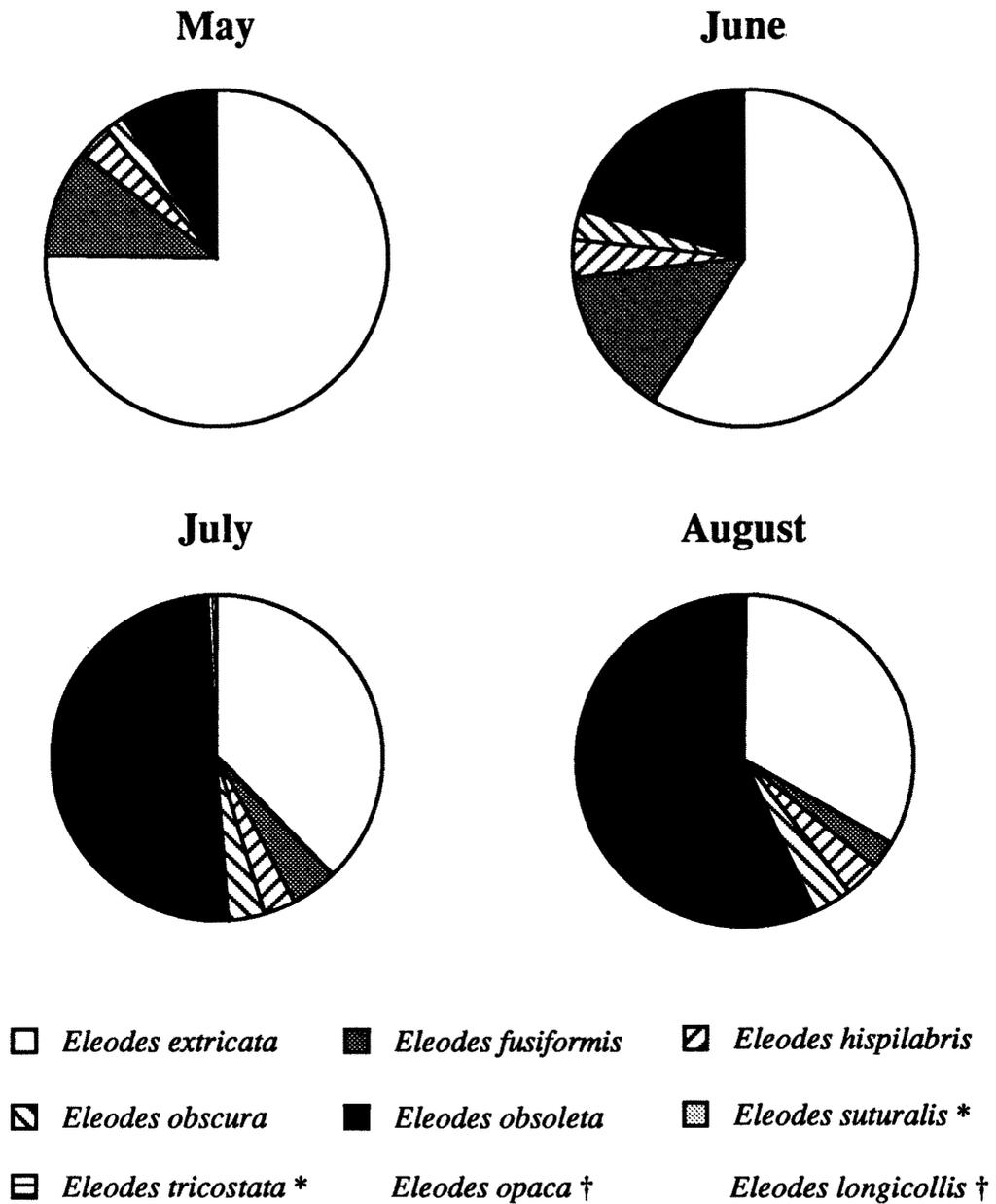


Fig. 2.2. Species composition (%) of pitfall-trap captures by month for shortgrass upland macrohabitat (sites 1-3, Table 2.1). Years (1994-1997) pooled. Species marked with an asterisk (*) comprised <1% of captures for all months. Species marked with a dagger (†) were not captured in any month.

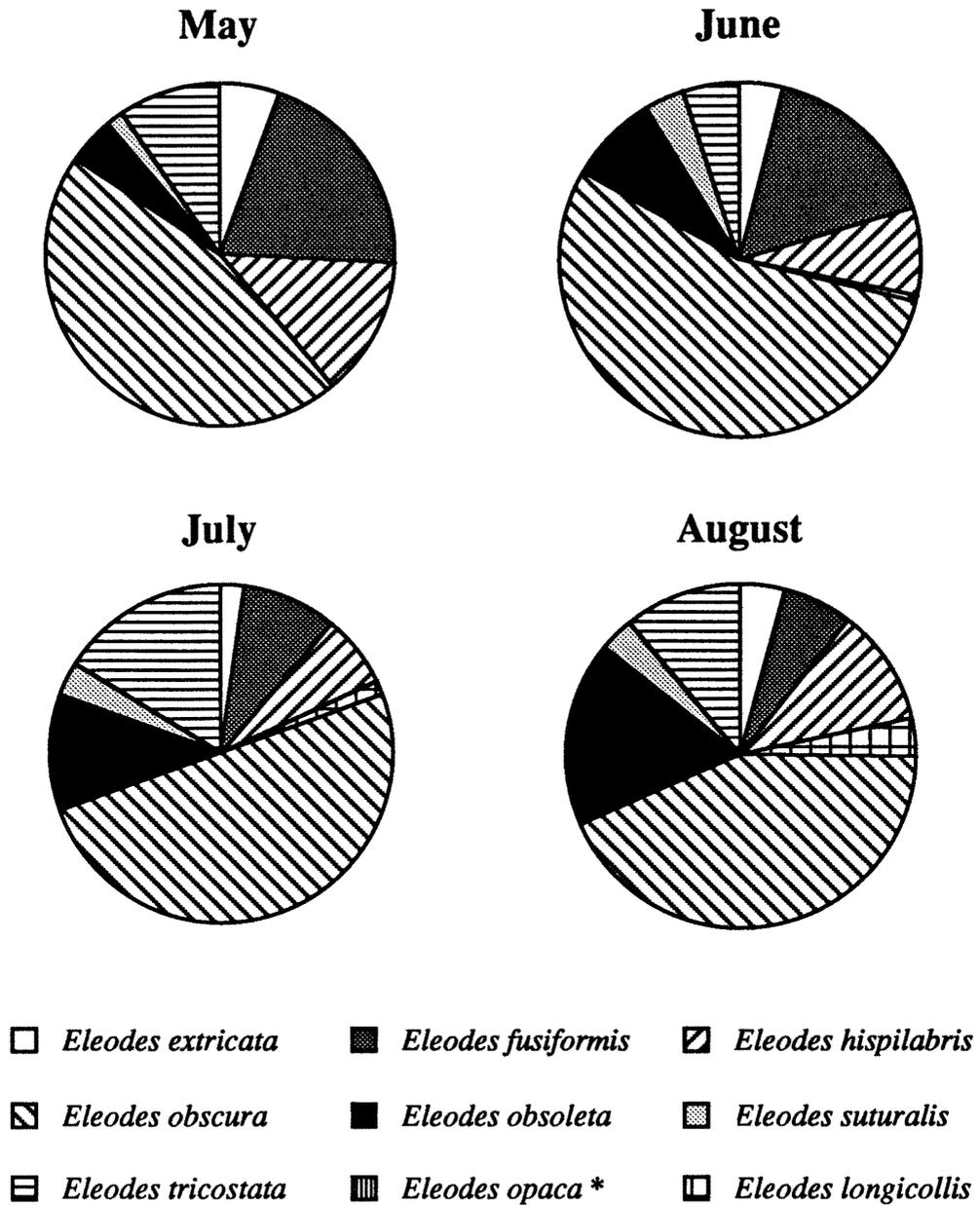


Fig. 2.3. Species composition (%) of pitfall-trap captures by month for shrub floodplain macrohabitat (sites 4-6, Table 2.1). Years (1994-1997) pooled. Species marked with an asterisk (*) comprised <1% of captures for all months.

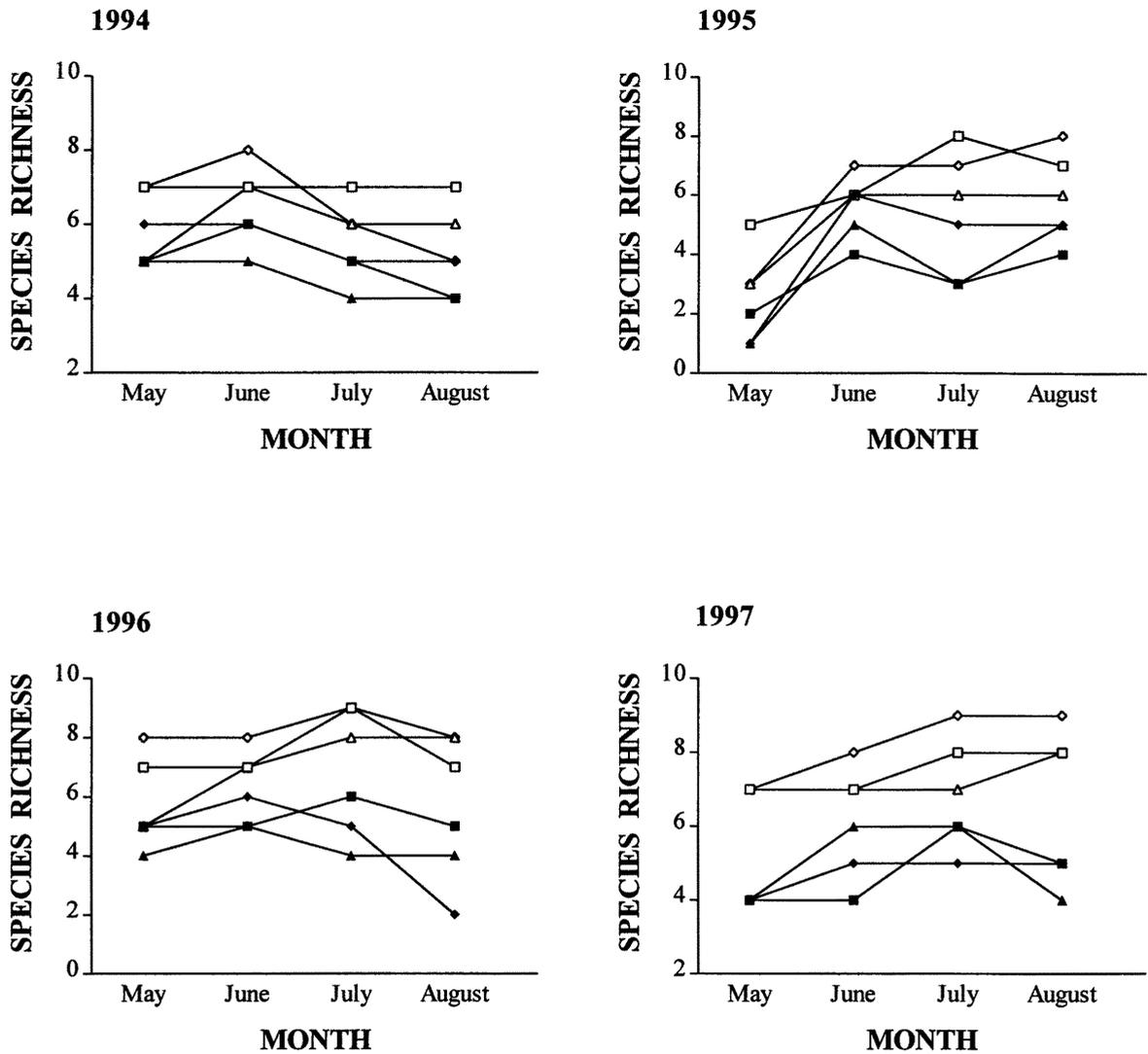


Fig. 2.4. Number of eleodid species captured by month at six sites at the Central Plains Experimental Range, Colorado, 1994-1997. Filled symbols represent shortgrass upland sites (sites 1-3 of Table 2.1) and open symbols represent shrub floodplain sites (sites 4-6 of Table 2.1).

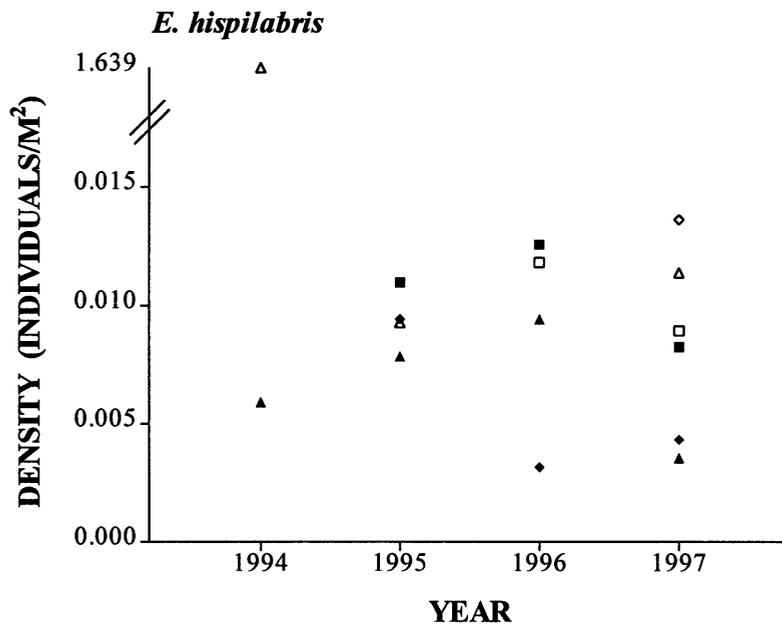
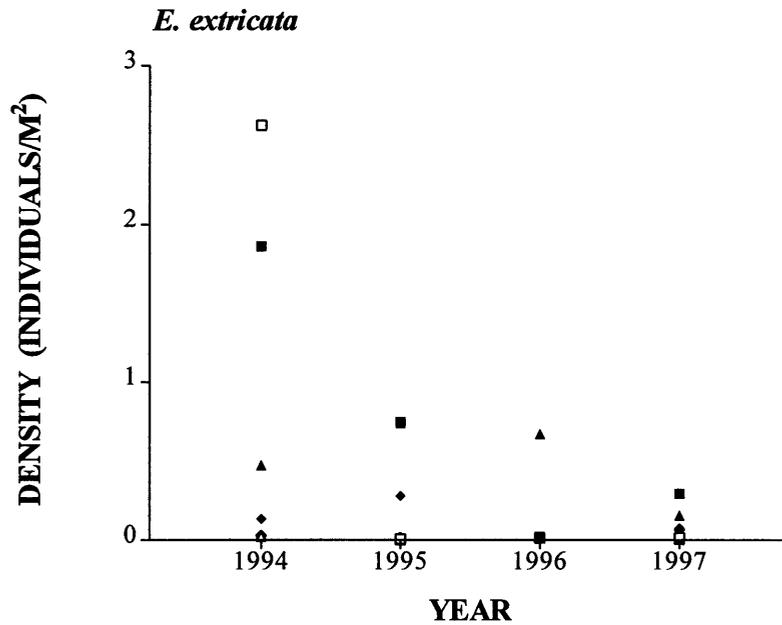


Fig. 2.5. Estimated population density for *E. extricata* (top) and *E. hispilabris* (bottom) at six sites at the Central Plains Experimental Range, Colorado, 1994-1997. Filled symbols represent shortgrass upland sites (sites 1-3 of Table 2.1), open symbols represent shrub floodplain sites (sites 4-6 of Table 2.1). Note differences in scale of Y-axes. Overlapping values are hidden. Confidence intervals are not shown for sake of clarity (site and year effects nonsignificant; see text for statistics).

Appendix 2.1. List of eleodid species captured at the Central Plains Experimental Range by year, 1994 - 1997, for two macrohabitat types (shortgrass upland and shrub floodplain). X denotes species was captured at least once in that broad habitat type that year.

	Shortgrass upland				Shrub floodplain			
	<u>1994</u>	<u>1995</u>	<u>1996</u>	<u>1997</u>	<u>1994</u>	<u>1995</u>	<u>1996</u>	<u>1997</u>
<i>Eleodes extricata</i> (Say)	X	X	X	X	X	X	X	X
<i>Eleodes fusiformis</i> LeConte	X	X	X	X	X	X	X	X
<i>Eleodes hispilabris</i> (Say)	X	X	X	X	X	X	X	X
<i>Eleodes longicollis</i> LeConte					X	X	X	X
<i>Eleodes obscura</i> (Say)	X	X	X	X	X	X	X	X
<i>Eleodes obsoleta</i> (Say)	X	X	X	X	X	X	X	X
<i>Eleodes opaca</i> LeConte						X	X	
<i>Eleodes suturalis</i> (Say)	X			X	X	X	X	X
<i>Eleodes tricostata</i> (Say)	X	X	X	X	X	X	X	X

Appendix 2.2. Number of eleodid species captured at six trapping areas at the Central Plains Experimental Range May-August 1994 - 1997. Trapping areas 1-3 are in shortgrass upland macrohabitats, areas 4-6 are in shrub floodplains. Species: EXTR=*E. extricata*, ELLO=*E. longicollis*, FUSI=*E. fusiformis*, HISP=*E. hispilabris*, OBSC=*E. obscura*, OBSO=*E. obsoleta*, ELOP=*E. opaca*, SUTU=*E. suturalis*, TRIC=*E. tricostrata*.

		Species								
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC
1994										
Trapping area 1										
37	May	135	0	35	9	2	12	0	0	0
	June	76	0	8	7	3	15	0	0	1
	July	25	0	0	6	5	11	0	1	0
	August	30	0	0	5	6	32	0	0	0
Trapping area 2										
	May	289	0	26	6	5	21	0	0	0
	June	143	0	13	4	2	29	0	0	0
	July	37	0	0	2	2	10	0	0	0
	August	64	0	0	6	8	16	0	0	0
Trapping area 3										
	May	68	0	33	2	1	32	0	0	1
	June	64	0	25	4	7	42	0	0	1
	July	36	0	4	5	3	47	0	0	0
	August	24	0	1	0	3	62	0	0	1

Appendix 2.2, continued

	Species								
	EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC
Trapping area 4									
May	23	0	86	37	169	20	0	14	3
June	13	0	23	17	109	11	0	12	10
July	6	0	3	10	64	12	0	2	4
August	5	0	2	33	78	26	0	10	3
Trapping area 5									
May	4	0	96	35	105	17	0	0	0
June	1	0	47	17	76	14	0	1	3
July	3	0	7	16	89	11	0	0	2
August	0	1	2	31	62	23	0	0	5
Trapping area 6									
May	24	0	55	21	131	8	0	4	29
June	9	2	30	13	65	5	0	3	14
July	3	0	2	9	18	0	0	2	2
August	2	5	0	0	10	2	0	0	7

Appendix 2.2, continued

		Species									
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC	
1995											
Trapping area 1											
39	May	8	0	0	1	0	0	0	0	0	
	June	39	0	0	4	1	10	0	0	0	
	July	16	0	0	0	2	6	0	0	0	
	August	24	0	0	2	3	33	0	0	0	
	Trapping area 2										
	May	9	0	0	0	0	0	0	0	0	
	June	101	0	1	2	2	17	0	0	0	
	July	22	0	0	0	8	13	0	0	0	
	August	50	0	4	2	4	51	0	0	0	
	Trapping area 3										
	May	0	0	0	0	0	1	0	0	0	
	June	7	0	6	1	1	12	0	0	1	
July	8	0	2	1	2	62	0	0	0		
August	17	0	4	4	1	113	0	0	0		

Appendix 2.2, continued

		Species								
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC
Trapping area 4										
	May	1	0	3	1	5	1	0	0	0
	June	0	0	9	13	187	14	0	14	7
	July	1	0	9	17	243	9	1	20	7
	August	3	0	9	10	166	10	0	5	11
Trapping area 5										
40	May	0	0	0	2	4	1	0	0	0
	June	0	0	11	10	90	11	0	2	0
	July	0	0	9	14	177	19	0	2	1
	August	1	0	10	15	103	23	0	0	1
Trapping area 6										
	May	1	0	0	2	2	0	0	0	0
	June	13	0	14	18	36	2	0	7	5
	July	1	0	4	10	56	7	0	10	6
	August	7	6	4	10	66	3	0	22	53

Appendix 2.2, continued

		Species								
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC
1996										
Trapping area 1										
	May	44	0	4	1	6	6	0	0	0
	June	22	0	9	2	3	12	0	0	0
	July	8	0	3	2	2	3	0	0	1
	August	9	0	1	3	4	40	0	0	0
Trapping area 2										
	May	29	0	2	0	4	2	0	0	0
	June	36	0	13	3	2	5	0	0	0
	July	20	0	7	4	0	17	0	0	0
	August	19	0	0	2	1	38	0	0	0
Trapping area 3										
	May	21	0	14	2	3	3	0	0	0
	June	7	0	28	1	3	6	0	0	1
	July	4	0	3	0	2	22	0	0	1
	August	2	0	0	0	0	101	0	0	0

Appendix 2.2., continued

		Species								
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC
Trapping area 4										
	May	5	0	13	6	85	6	0	5	3
	June	10	1	8	7	117	13	0	7	1
	July	10	2	20	20	167	19	1	5	35
	August	3	0	2	24	100	58	0	3	20
Trapping area 5										
42	May	0	0	19	8	27	5	0	0	2
	June	1	1	30	9	88	16	0	0	1
	July	4	3	23	17	88	35	0	2	5
	August	1	5	10	11	37	72	1	0	4
Trapping area 6										
	May	5	1	22	23	53	6	0	3	12
	June	14	6	19	16	58	9	0	11	21
	July	2	15	16	15	37	20	1	8	108
	August	11	33	5	33	58	29	0	6	45

Appendix 2.2, continued

		Species									
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC	
1997											
Trapping area 1											
43	May	135	0	0	8	1	8	0	0	0	
	June	21	0	6	3	0	14	0	0	0	
	July	59	0	4	2	2	51	0	1	0	
	August	31	0	3	1	3	13	0	0	0	
	Trapping area 2										
	May	90	0	1	4	0	8	0	0	0	
	June	21	0	1	1	2	9	0	0	1	
	July	82	0	5	2	3	116	0	0	1	
	August	25	0	3	2	0	6	0	0	0	
	Trapping area 3										
	May	22	0	2	4	0	7	0	0	0	
	June	15	0	22	1	2	15	0	0	0	
July	21	0	11	3	0	93	0	0	3		
August	11	0	9	3	1	22	0	0	0		

Appendix 2.2., continued

		Species								
		EXTR	ELLO	FUSI	HISP	OBSC	OBSO	ELOP	SUTU	TRIC
Trapping area 4										
	May	16	0	11	2	52	9	0	2	24
	June	8	0	22	6	98	34	0	5	16
	July	7	0	25	8	117	30	1	10	50
	August	12	0	21	18	86	20	1	6	27
Trapping area 5										
44	May	1	0	35	9	74	2	0	1	4
	June	2	0	77	7	39	15	0	1	6
	July	5	0	90	18	99	79	0	1	18
	August	4	0	43	10	33	47	4	2	5
Trapping area 6										
	May	20	0	23	90	116	5	0	4	90
	June	4	1	15	17	56	5	0	5	10
	July	13	13	13	20	100	33	6	24	167
	August	33	22	19	24	42	24	3	11	25

"The question is always asked by the curious travelers who have crossed the Plains at Interstate speeds, 'How can you live here without the mountains, the ocean, the woods?' But what they are really speaking to is their desire to 'get it' right away. The sublime of this place that we call the prairie is one of patience and looking. There is no quick fix...The coming to grips with the prairie...has to do with a long and expansive relationship...If one is to understand the beauty of this place, the old answers just won't do."

Keith Jacobshagen

"Personal Journal," *The Changing Prairie* (1995, A. Joern and K. Keeler, eds.)

Oxford University Press, Oxford

CHAPTER III

SCALE-DEPENDENT HABITAT SELECTION BY THE DARKLING BEETLE *ELEODES HISPILABRIS* (COLEOPTERA: TENEBRIONIDAE)

McIntyre, N.E. 1997. Scale-dependent habitat selection by the darkling beetle Eleodes hispilabris (Coleoptera: Tenebrionidae). American Midland Naturalist 138:230-235.

ABSTRACT

Habitat selection in the darkling beetle *Eleodes hispilabris* Say (Coleoptera: Tenebrionidae) on the shortgrass prairie of the central United States was non-random at both a broad (km²) and a fine (cm²) scale, relative to the abundance of broadly defined habitat types and, within these, microhabitats. On a broad habitat scale, darkling beetles were more numerous and had longer residency times (as assessed by recapture rates) in shrub floodplains than in shortgrass uplands. On a microhabitat scale, beetles used patches of vegetative detritus more and bare ground areas less than expected, based upon the abundances of these microhabitats. Broad-scale patterns of habitat selection may reflect microhabitat preferences, as shrub floodplains possessed relatively more vegetative detritus (a darkling beetle food source) than did shortgrass uplands. Such an ability to explain how a phenomenon at one scale affects a pattern at another scale will allow for patterns of habitat selection across multiple scales to be predicted.

Key words: Coleoptera, *Eleodes hispilabris*, habitat selection, scale, Tenebrionidae

INTRODUCTION

Habitat selection--the non-random use of habitats in relation to their availability--is a scale-dependent phenomenon. Animals may occupy broad-scale habitat types (such as "beech forest," "serpentine grassland," or "alpine meadow") based upon general feeding, reproductive, or other requirements, and then use only particular portions of that habitat (finer-scaled microhabitats) to fulfill those requirements. Although some researchers have acknowledged that there is a hierarchical "ordering" to habitat selection (as from geographic range down to microhabitat; Johnson, 1980), the mechanisms by which patterns of habitat occupation at one spatial scale are directly affected by habitat selection at another scale are poorly understood. Understanding the mechanisms behind habitat selection at multiple scales allows for more accurate predictions about animal occurrences and behaviors. To this end, I investigated habitat use by the darkling beetle *Eleodes hispilabris* (Coleoptera: Tenebrionidae) at two spatial scales (a broad habitat scale of square kilometers and a fine microhabitat scale of square centimeters) to determine whether habitat use by this species is nonrandom at multiple scales and, if so, what habitat preferences were exhibited.

Darkling beetles are among the most common macroinvertebrates in arid and semiarid ecosystems of North America (Crawford, 1981). As generalist detritivores, they feed primarily on vegetative matter from a variety of plant species (Yount, 1971; Rogers *et al.*, 1988). Being highly mobile, they wander freely over hundreds of meters (Parmenter *et al.*, 1989a; Johnson *et al.*, 1992; Wiens and Milne, 1989), thereby encountering a variety of habitats at both broad and fine spatial scales. Detection of nonrandom or preferential habitat use provides information about broad and fine habitat features that these beetles may deem important or favorable (e.g. feeding or oviposition areas, thermoregulatory sites, refugia from predators), contributing to a better understanding of the ecology of this species. In a more general sense, such a technique can be used to gather basic information about a variety of animal species and to determine empirically the effects of scale on biological patterns and processes.

METHODS

I studied habitat selection by *Eleodes hispilabris* from May through August 1994-1995 at the 6280-ha Central Plains Experimental Range (CPER), Colorado. As part of the shortgrass prairie ecosystem of the central United States, the CPER consists of two major habitat types that extend for thousands of square kilometers. Upland areas (composing approximately two-thirds of the CPER) are dominated by shortgrasses (approximately 90% grass cover, primarily consisting of *Bouteloua gracilis* and *Buchloë dactyloides*), occasionally interspersed with a few low shrubs (2%, primarily *Artemisia frigida* and *Eriogonum effusum*), whereas in adjacent lowland floodplains associated with the ephemeral channels of Owl Creek, this habitat matrix (56% grass) is interspersed with numerous low and larger shrubs (18%, primarily *A. frigida*, *Atriplex canescens*, *Chrysothamnus nauseosus*, *E. effusum* and *Gutierrezia sarothrae*). Upland areas average 1642 m in elevation and are primarily composed of sandy loam soils, whereas the floodplain sites average 1621 m in elevation and consist of sands and loamy sands. On a finer scale (< 1m²), both of these broad habitat types contain microhabitats of bare ground, *Opuntia polyacantha* cactus clumps and vegetative detritus ("litter").

Eleodes hispilabris darkling beetles were chosen for study because of their abundance at the CPER and because they occur in both of the broad habitat types (Whicker and Tracy, 1987; Crist *et al.*, 1992). Averaging 418.9±105.8 mg in live mass (N = 15, Crist *et al.*, 1992) and 16.1±2.2 mm in length (N = 15, this study), *E. hispilabris* is one of the largest of the ~100 North American *Eleodes* species (Whicker and Tracy, 1987). It is a diurnal, flightless beetle that may live two years as an adult (Allsopp, 1980). This species occurs in grasslands of the western United States (Whicker and Tracy, 1987). Individuals possess no true home range and may range over several dozen meters in a day (Kramm and Kramm, 1972; Calkins and Kirk, 1973; Doyen and Tschinkel, 1974). Adults are detritivorous, feeding primarily on dead grass and forbs (Yount, 1971; Rogers *et al.*,

1988). More detailed information on darkling beetle natural history may be found in Allsopp (1980), Whicker and Tracy (1987) and Rogers *et al.* (1988). Habitat affiliations in this genus has been researched by Doyen and Tschinkel (1974), Parmenter and MacMahon (1984), Sheldon and Rogers (1984) and Parmenter *et al.* (1989b).

To assess broad-scale differences in habitat selection by *E. hispilabris*, individuals were trapped in 480 live pitfall traps arrayed in six 638-m² trapping webs of 80 unbaited traps each (spaced 1.5 m apart in ten concentric rings, following the design of McIntyre [1995]), with three trapping webs in each of the two broad habitat types (shortgrass upland, shrub floodplain). Beetles were marked on the elytra with a dot of colored enamel paint to distinguish recaptured individuals from new captures, as adult darkling beetles can live for over a year (Allsopp, 1980). Trapping was conducted for 6 consecutive days during the third week of each month from May through August 1994 and 1995, during which traps were checked once daily (23,040 total trap-days). Recapture percentages (defined as number of recaptures divided by total number of beetles captured) in each of the two broad habitats were then compared to assess in which habitat beetles spent more time (with larger recapture rates indicating longer residency).

To assess fine-scale, microhabitat selection by *E. hispilabris*, 32 individuals (16 per broad habitat type) were followed for 30 min each and their locations marked at 15-s intervals, following the protocol of Wiens and Milne (1989). Beetles were followed during the third week of each month from May through August 1994-1995 (two beetles per month per year) when unshaded air temperatures 1 cm above the soil (beetle height) lay between 16-30 C (mean = 21.5 C), corresponding to temperatures when darkling beetles are normally active (Whicker and Tracy, 1987). Observations were made simultaneously by two observers between 0700-1100 MDT. The microhabitat type (grass, litter, bare ground, cactus, shrub or other items [i.e., cattle fecal pats]) was determined at each of the 15-s locations. The proportions of each of these microhabitat types used was compared to the proportion of each type available, which was assessed by determining the microhabitat type

at 300 randomly selected points (75 per broad habitat type per year). The microhabitat type was recorded at 75 points in a 5 x 5 m quadrat (with the 75 points randomly selected from 441 possible points, sited at 0.25-m intervals) in each broad habitat type. A chi-square goodness-of-fit test was used to detect significant differences in microhabitat use versus microhabitat availability, following Cochran's (1954) conservative standards of discarding analyses in which more than 20% of the microhabitat types contained fewer than 5 observations. For those microhabitat categories that did not meet Cochran's standards, no statistics could be calculated and the values are reported for descriptive purposes only. For significant differences in microhabitat use versus availability, a Bonferroni z statistic was used to calculate 95% confidence intervals to indicate microhabitats used more or less often than expected at random (Neu *et al.*, 1974; Sparks *et al.*, 1994). This technique has performed well in analyses of habitat selection with a large (≥ 20) number of observations and relatively fewer habitats available (Alldredge and Ratti, 1986, 1992).

RESULTS

A total of 524 darkling beetles were captured over the two-year period (139 in 1994, 385 in 1995). Recapture data from both years were pooled, as analysis of variance revealed no significant differences in the percentage of beetles recaptured by year ($F = 1.00$, $df = 1$, $P = 0.500$) or with trapping web within habitat by year ($F = 3.60$, $df = 1$, $P = 0.087$). Recapture rates did differ by broad habitat type ($F = 312.11$, $df = 1$, $P = 0.036$). On this scale, *E. hispilabris* had a longer residency time in shrub-dominated lowland floodplains than in shortgrass upland areas because not only were more beetles were captured in floodplains (437) than in uplands (87), there were relatively more recaptures in floodplains (26.09%) than in uplands (9.20%).

On a fine scale, because there were no significant differences between the two years in the proportions of microhabitats used for either broad habitat type (shortgrass uplands:

$F = 3.22$, $df = 1$, $P = 0.106$; lowland floodplains: $F = 3.98$, $df = 1$, $P = 0.068$), data from both years were pooled for analysis. *E. hispilabris* non-randomly selected (use > availability, *sensu* Ben-David *et al.*, 1996) certain microhabitats ($\chi^2 = 29.031$, $df = 6$, $P = 0.001$). In shortgrass upland areas, *E. hispilabris* used grass patches less often than expected ($\chi^2 = 13.656$, $df = 2$, $P = 0.001$), instead preferring areas of litter, a relatively rare microhabitat type (Fig. 3.1a). Bare ground areas and the relatively few areas of more complex structure (e.g. shrub and cactus patches) present in this habitat were used in proportion to their occurrence. In shrub floodplains, beetles again avoided grass clumps and preferentially used areas of litter ($\chi^2 = 18.538$, $df = 4$, $P = 0.001$; Fig. 3.1b). Bare ground areas were more common in this broad habitat type and used less often than expected from their abundance. Other microhabitats (shrubs, cactus, cattle fecal pats) were relatively uncommon and used infrequently.

DISCUSSION

Eleodes hispilabris of the Colorado shortgrass prairie ecosystem differed in habitat selection with spatial scale. They occurred more often in shrub-dominated lowland floodplains than in shortgrass uplands, as shown by higher capture and recapture rates in the floodplain sites. The coarsely textured soils and complex vegetational structure of floodplains may provide refugia from predators such as rodents or thermoregulatory or oviposition opportunities that the more compact soils and structurally more simple vegetation of the uplands do not (Parmenter and MacMahon, 1984; Parmenter *et al.*, 1989b), resulting in this pattern of habitat selection. This broad-scale pattern of habitat selection reflects microhabitat preferences, as shrub floodplains possessed relatively more vegetative detritus (a darkling beetle food source; Yount, 1971; Rogers *et al.*, 1988; Fig. 3.1), possibly because shrubs produce as well as accumulate wind-blown vegetative detritus. When coupled with the occurrence of the more complex vegetative structure of

shrub floodplains, the presence of vegetative detritus is a good indicator of the presence of *E. hispilabris*.

Knowledge about the microhabitats that beetles use thus allows for larger-scaled predictions about patterns of *E. hispilabris* habitat selection to be made. Although constrained by the darkling beetles' physiological requirements (i.e., within the beetles' geographic range), locations that accumulate more vegetative detritus are predicted to support more beetles, because beetles were followed during temperatures associated with activity for these species (Whicker and Tracy, 1987). However, other microhabitats may be important during colder or warmer periods, making such translations across scales indefinite (Crist *et al.*, 1992). More research on this possibility is warranted.

Beyond the knowledge gained about *E. hispilabris* habitat preferences, these results demonstrate in a more general sense how individual behaviors (like microhabitat preferences) may collectively define population parameters (such as density). Determination of habitat preference is thus of fundamental importance in understanding the basic ecology and life history of any animal species (Johnson, 1980; Thomas and Taylor, 1990; Arthur *et al.*, 1996). The determination of such a preference, however, is scale-dependent. Thus, one must consider both macro- and microhabitat components when trying to assess habitat selection, as habitat use and availability are affected by the scale perceived by the animal. Even the concept itself is scale-dependent, as habitat selection may be a pattern or a process depending on the temporal scale at which it is considered. Emphasis on the importance of scale-dependent effects on biological processes has only recently come about (Wiens, 1989; Wiens and Milne, 1989; Kotliar and Wiens, 1990; Crist and Wiens, 1994; Li and Reynolds, 1995). Future analyses of habitat selection should incorporate this effect if they are to be realistic.

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LITERATURE CITED

- Allredge, J.R., and J.T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 50:157-165.
- Allredge, J.R., and J.T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 56:1-9.
- Allsopp, P.G. 1980. The biology of false wireworms and their adults (soil-inhabiting Tenebrionidae) (Coleoptera): A review. *Bulletin of Entomological Research* 70:343-379.
- Arthur, S.M., B.F. J. Manly, L.L. McDonald, and G.W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* 77:215-227.
- Ben-David, M., R.T. Bowyer, and J.B. Faro. 1996. Niche separation by mink and river otters: Coexistence in a marine environment. *Oikos* 75:41-48.
- Calkins, C.O., and V.M. Kirk. 1973. Distribution and movement of adult false wireworms in a wheat field. *Annals of the Entomological Society of America* 66:527-532.
- Cochran, W.G. 1954. Some methods for strengthening the common χ^2 test. *Biometrics* 10:417-451.
- Crawford, C.S. 1981. *Biology of desert invertebrates*. Springer-Verlag, New York, NY.

- 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* 6:536-544.
- Crist, T.O., and J. A. Wiens. 1994. Scale effects of vegetation on forager movements and seed harvesting by ants. *Oikos* 69:37-46.
- Doyen J. T., and W.F. Tschinkel. 1974. Population size, microgeographic distribution and habitat separation in some Tenebrionid beetles (Coleoptera). *Annals of the Entomological Society of America* 67:617-626.
- Johnson, A.R., B.T. Milne, and J.A. Wiens. 1992. Diffusion in fractal landscapes: Simulations and experimental studies of tenebrionid beetle movements. *Ecology* 73:1968-1983.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- 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.
- Kramm, R.A., and K.P. Kramm. 1972. Activities of certain species of *Eleodes* in relation to season, temperature, and time of day and Joshua Tree National Monument (Coleoptera: Tenebrionidae). *Southwestern Naturalist* 16:341-355.
- Li, H., and J.F. Reynolds. 1995. On definition and quantification of heterogeneity. *Oikos* 73:280-284.
- McIntyre, N.E. 1995. Methamidophos application effects on *Pasimachus elongatus* (Coleoptera: Carabidae): An update. *Environmental Entomology* 24:559-563.
- Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541-545.
- Parmenter, R.R., and J.A. MacMahon. 1984. Factors influencing the distribution and abundance of ground-dwelling beetles (Coleoptera) in a shrub-steppe ecosystem: The role of shrub architecture. *Pedobiologia* 26:21-34.
- Parmenter, R.R., J.A. MacMahon, and D.R. Anderson. 1989a. Animal density estimation using a trapping web design: Field validation experiments. *Ecology* 70:169-179.

- Parmenter, R.R., C. A. Parmenter, and C.D. Cheney. 1989b. Factors in microhabitat partitioning in arid-land darkling beetles (Tenebrionidae): Temperature and water conservation. *Journal of Arid Environments* 17:57-67.
- Rogers, L.E., N.E. Woodley, J.K. Sheldon, and P.A. Beedlow. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within a shrub-steppe ecosystem. *Annals of the Entomological Society America* 81:782-791.
- Sheldon, J.K., and L.E. Rogers. 1984. Seasonal and habitat distribution of tenebrionid beetles in shrub-steppe communities of the Hanford site in eastern Washington. *Environmental Entomology* 13:214-220.
- Sparks, E.J., J.R. Belthoff, and G. Ritchison. 1994. Habitat use by Eastern Screech-Owls in central Kentucky. *Journal Field Ornithology* 65:83-95.
- Thomas, D.L., and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322-330.
- Whicker, A.D., and C.R. Tracy. 1987. Tenebrionid beetles in the shortgrass prairie: Daily and seasonal patterns of activity and temperature. *Ecological Entomology* 12:97-108.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, J.A., and B.T. Milne. 1989. Scaling at 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* 3:87-96.
- Yount, V.A. 1971. Diets of selected insects in a grassland ecosystem. M.S. Thesis, Colorado State University, Fort Collins, CO.

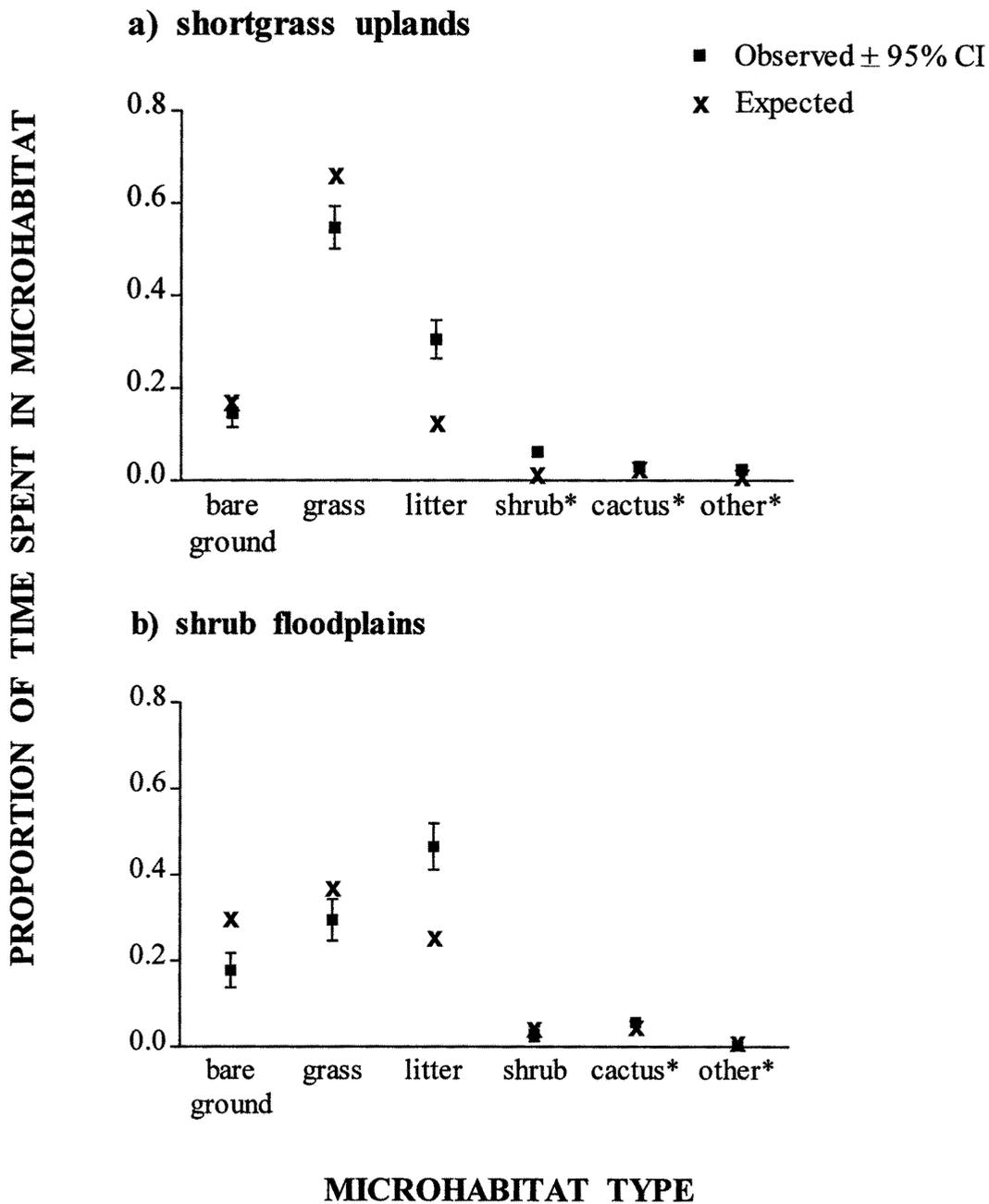


Fig. 3.1. Expected and observed proportions of time (with 95% confidence intervals) spent by darkling beetles in different microhabitat types for two broad habitats (Fig. 3.1a: shortgrass uplands, Fig. 3.1b: shrub floodplains). Microhabitat types denoted with * do not conform to Cochran's (1954) chi-square criteria (see text) and have no confidence intervals associated with them.

"There is no describing [the grasslands]...They inspire feelings so unique, so distinct from anything else, so powerful, yet vague and indefinite, as to defy description, while they invite the attempt."

John Van Tramp

Prairie and Rocky Mountain Adventures (1860; 1869 ed.)

Segner and Condit, Columbus, OH

CHAPTER IV

INTERACTIONS BETWEEN LANDSCAPE STRUCTURE AND ANIMAL BEHAVIOUR: 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 behaviours 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-m² 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. The interaction between landscape structure and an organism's internal state therefore contributes to environment-specific movement patterns.

Key words: Movement, resource distribution, food deprivation, landscape ecology

INTRODUCTION

Theory (De Roos et al. 1991, Wiens et al. 1993b), models (Turchin 1991, Gustafson and Gardner 1996), and empirical observations (Kareiva 1985, Crist et al. 1992) 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). 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 these movement-landscape relationships by permitting testing of hypotheses about the ecological consequences of landscape structure at tractable scales with empirical rigour (Ims et al. 1993, Wiens et al. 1993b, Wiens et al. 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 EMS 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, 1996b). 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, McIntyre and Wiens in review). 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).

Such studies have focused on how the fine-scale movement patterns of individuals reflect the spatial properties of mosaics, but they have not explored the factors that may explain why individuals move in particular ways. One obvious factor is food. The distribution of food resources should be expected to influence movements (Arditi and Dacorogna 1988, Bernstein et al. 1988), and we might therefore expect a hungry animal to respond differently to food distributions than a satiated one (Bell 1991). 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. On the basis of patch-foraging theory (Hassell and Southwood 1978; Bell 1990, 1991; Kareiva 1985; Fromm and Bell 1987) and observations of area-restricted search (Tinbergen et al. 1967), we predicted that: 1) movements by foraging animals in areas with aggregated food resources would be less linear than in areas where food resources are randomly or uniformly dispersed, where distances between food patches would be smaller; and 2) these effects would be more pronounced in food-deprived than in fed individuals, whose motivation to find food would be less intense. Since 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 satiated individuals because of more intense searching behaviour. 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. Darkling 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, and diurnal. They are generalist detritivores, feeding primarily on plant matter (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, Wiens et al. 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, USA. All vegetation in an enclosed 5 x 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). 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.

Resource distributions

In the shortgrass steppe, darkling beetles forage in a heterogeneous mosaic consisting primarily of grass and bare ground areas (created by erosion, cultivation,

harvester ants [*Pogonomyrmex occidentalis*], rodents such as prairie dogs [*Cynomys ludovicianus*], and wallowing cattle [*Bos taurus*] or bison [*Bison bison*] (Crist et al. 1992). 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 six replicate 5.1-m line transects spaced 0.5 km apart in the area surrounding our experimental sandbox arena. Vegetation was categorized as potential darkling beetle food (grass or forb) versus non-food (bare ground, cactus, or shrub) (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"; Fig. 4.1) 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, 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 colour 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 piles, two of which consisted of 50 g each and the other two of 350 g each. Pile locations were determined by gridding the arena into 1 x 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 in four 200-g piles that were clustered into groups of two. In addition, a control was

used in which no food was present in the enclosure. All piles covered the same surface area (a 7-cm-diameter circle), varying only in volume (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 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. The total surface area of the sandbox arena covered by food was identical between the random and clumped treatments (4 piles $\times \pi r^2 = 616 \text{ cm}^2$) but less than that of the uniform treatment (16 piles $\times \pi r^2 = 2464 \text{ cm}^2$). Consequently, we may predict 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 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.

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 x 25 x 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 behaviour (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 when unshaded soil temperatures were 16-30°C (0700-1100 MDT), a range that is inclusive of temperatures and times when the beetles are normally active (Whicker and Tracy 1987). 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 naive about the experimental surroundings. Therefore, we did not familiarize the beetles with the experimental arena, and each individual was tested only once. The movement pathways of food-deprived and fed beetles were compared in each of the four experimental conditions (random, uniform, clumped, and control). We measured seven pathways per hunger treatment per resource distribution ($N = 56$ paths; 16 paths in 1995, 40 in 1996). For each pathway, we calculated: (1) total path length; (2) net linear displacement; (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. The fractal dimension theoretically ranges from 1 to 2, with values near 1 indicating a linear, directional path and values near 2 denoting a random path (Hastings and Sugihara 1993). We also recorded whether a beetle contacted and ate from a food pile; the frequency of contacting a food pile as affected by treatment was assessed with Yates' continuity-corrected chi-square test (Sokal and Rohlf 1981). Fisher's Protected Least Significant Difference (LSD) test (Sokal and Rohlf 1981) was performed to detect statistically significant differences in movement path characteristics with level of food deprivation and with food distribution.

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 ($s^2 = 19.78$, $x = 15.00$; $\chi^2 = 6.60$, $df = 5$, $P = 0.25$). 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 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 (Fig. 4.2a). As a consequence, food-deprived beetles covered a smaller overall area in a given time period (smaller net displacement, Fig. 4.2b). Again, this difference was consistent across all of the food-dispersion treatments.

Experimental resource distributions

The level of food deprivation and the distribution of food patches affected both the total distance moved by beetles and the tortuosity (fractal dimension) of their pathways. In treatments with randomly distributed food patches, food-deprived beetles exhibited the greatest overall path length and the highest fractal dimensions (Fig. 4.2c, 4.2d). In contrast, hungry beetles had significantly shorter overall path lengths (but not fractal dimensions) in treatments with clumped and with uniformly distributed resources (Fig. 4.2c, 4.2d). 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 (Fig. 4.2d) for pathways of all beetles in all treatments was < 1.50 (the midpoint value of

the two-dimensional fractal value range), indicating that beetle movements were not simply random walks.

DISCUSSION

In our experiments, both food deprivation and landscape structure (in the form of food distribution) affected darkling beetle movements. Food-deprived beetles moved more slowly and over shorter overall distances than did fed beetles across all treatments. When food was clumped or uniformly distributed, foraging movements of hungry beetles also covered less ground (smaller total path length) 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 behaviour 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 (≥ 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 behaviour (“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 amount of surface area covered by food (compared to the random and clumped treatments). This indicates that total surface 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.

When confronted with a random distribution of food patches, beetles followed a more tortuous pathway that covered a greater overall distance (path length) than did beetles (fed or hungry) in any of the other treatments, which meant that they took longer to find a food patch than did 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 food-dispersion pattern are less effective in locating food patches than when food is distributed in different patterns. In other words, beetles are more effective in locating food resources when the food is clumped or uniformly distributed than when it is randomly arrayed.

Contrary to our initial predictions, the strongest movement responses were elicited by areas with randomly dispersed resources, rather than 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 satiated individuals, presumably because of more intense searching behaviour by 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) affect the behaviour of a variety of organisms under field, laboratory, and simulation conditions. Exactly what sort of movement pattern might be “optimal” under differing resource distributions, however, is open to debate. When animals have no information about the spatial location of resources, some (e.g. Jander 1975, Dusenbery 1989) have argued that a linear path may be the most energetically effective movement strategy. Indeed, the relatively low fractal dimensions of beetle movements in all treatments (Fig. 4.2d) 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 in press), EMS experiments (e.g. Ims et al. 1993, McIntyre and Wiens in

review), 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 behaviours 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.

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 simple sandbox arenas. Nonetheless, our experiments have revealed some of the behavioural mechanisms that may underlie variations in how organisms move through heterogeneous landscape mosaics (Ims 1995). 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).

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LITERATURE CITED

- Andreassen, H.P., S. Halle, R.A. Ims. 1996a. Optimal width of movement corridors for root voles: Not too narrow and not too wide. *Journal of Applied Ecology* 33:63-70.
- Andreassen, H.P., R.A. Ims, and O.K. Steinset. 1996b. Discontinuous habitat corridors: Effects on male root vole movements. *Journal of Applied Ecology* 33:555-560.
- Arditi, R., and B. Dacorogna. 1988. Optimal foraging on arbitrary food distribution and the definition of habitat patches. *American Naturalist* 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. *Annual Review of Entomology* 35:447-467.
- Bell, W.J. 1991. *Searching Behaviour: The Behavioural Ecology of Finding Resources*. Chapman and Hall, London.
- Bell, W.J., and E. Kramer 1979. Search and anemotactic orientation of cockroaches. *Journal of Insect Physiology* 25:631-640.
- Bell, W.J., C. Tortorici, R.J. Roggero, L.R. Kipp, and T.R. Tobin. 1985. Sucrose-stimulated searching behaviour of *Drosophila melanogaster* in a uniform habitat: Modulation by period of deprivation. *Animal Behaviour* 33:436-448.
- Bernstein, C., A. Kacelnik, and J.R. Krebs 1988. Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology* 57:1007-1026.
- Calkins, C.O., and V.M. Kirk 1973. Distribution and movement of adult false wireworms in a wheat field. *Annals of the Entomological Society of America* 66:527-532.

- Carter, M.C., and A.F.G. Dixon. 1982. Habitat quality and the foraging behaviour of coccinellid larvae. *Journal of Animal Ecology* 51:865-878.
- Crawford, C.S. 1981. *Biology of Desert Invertebrates*. Springer-Verlag, New York, NY.
- 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* 6:536-544.
- De Roos, A.M., E. McCauley, and W.F. Wilson 1991. Mobility versus density-limited predator-prey dynamics on different spatial scales. *Proceedings of the Royal Society of London* B246:117-122.
- Dicke, M., and P.A. Burrough. 1988. Using fractal dimensions for characterizing tortuosity of animal trails. *Physiological Entomology* 13:393-398.
- Doyen, J.T., and W.F. Tschinkel. 1974. Population size, microgeographic distribution, and habitat separation in some tenebrionid beetles. *Annals of the Entomological Society of America* 67:617-626.
- Dusenbery, D.B. 1989. Ranging strategies. *Journal of Theoretical Biology* 136:309-316.
- Duvall, D., D. Chiszar, and R.A. Mintzer. 1994. Plane geometry for naïve searchers: some results of the simulation Rattlesnake[®]. *American Zoologist* 34:78A.
- Edwards, G.R., J.A. Newman, A.J. Parsons, and J.R. Krebs. 1994. Effects of the scale and spatial distribution of the food resource and animal state on diet selection: An example with sheep. *Journal of Animal Ecology* 63:816-826.
- Evans, H.F. 1976. The searching behaviour of *Anthocoris confusus* (Reuter) in relation to prey density and plant surface topography. *Ecological Entomology* 1:163-169.
- Fromm, J.E., and W.J. Bell. 1987. Search orientation of *Musca domestica* in patches of sucrose drops. *Physiological Entomology* 12:297-307.
- Gardner, R.H., R.V. O'Neill, M.G. Turner, and V.H. Dale. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecology* 3:217-227.

- Gardner, R.H., M.G. Turner, R.V. O'Neill, and S. Lavorel. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. Pp. 76-89 in: *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments* (M.M. Holland, P.G. Risser, and R.J. Naiman, eds.). Chapman and Hall, New York, NY.
- Gustafson, E.J., and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77:94-107.
- Hassell, M.P., and T.R.E. Southwood. 1978. Foraging strategies of insects. *Annual Review of Ecology and Systematics* 9:75-98.
- Hastings, H.M., and G. Sugihara. 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. *Memoirs of the Entomological Society of Canada* 48.
- Ims, R.A. 1995. Movement patterns related to spatial structures. Pp. 85-109 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- Ims, R.A., J. Rolstad, and P. Wegge. 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? *Biological Conservation* 63:261-268.
- Jander, R. 1975. Ecological aspects of spatial orientation. *Annual Review of Ecology and Systematics* 6:171-188.
- Johnson, A.R., B.T. Milne, and J.A. Wiens. 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 J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.

- Lauenroth, W.K., and D.G. Milchunas. 1991. Short-grass steppe. Pp. 183-226 in: *Ecosystems of the World 8A: Natural Grasslands* (R.T. Coupland, ed.). Elsevier, Amsterdam.
- Ludwig, J.A., and J.F. Reynolds. 1988. *Statistical Ecology: A Primer on Methods and Computing*. John Wiley and Sons, New York, NY.
- McIntyre, N.E. 1997. Scale-dependent habitat selection by the darkling beetle *Eleodes hispilabris* (Coleoptera: Tenebrionidae). *American Midland Naturalist* 138: 230-235.
- McIntyre, N.E., and T.T. Vaughn. 1997. Effects of food deprivation and olfactory and visual cues on the movement patterns of two *Eleodes* species (Coleoptera: Tenebrionidae) in a wind tunnel. *Annals of the Entomological Society of America* 90:260-265.
- McIntyre, N.E., and J.A. Wiens. In review. How does the scale of landscape patchiness affect animal movement?: An experiment with darkling beetles. *Ecology*.
- Merriam, G. 1988. Landscape dynamics in farmland. *Trends in Ecology and Evolution* 19:16-20.
- Milne, B.T., M.G. Turner, J.A. Wiens, and A.R. Johnson. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. *Theoretical Population Biology* 41:337-353.
- Mitchell, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). I. Life cycles and feeding behaviour. *Journal of Animal Ecology* 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. In: *Miscellaneous Papers 18 of the Agricultural University, Wageningen, The Netherlands* (P.J. DenBoer, H.U. Thiele, and F. Weber F, eds.). H. Veenman and Zonen BV, 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 Phytopathologica Entomologica Hungarica* 22:187-205.
- Rogers, L.E., N.E. Woodley, J.K. Sheldon, and P.A. Beedlow. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within a shrub-steppe ecosystem. *Annals of the Entomological Society of America* 81:782-791.

- Rose, G., and W. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. *Ecology* 71:33-43.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry* (2nd ed.). WH Freeman, New York, NY.
- Tinbergen, N., M. Impeken, and D. Franck. 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28:307-321.
- Tortorici, C., A. Brody, W.J. Bell. 1986. Influence of spatial patterning of resources on search orientation of adult *Drosophila melanogaster*. *Animal Behaviour* 34:1568-1570.
- 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. *American Naturalist* 141:199-216.
- Whicker, A.D., and C.R. Tracy. 1987. Tenebrionid beetles in the shortgrass prairie: daily and seasonal patterns of activity and temperature. *Ecological Entomology* 12:97-108.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, J.A. 1995. Landscape mosaics and ecological theory. Pp. 1-26 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- Wiens, J.A., T.O. Crist, and B.T. Milne. 1993a. On quantifying insect movements. *Environmental Entomology* 22:709-715.
- 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. 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. 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 Ecology* 9:25-36.
- With, K.A., and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76:2446-2459.
- Yount, V.A. 1971. Diets of selected insects in a grassland ecosystem. M.S. Thesis, Colorado State University, Fort Collins, CO.

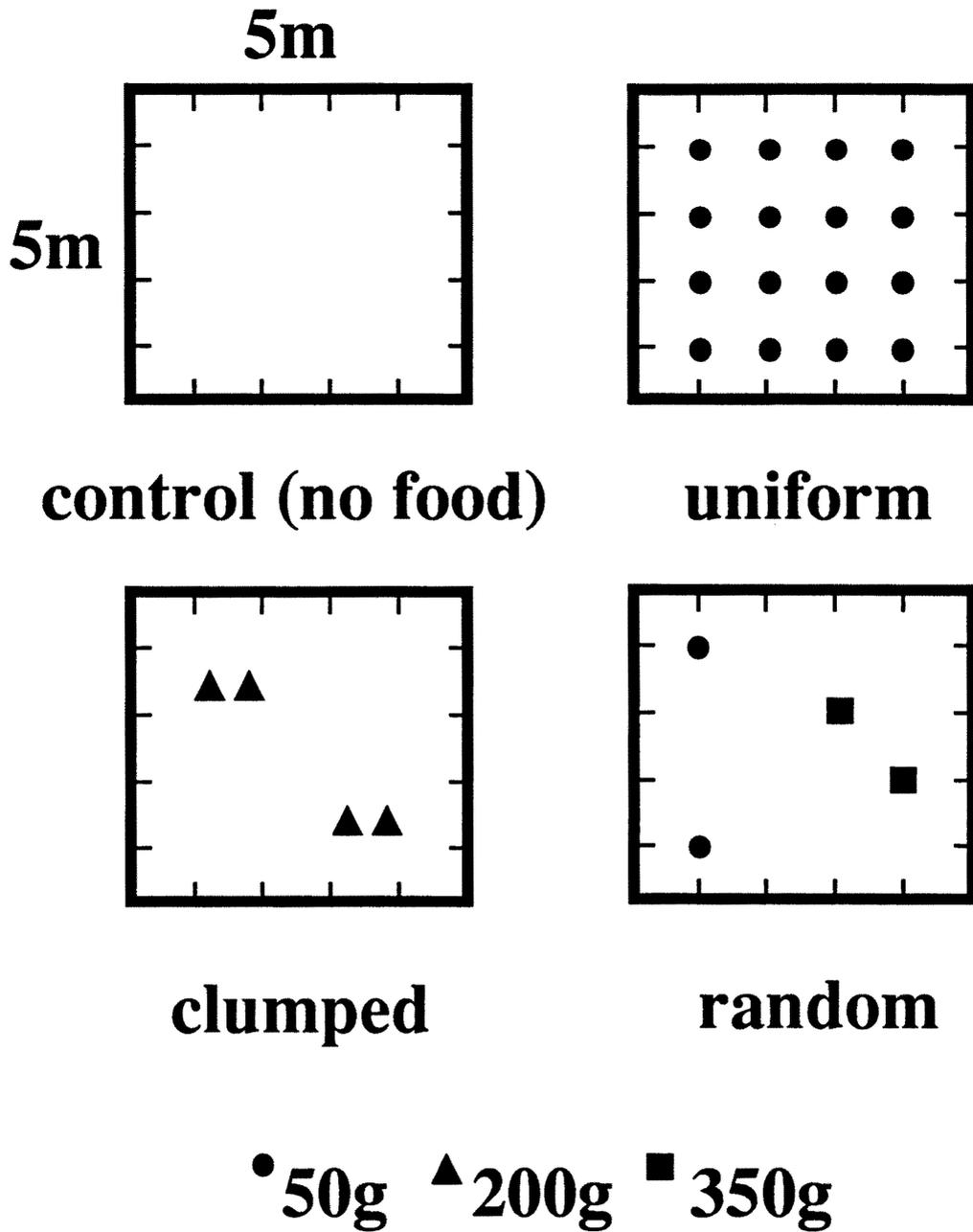


Fig. 4.1. Experimental model system (sandbox arena) used. Small hash marks along arena border mark 1-m increments. Amount of food was held constant at 800 g across treatments. All food piles covered the same area (7-cm diameter circle), differing only in volume (height).

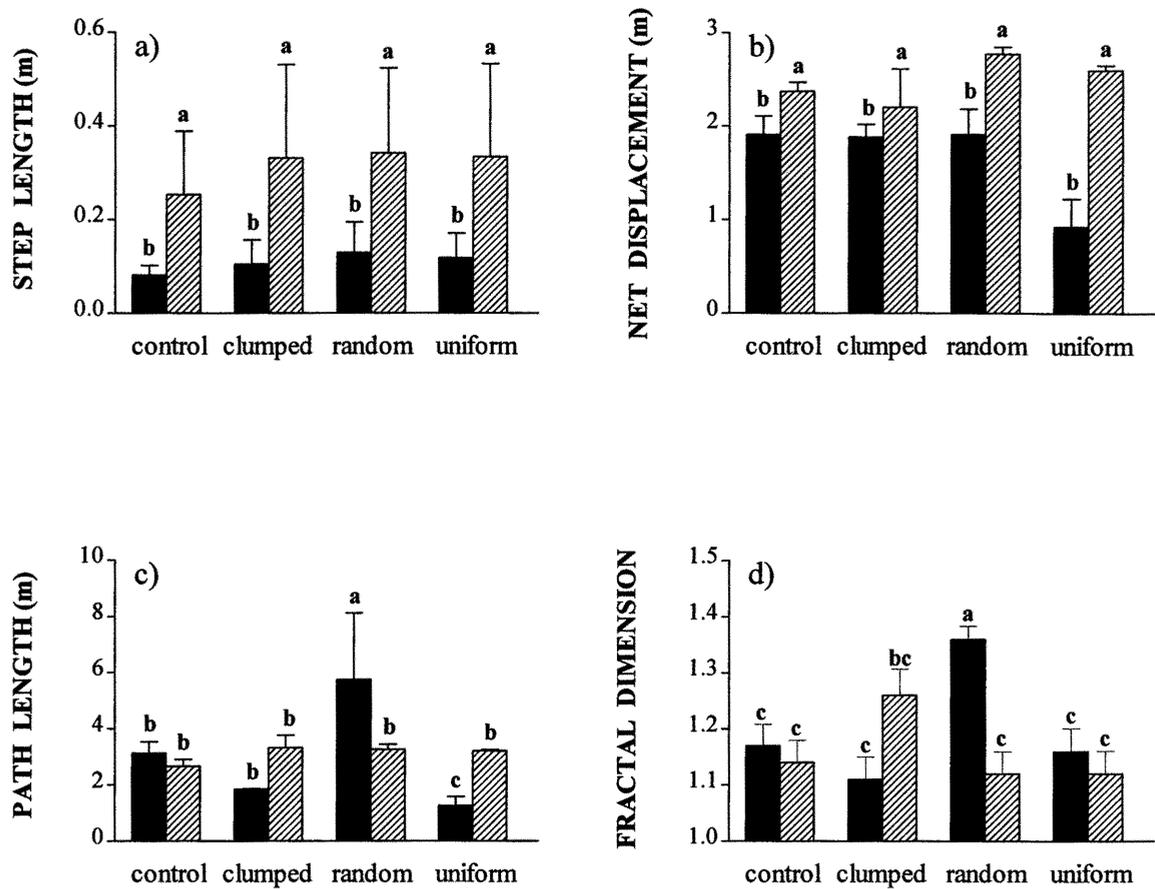


Fig. 4.2. Mean (+ SE) path metrics for food-deprived (solid bars) and fed (hatched bars) *E. extricata* in areas with no food resources (control) and resources in clumped, random, and uniform distributions. Means denoted with different letters are significantly different ($P < 0.05$ Fisher's Protected LSD). a) length of 15-s steps, b) net linear displacement, c) total path length, d) fractal dimension.

"...spatial variability...is a dynamically interesting quantity rather than a statistical nuisance to be overcome."

David Schneider

Quantitative Ecology (1994)

Academic Press, San Diego, CA

CHAPTER V

HOW DOES THE SCALE OF LANDSCAPE PATCHINESS AFFECT ANIMAL MOVEMENT?: AN EXPERIMENT WITH DARKLING BEETLES

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ABSTRACT

We used an experimental model system comprised of darkling beetles (Coleoptera: Tenebrionidae, *Eleodes obsoleta* Say) and the microlandscape they occupied to assess the effects of the scale of landscape heterogeneity on the movement patterns of animals. The ratio of habitat area to non-habitat in a 25-m² experimental landscape was held constant while the scale of patchiness (size of patches) was varied in three treatments. Beetle movement pathways were electronically surveyed, and seven metrics were used to quantify movement characteristics. Multivariate analysis of variance and Fisher's Protected Least Significant Difference post-hoc comparisons revealed that finely fragmented landscapes with small habitat patches elicited significantly shorter and less linear beetle movement paths than did coarsely fragmented landscapes with larger habitat patches, suggesting that beetles may perceive habitat patches of different sizes as having different ecological functions. Lacunarity analysis revealed that darkling beetles exhibited patterns of landscape use that did not match patterns of landscape structure. These results indicate that different landscapes may be structurally dissimilar and yet functionally equivalent, and the scale of spatial heterogeneity may be as important as the presence of heterogeneity in affecting

animal movements. Predicting how organisms respond to spatial heterogeneity will thus require not only a description of spatial pattern but also its functional role.

Key words: Scale, patchiness, movement, spatial heterogeneity, landscape ecology

INTRODUCTION

A primary goal of landscape ecology is to determine how spatial patterning of the environment influences the abundance and distribution of organisms (Ims 1995, Wiens 1995). Because spatial patterns change with changes in scale, issues of scale are central to landscape ecology (Meentemeyer and Box 1987, Dale et al. 1994), as they are to many other areas of ecology (Wiens 1989; Levin 1992, 1993). Understanding how landscape pattern affects the abundance and distribution of organisms therefore requires an understanding of scale-dependency. Because we do not yet have anything resembling a "theory of scaling" (Meentemeyer and Box 1987), we must rely on empirical studies to derive insights about scaling effects in landscape ecology (Wiens 1995).

The linkage between animal behavior and landscape pattern is particularly amenable to empirical analysis. Behaviors such as movement are strongly influenced by landscape pattern (Wiens and Milne 1989, Crist et al. 1992, With 1994, Ims 1995, Cresswell 1997, McIntyre 1997), and movement patterns, in turn, alter the genetic and demographic composition of populations (Levins 1969, McCauley 1995, Cresswell 1997), affect the spread of diseases and parasites (Holmes 1993), and impact 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 (Kareiva 1990; Wiens 1989, 1990; Ims 1995).

Conceptually, it seems obvious that animal movements will be influenced by the scale (or grain; Wiens 1989) on which landscape pattern is expressed or on which it is perceived by organisms (Kotliar and Wiens 1990, With 1994). 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 scale of landscape pattern on animal movements. We used an experimental model system (EMS; Ims et al. 1993, Wiens et al. 1993b) consisting of darkling beetles (Coleoptera: Tenebrionidae, *Eleodes obsoleta* Say) moving in microlandscapes in which the proportion of different landscape elements was held constant but the scale of the pattern was varied. As the scale of patchiness becomes broader (*i.e.*, as the patches become larger), the ratio of patch perimeter to patch area decreases, resulting in fewer patch boundary zones. Because beetle movements differ in the different landscape elements (Wiens et al. 1985, Wiens and Milne 1989, Crist et al. 1992, Wiens et al. 1997) and are likely to be affected by patch boundaries, we predict that movements will be more constrained and localized in fine-scale landscapes. This is because the frequent boundaries between patches will interrupt the flow of movements in a particular patch type and cause repeated transitions to movement patterns characteristic of other patch types. Percolation models also predict a nonlinear relationship between the scale of landscape patchiness and movement patterns (Wiens et al. 1997, With et al. 1997, With 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 approximately 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 *Buchloë 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

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.

The experimental landscape treatments were 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 used buffalograss (*Buchloë dactyloides*) sod to make habitat patches in the sand (non-

habitat) matrix. Buffalograss 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 scales of landscape patchiness, were used (Fig. 5.1). The size of grass patches was varied, creating 0.125 x 0.125 m, 0.25 x 0.25 m, 0.5 x 0.5 m, and 1 x 1 m grass patches. 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). 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 this design, then, the five landscape configurations represented *treatments*; within each of these treatments, individual movement pathways were the *replicates* (see Movement Analyses section, below).

Landscape pattern was quantified by calculating the *lacunarity* of the microlandscape. Lacunarity (Λ) is an index of landscape patchiness that describes habitat contagion and pattern at multiple scales (Plotnick et al. 1993). Although there are several indices that quantify habitat contagion (see Riitters et al. 1996), only lacunarity includes a multi-scaled approach to describing habitat aggregation. Because we were interested in how movement behaviors were affected by landscape treatments that differed only with respect to pattern at multiple scales, lacunarity (hereafter, "landscape-pattern lacunarity") was chosen to describe habitat patterning.

To assess landscape-pattern lacunarity, the microlandscape arena was gridded into 1 x 1 m squares, with squares containing habitat (grass patches) denoted "1" and squares of non-habitat (sand) denoted "0". This procedure was repeated over a range of square sizes to assess patchiness at a range of spatial scales (the "gliding box" technique of Allain and Cloitre 1991). The frequency of squares containing grass habitat was then used to calculate the probability (Λ) of selecting two points on the landscape that are grass, given the spatial arrangement of such patches. The gliding box technique produced a range of landscape-pattern lacunarity values for the range of square sizes (*i.e.*, scales). Landscape-pattern lacunarity values were plotted against these scales, producing a curve for each spatial scale. Areas under inflection points of these curves indicate "domains of scale" that result from different ecological processes acting at different scales (Plotnick et al. 1993).

A landscape-pattern lacunarity value of 1 indicates that habitat patches are uniformly dispersed at a given scale. Landscape-pattern lacunarity values $\neq 1$ indicate nonuniformity in the distribution of habitat. For a given gliding-box size, lower values of Λ indicate a random distribution of habitat, whereas higher values of Λ indicate aggregation of habitat (see Fig. 2 in Plotnick et al. 1993). Because it assesses the dispersion of one habitat type embedded within another, landscape-pattern lacunarity is applicable only to non-homogeneous landscapes. Therefore, landscape-pattern lacunarity could not be calculated for the control landscape, which was entirely sand.

Movement analyses

Movement analyses followed the protocol of Wiens et al. (1993a) and Wiens et al. (1997). Because we wanted to use movement data for the 0.25 x 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) as closely as possible. We used the same sandbox arena, the same species of beetle and grass sod (both of which we obtained from the same sources as Wiens and his colleagues), and 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. If there were between-year effects, we would expect that the 0.25 x 0.25 m treatment to differ from the other treatments for all path metrics. However, multivariate analysis of variance (MANOVA) revealed that the movement-path data we collected were not significantly different from those of Wiens et al. (1997) ($F_{6,13} = 1.3076$, $P = 0.3205$). Accordingly, we combined the data sets in our analyses. Any significant differences between the 0.25 x 0.25 m treatment and the other treatments therefore should reflect actual treatment effects rather than temporal artifacts.

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 x 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 marked at 5-s intervals with sequentially numbered flags. Each individual beetle was used in only one trial. Beetles were followed for 100 such time-steps ($N = 6$) or until they reached the boundary fence ($N = 84$), which usually occurred between 25 and 50 time-steps (mean = 39 time-steps). Their movement paths were then recorded electronically with a Pentax PTS-II₀₅ surveying station. Field data were downloaded into a Corvallis Microtechnology CMT MC-II field microcomputer and translated into Cartesian coordinates with computer software designed by the Maptech Corporation (Loveland, Colorado, USA).

Movement pathways were described by seven path metrics. Net linear displacement quantified the distance covered by a beetle, fractal dimension described path tortuosity, and average movement distance (step length) per 5-s interval and displacement

rate quantified a beetle's velocity. The number of 5-s movements intervals occurring on sand and on grass and the number of pauses (time intervals without movements) were also counted.

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, Wiens et al. 1995). The fractal dimension 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).

Just as a landscape may be heterogeneous in composition, an animal's use of the landscape may also be patchy, with use concentrated in only certain portions of the landscape. We assessed the relative homogeneity of beetle use of the microlandscape by calculating lacunarity in a manner similar to that applied in the microlandscape analysis. As with landscape-pattern lacunarity, the microlandscape arena was divided into squares. Squares in which a beetle moved were treated like "habitat" ("1") in the landscape-pattern lacunarity analysis, whereas squares into which a beetle did not move were treated like "non-habitat" ("0"). This approach allowed a direct comparison between landscape patchiness and the patchiness of an animal's use of that landscape at different scales. This use of lacunarity (hereafter, "landscape-use lacunarity") represents a new way of linking landscape pattern and the effects of that pattern on animal movements (R. Plotnick *personal communication*). As with landscape-pattern lacunarity, higher landscape-use lacunarity values for a given gliding-box size indicate concentration of movements in a localized area, whereas lower values of Λ indicate more free-ranging movements. Recall that grass patches were randomly located in each of the treatments and differed in size; if beetles are insensitive to the scale of landscape patchiness, we would expect landscape-use lacunarity values similar to those of landscape-pattern lacunarity.

MANOVA was used to detect significant differences in movement-path metrics with changes in the scale of landscape patchiness over all treatments. If significant overall effects were found, Fisher's protected least significant difference (LSD) tests (Sokal and Rohlf 1981) were performed to detect significant differences in path metrics among treatments. A Spearman rank correlation test was used to compare landscape-pattern and landscape-use lacunarity values.

RESULTS

Movement patterns in the control area, which lacked vegetation, differed significantly from those in all other treatments. In addition, the scale of landscape patchiness significantly affected beetle movement patterns (MANOVA: $F_{53,445} = 5.3626$, $P = 0.0001$). Beetles in landscapes with larger habitat patches generally moved in a more linear fashion and paused more often than did those in more finely fragmented landscapes with 0.125 x 0.125 m habitat patches. Heterogeneous landscapes elicited shorter pathways than did the homogeneous control (Fig. 5.2a). Beetles also moved more slowly in fragmented landscapes than in the homogeneous control (Fig. 5.2b, 5.2c). Beetles spent more time in movement (taking more time-steps) in heterogeneous landscapes (Fig. 5.2d). This response is also reflected in the amount of time they spent in habitat patches. Intermediate levels of patchiness elicited longer patch residency times (Fig. 5.2e), probably because beetles paused more often in such microlandscapes (Fig. 5.2f). Heterogeneous landscapes also induced beetles to move in a less linear fashion (Fig. 5.3).

Beetles clearly responded to changes in the scale of patchiness of the microlandscapes (Figs. 5.2, 5.3). Many of the strongest responses were associated with intermediate scales of patchiness (0.25 x 0.25 m and 0.5 x 0.5 m grass patches). Movement responses for most variables were similar in smaller (0.125 x 0.125 m) and larger (1 x 1 m) grass patches (Fig. 5.2), although the smallest grass patches evoked the most convoluted pathways (Fig. 5.3).

Landscape-use lacunarity values generally were higher than landscape-pattern lacunarity values (Fig. 5.4), indicating that beetle use of a landscape is more localized than is the habitat configuration of that landscape. Landscape-pattern and landscape-use lacunarity were highly correlated ($R_s = 0.8974$, $P = 0.0001$): movements were more localized in more highly fragmented landscapes with smaller habitat patches (Fig. 5.5). Similarly, movements did not exhibit a linear response to landscape patchiness (Figs. 5.4, 5.5), indicating that movements become more restricted (higher landscape-use lacunarity values) as landscapes become more patchy and habitat becomes more aggregated (higher landscape-pattern lacunarity values).

DISCUSSION

Our experiments show that the scale of landscape pattern affected the characteristics of beetle movements. These effects were especially evident at intermediate scales of patchiness. 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. With respect to translating individual movement responses into patterns of abundance and distribution of animals such as darkling beetles, this scale-dependent effect illustrates how organisms are "retained" by a landscape's pattern. Based upon our results, for example, *E. obsoleta* darkling beetles should occur most often in heterogeneous landscapes that possess discrete patches of vegetation approximately 0.25 x 0.25 m in size—this configuration would better deter linear movements that would direct a beetle out of the area, thereby eliciting longer local residency times, 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, an examination of the literature does reveal that *E. obsoleta* and other darkling beetle species are more common in heterogeneous areas than in relatively

homogeneous regions of the shortgrass steppe (Crist et al. 1992, Whicker 1983, Stapp 1997).

Our results indicate that the scale of spatial heterogeneity may be as important as the presence of heterogeneity in affecting animal movements. The peaked distributions of most variables (Fig. 5.2) illustrate that landscapes may be structurally dissimilar and yet functionally equivalent. 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 also suggest that beetles perceive patches of different sizes as having different ecological functions. They may see very small patches as being unable to provide adequate levels of resources, responding to them in a quite different manner than to large patches. This would create the increase in response to patch size observed for most variables. This effect is similar to the manner in which the presence of different fractal domains indicate different mechanisms or constraints acting at different spatial scales (see Krummel et al. 1987). For example, the "left" domain of Fig. 5.3 may reflect beetle movements around the small grass patches, whereas the "right" domain may reflect beetle movements within the large grass patches. In other words, small grass patches were perceived as obstacles, whereas larger patches were colonized as habitat. When a habitat patch's area is quite large or when such patches are abundant, however, a beetle may use habitat in a lesser proportion than the habitat's occurrence on the landscape, resulting in a decrease in the magnitude of response past some threshold size or amount of habitat. This would explain why some large and small patch sizes in Fig. 5.3 are statistically indistinguishable from one another and yet evoke different responses than do patches of intermediate size.

The most highly fragmented landscapes with the smallest grass patches evoked the most convoluted movement paths (Fig. 5.3). As grass is more viscous than sand, it is not surprising that the presence of more grass patches would cause beetles to move in a more

tortuous fashion so as to avoid these obstacles (an effect also noted by Wiens and Milne 1989 and Crist et al. 1992). Beetle movements differ when entirely on grass than when in a heterogeneous grass-sand landscape (Crist et al. 1992, Wiens et al. 1997, NEM unpublished data). The presence of numerous small grass patches exposed beetles to more habitat transitions. As 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.

If beetles are insensitive to the scale of landscape patchiness, we would expect to see similar lacunarity values for landscape pattern and landscape use. However, landscape-use Λ were consistently and significantly larger than landscape-pattern Λ over most scales (Fig. 5.4). Once again, therefore, there is evidence that animal movements are impacted by landscape pattern.

Differences in landscape-pattern and landscape-use lacunarity values (Fig. 5.5) illustrate that there is a disparity between landscape pattern and landscape function (i.e., use) (see also With and King 1997). Contrasting the lacunarity of landscape pattern with that of landscape use demonstrates how an animal may respond in a nonlinear or unpredictable manner to a given level of landscape patchiness. Darkling beetles exhibited patterns of landscape use that did not correspond exactly to patterns of landscape pattern, and these patterns of landscape use varied with patch scale. 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 multi-scaled, landscape ecology approach to understand organism-environment interactions (Fahrig and Merriam 1994, Wiens 1996).

Our study represents one of the few field tests of how manipulating landscape pattern alters movement parameters. 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. Because of

the scale-dependent nature of ecological phenomena like animal movement, a mapping-oriented approach to landscape ecology may not by itself be particularly useful in assessing the responses of organisms to spatial pattern. Experimentation may provide a useful way to determine the presence and nature of scale-dependent effects. This approach will entail focusing less on the pattern of landscapes and more on their functions--that is, we need to focus on the *ecology* in landscape ecology. Taking a functionally based approach to landscape ecology would necessitate a paradigm shift (Golley 1989), which is never an easy task. If the discipline is to make a lasting impact upon our understanding of how organisms interact with their environment, however, its practitioners must try.

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LITERATURE CITED

- Allain, C., and M. Cloitre. 1991. Characterizing the lacunarity of random and deterministic fractal sets. *Physical Review A*44:3552-3558.
- 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., D.S. Guertin, J.A. Wiens, and B.T. Milne. 1992. Animal movements in heterogeneous landscapes: an experiment with *Eleodes* beetles in short grass prairie. *Functional Ecology* 6:536-544.
- Dale, V.H., S.M. Pearson, H.L. Offerman, and R.V. O'Neill. 1994. Relating patterns of landuse change to faunal biodiversity in the central Amazon. *Conservation Biology* 8:1027-1036.
- Elmes, G.W. 1991. Ant colonies and environmental disturbance. *Symposium of the Zoological Society of London* 63:15-32.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50-59.
- Forman, R.T.T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- Gardner, R.H., M.G. Turner, V.H. Dale, and R.V. O'Neill. 1992. A percolation model of ecological flows. Pp. 259-269 in: *Landscape Boundaries* (O.L. Lange, H.A. Mooney, and H. Remmert, eds.). Springer-Verlag, New York, NY.
- Golley, F.B. 1989. Paradigm shift. *Landscape Ecology* 3:65-66.
- Holmes, E.E. 1993. Are diffusion models too simple? A comparison with telegraph models of invasion. *American Naturalist* 142:779-795.
- Ims, R.A. 1995. Movement patterns related to spatial structures. Pp. 85-109 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- Ims, R.A., J. Rolstad, and P. Wegge. 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? *Biological Conservation* 63:261-268.
- Johnson, A.R., B.T. Milne, and J.A. Wiens. 1992. Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements. *Ecology* 73:1968-1983.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: Theory and data. Pp. 53-68 in: *Population Regulation and Dynamics* (M.P. Hassell and R.M. May, eds.). Royal Society, London.

- 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.
- Krummel, J.R., R.H. Gardner, G. Sugihara, R.V. O'Neill, and P.R. Coleman. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321-324.
- Lauenroth, W.K., and D.G. Milchunas. 1991. Short-grass steppe. Pp. 183-226 in: *Ecosystems of the World 8A: Natural Grasslands* (R.T. Coupland, ed.). Elsevier, Amsterdam.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Levin, S.A. 1993. Concepts of scale at the local level. Pp. 7-19 in: *Scaling Physiological Processes: Leaf to Globe* (J.R. Ehleringer and C.B. Field, eds.). Academic Press, New York, NY.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237-240.
- Mandelbrot, B.B. 1983. *The Fractal Geometry of Nature*. W.H. Freeman and Co., New York, NY.
- McCauley, D.E. 1995. Effects of population dynamics on genetics in mosaic landscapes. Pp. 178-198 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- McIntyre, N.E. 1997. Scale-dependent habitat selection by the darkling beetle *Eleodes hispilabris* (Coleoptera: Tenebrionidae). *American Midland Naturalist* 138:230-235.
- Meentemeyer, V., and E.O. Box. 1987. Scale effects in landscape studies. Pp. 15-34 in: *Landscape Heterogeneity and Disturbance* (M.G. Turner, ed.). Springer-Verlag, New York, NY.
- Merriam, G. 1995. Movement in spatially divided populations: responses to landscape structure. Pp. 64-77 in: *Landscape Approaches in Mammalian Ecology and Conservation* (W.Z. Lidicker, ed.). University of Minnesota Press, Minneapolis, MN.

- Plotnick, R.E., R.H. Gardner, and R.V. O'Neill. 1993. Lacunarity indices as measures of landscape texture. *Landscape Ecology* 8:201-211.
- Riitters, K.H., R.V. O'Neill, J.D. Wickham, and K.B. Jones. 1996. A note on contagion indices for landscape analysis. *Landscape Ecology* 11:197-202.
- Rogers, L.E., N.E. Woodley, J.K. Sheldon, and P.A. Beedlow. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within a shrub-steppe ecosystem. *Annals of the Entomological Society of America* 81:782-791.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry* (2nd ed.). W.H. Freeman and Co., New York.
- Stapp, P. 1997. Microhabitat use and community structure of darkling beetles (Coleoptera: Tenebrionidae) in shortgrass prairie: effects of season, shrub cover and soil type. *American Midland Naturalist* 137:298-311.
- Whicker, A.D. 1983. Spatial and temporal distributions of tenebrionid beetles, genus *Eleodes*, in a grassland community. Ph.D. Dissertation, Colorado State University, Fort Collins, CO.
- Whicker, A.D., and C.R. Tracy. 1987. Tenebrionid beetles in the shortgrass prairie: daily and seasonal patterns of activity and temperature. *Ecological Entomology* 12:97-108.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, J.A. 1990. Ecology 2000: an essay on future direction in ecology. *Revista Chilena de Historia Natural* 63:309-315.
- Wiens, J.A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pp. 217-235 in: *Landscape Boundaries* (O.L. Lange, H.A. Mooney, and H. Remmert, eds.). Springer-Verlag, New York, NY.
- Wiens, J.A. 1995. Landscape mosaics and ecological theory. Pp. 1-26 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- Wiens, J.A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and management. Pp. 53-84 in: *Metapopulations and Wildlife Conservation* (D.R. McCullough, ed.). Island Press, Washington, D.C.

- Wiens, J.A., C.S. Crawford, and J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421-427.
- Wiens, J.A., T.O. Crist, and B.T. Milne. 1993a. On quantifying insect movements. *Environmental Entomology* 22:709-715.
- Wiens, J.A., T.O. Crist, K. 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. 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. 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 Ecology* 9:25-36.
- With, K.A., and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76:2446-2459.
- 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., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151-169.
- Yount, V.A. 1971. Diets of selected insects in a grassland ecosystem. M.S. Thesis, Colorado State University, Fort Collins, CO.

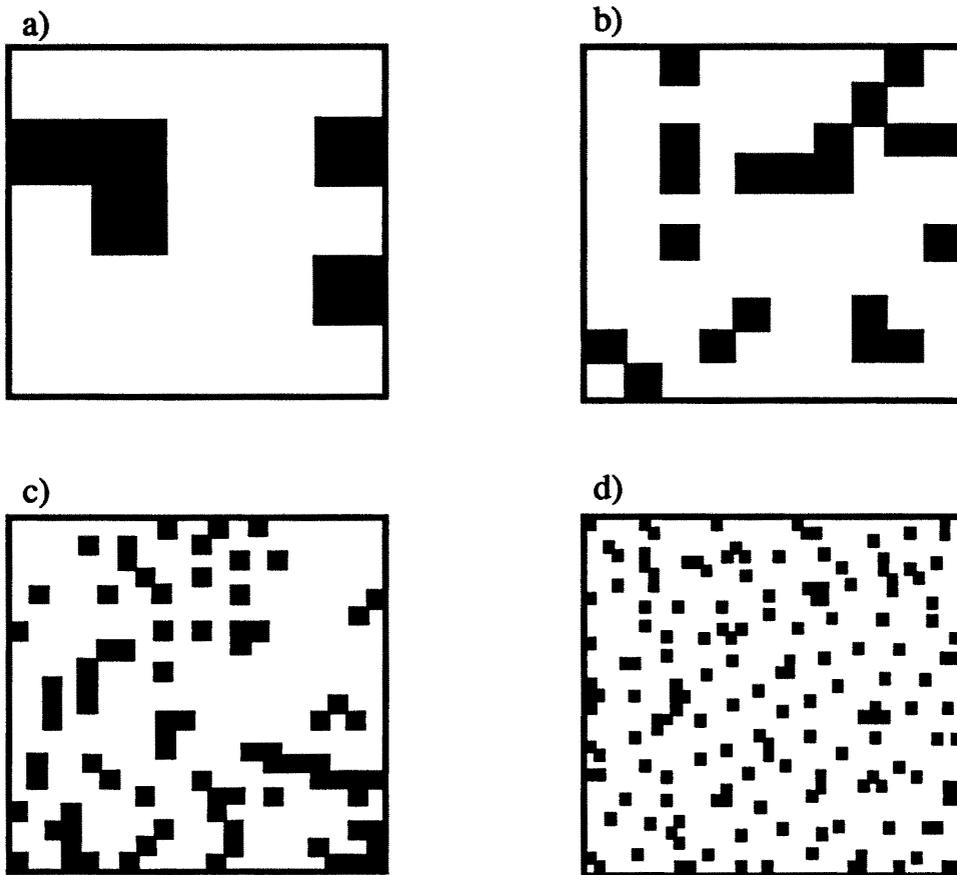


Fig. 5.1. Treatments created in sandbox microlandscape. The overall ratio of grass (dark squares) to sand (light background) was held constant at 20:80, except for a control of 100% sand (not shown). a) 1 x 1 m grass patches, b) 0.5 x 0.5 m grass patches, c) 0.25 x 0.25 m grass patches, d) 0.125 x 0.125 m grass patches.

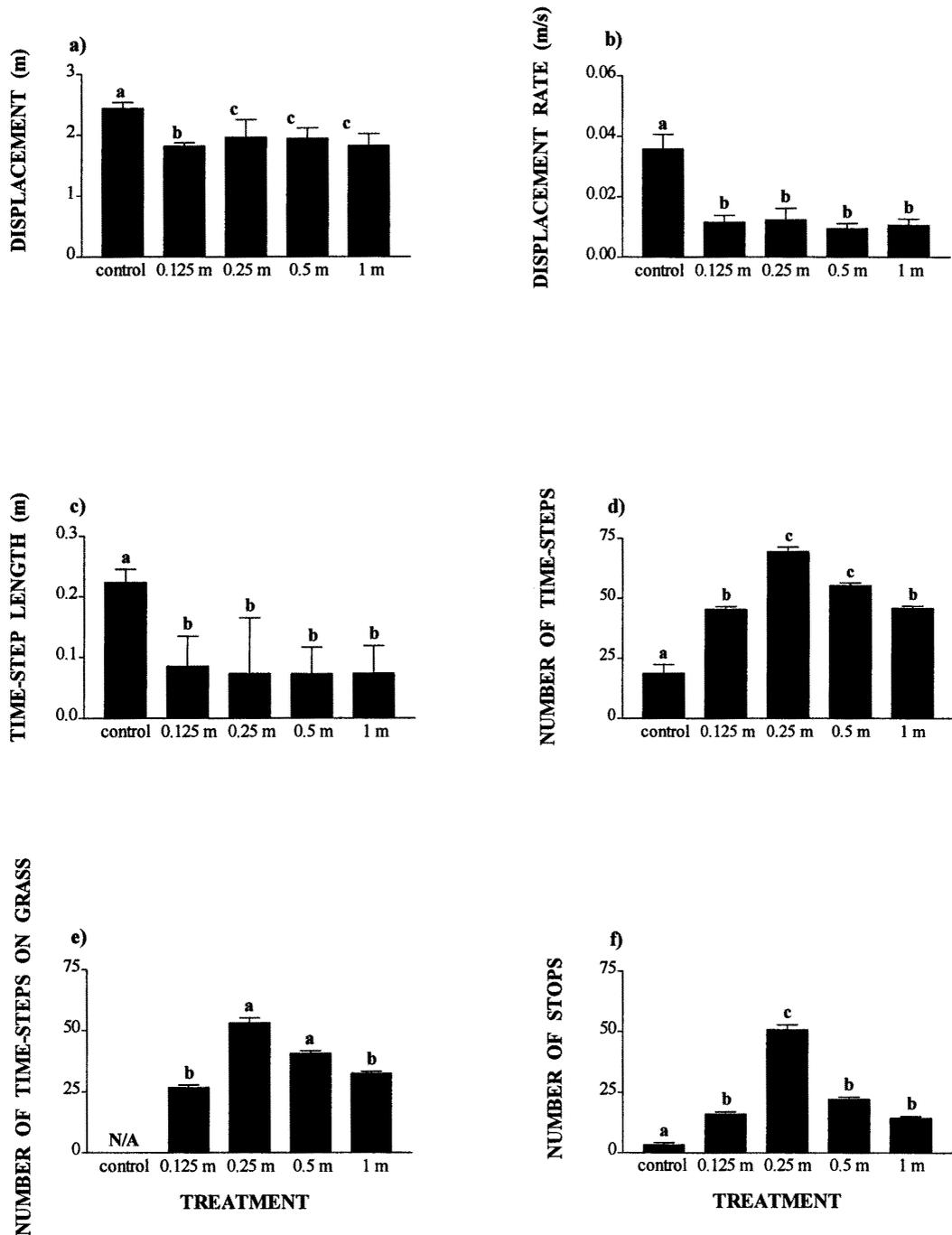


Fig. 5.2. Mean (\pm SE) response variables by treatment. Abscissa indicates treatment levels as in Fig. 5.1. Means denoted with the same letter do not differ significantly (Fisher's protected least significant difference test, $P > 0.05$). a) net linear displacement, b) displacement rate, c) step length per 5-s interval, d) number of time-steps (5-s movement intervals) taken, e) number of time-steps taken on grass, f) number of stops. "N/A" in Fig. 5.2e indicates that no time-steps on grass could have been made in the control plots.

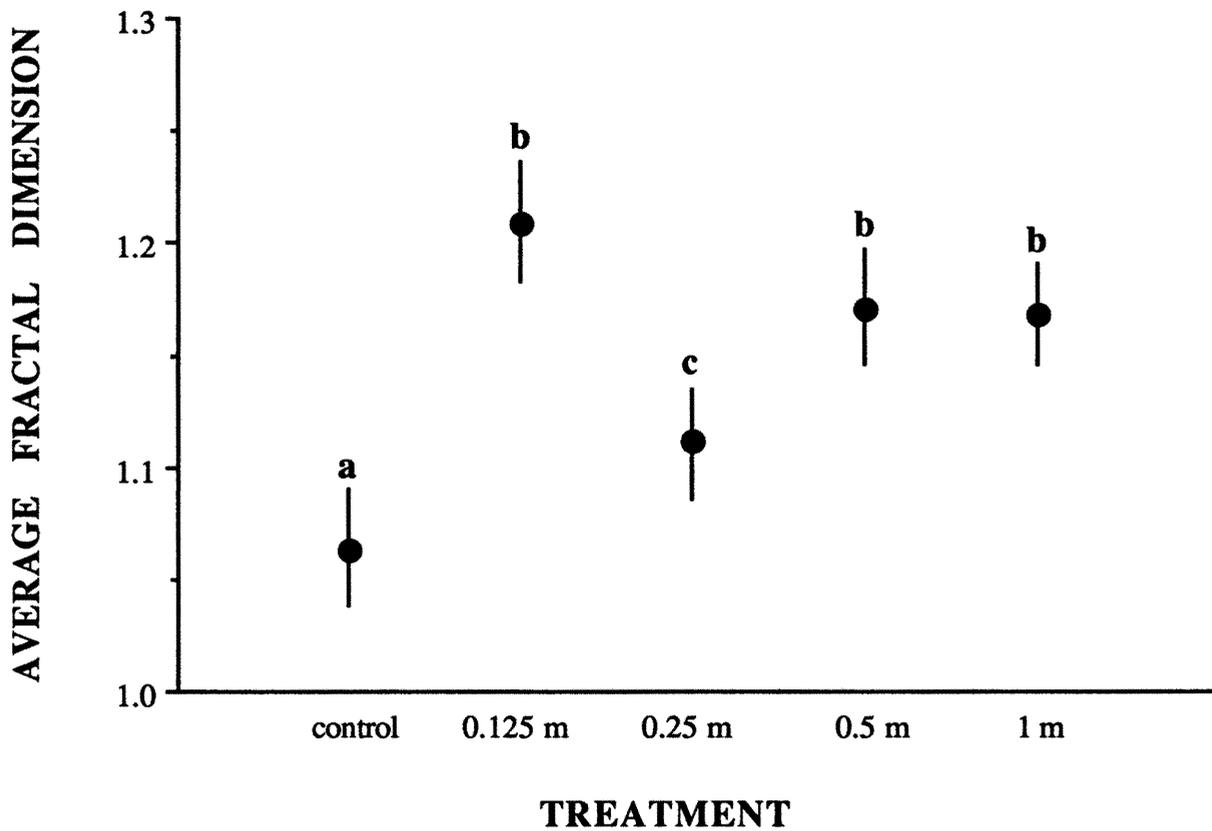


Fig. 5.3. Mean fractal dimension of movement pathways (\pm SE) by treatment. Abscissa indicates treatment levels as in Fig. 5.1. Means denoted with the same letter do not differ significantly (Fisher's protected least significant difference test, $P > 0.05$).

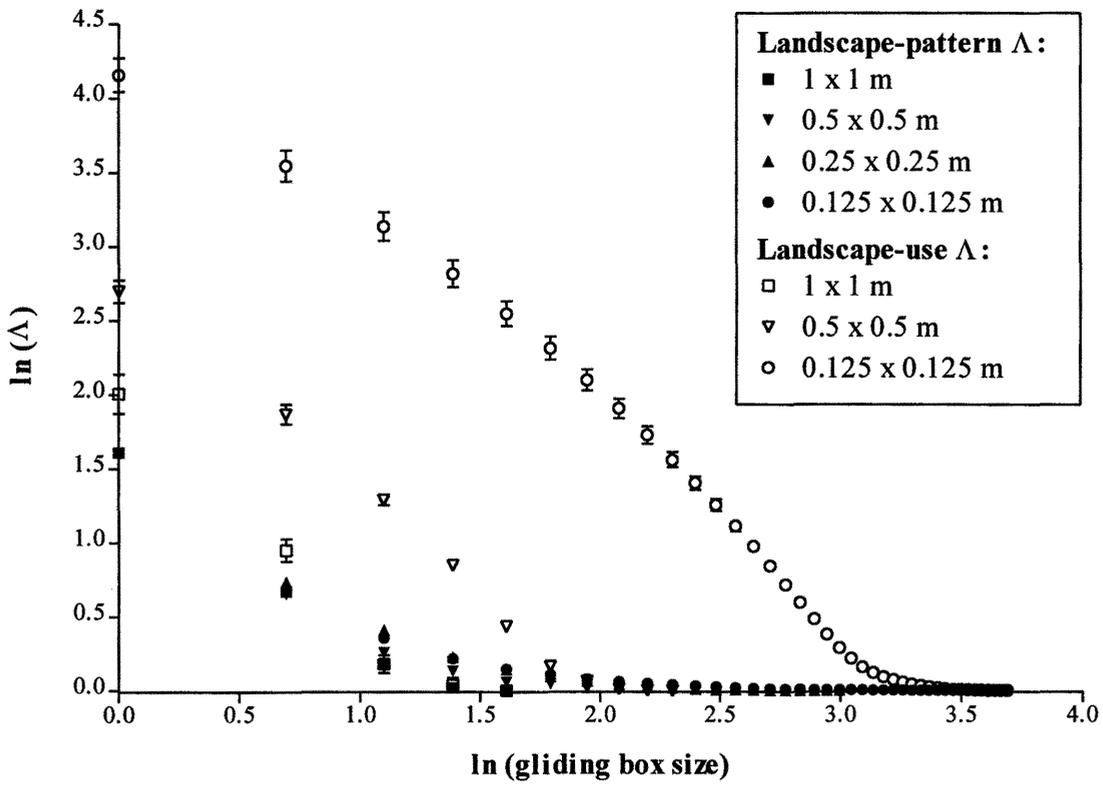


Fig. 5.4. Log-log plot of mean (\pm SE) lacunarity (Λ) as a function of gliding box size for landscape-pattern lacunarity (open symbols) and landscape-use lacunarity (filled symbols) in treatments with 0.125 x 0.125 m, 0.25 x 0.25 m, 0.5 x 0.5 m, and 1 x 1 m grass patches. Points represent means for landscape-use lacunarity over replicated pathways (N = 20 per treatment). Landscape-use lacunarity was not calculated for 0.25 x 0.25 m grass patches because data on path configuration relative to habitat patch configuration were not collected for that treatment.

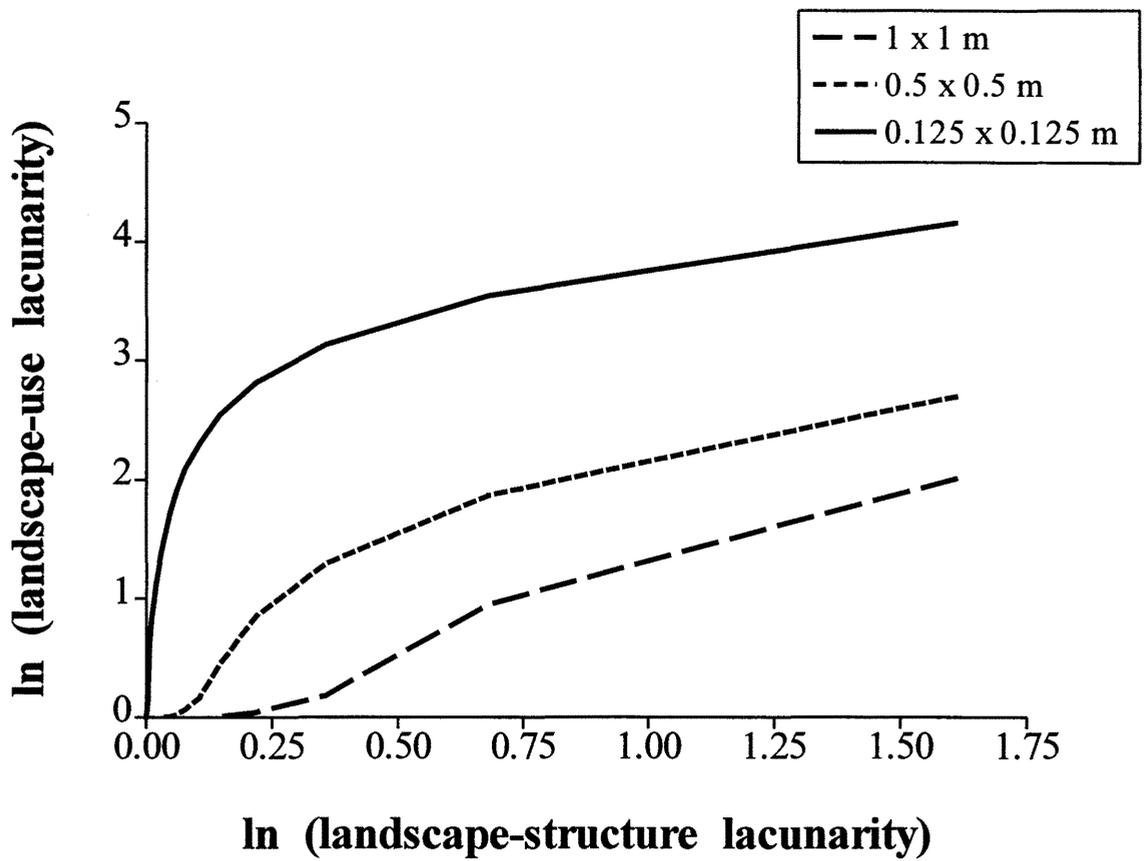


Fig. 5.5. Regression of mean ln (landscape-use lacunarity) versus mean ln (landscape-structure lacunarity) for different scaling treatments.

"Eternal prairie and grass...[Explorer John] Fremont prefers this to every other landscape.
To me it is as if someone would prefer a book with blank pages to a good story."

Charles Preuss

Exploring with Fremont (1842)

University of Oklahoma Press, Norman, OK

CHAPTER VI

INTERACTIONS BETWEEN HABITAT ABUNDANCE AND CONFIGURATION: AN EXPERIMENTAL TEST OF PERCOLATION THEORY

ABSTRACT

Recent neutral landscape models derived from percolation theory predict that a landscape with sparse but contagious habitat coverage is functionally equivalent to one with more abundant but randomly situated habitat patches. I tested this prediction in a field experiment that determined how habitat-patch abundance and configuration affect landscape use by animals. Using a 2x2 factorial design in a 25-m² landscape, I created four treatments by varying the ratio of habitat (grass) to non-habitat (sand) patches (10%:90% vs. 20%:80%) and the clustering of grass habitat patches (random vs. contagious). I then allowed tenebrionid beetles (Coleoptera: Tenebrionidae) to move through these treatment landscapes and measured their pathway characteristics. My results were largely consistent with model predictions. The amount of habitat present had a greater influence than did habitat configuration, particularly when habitat patches were situated at random within a landscape. Habitat abundance exerted its strongest influence on movement behaviors when habitat was sparse, regardless of spatial pattern. These individual-level results also supported a recent population-level landscape model that predicted that the amount of habitat was relatively more important than habitat pattern in long-term population survival. These results have important implications for conservation efforts that endeavor to preserve landscape function by maintaining some minimum amount of habitat coverage because

interactions between habitat amount and habitat pattern complicate how landscape function is detected and defined.

Key words: Connectivity, *Eleodes*, habitat abundance, habitat configuration, landscape structure, movement, percolation

INTRODUCTION

The influence of environmental patterns on biological processes that is the focus of ecology has only recently been examined with respect to how spatial structure determines landscape function (With and King 1997). Movement represents one manifestation of this pattern-process relationship (With 1994). The *functionality* of a landscape for movement (landscape *connectivity*; Taylor et al. 1993, With and Crist 1995, Keitt et al. 1997, With 1997, With et al. 1997) is thought to be determined by the spatial arrangement of habitat patches as well as movement behaviors within and between patches (Wiens et al. 1997, With 1997), particularly since the amount of habitat present may not be a good predictor of population size or dynamics (Wiens 1997a). Considering the functionality of landscape elements rather than just their spatial characteristics promotes a more realistic picture of how environmental features affect the abundance and distribution of organisms (With and Crist 1995). Landscape functionality is thus a central concern of conservation biology, although little experimental research has been conducted on it (With 1997).

Percolation theory from mathematics and physics provides one means of determining landscape functionality. Percolation theory was originally developed to describe movement of liquids through lattice networks (Orbach 1986). It has since been used as a simple neutral model of the movement through a heterogeneous landscape (Gardner et al. 1987, 1989; Gardner and O'Neill 1991). Percolation theory has been used to understand the movement of disturbance (Turner et al. 1989, Li and Archer 1997), ecotones in habitat phase transitions (Loehle et al. 1996), and organisms (Wiens et al.

1997). Under the percolation theory of organism movement, organisms move randomly through a landscape composed of permeable (i.e., habitat) and impermeable (nonhabitat) patches. When the proportion p of habitat patches in the landscape is low relative to total landscape area, organisms are confined to isolated areas of habitat and are unable to disperse to other habitat patches. As the proportion of habitat present in a landscape increases, however, habitat patches grow in size and begin to merge with neighboring clusters of habitat, forming larger aggregations. As this trend continues, eventually there is enough habitat present in contiguous aggregations to stretch from one edge of a landscape to the opposite edge, thereby permitting an organism to traverse the landscape; this critical threshold amount of habitat has been termed p_{crit} (Stauffer and Aharony 1985).

P_{crit} represents a transition point in the functionality of a landscape (a "threshold phenomenon" of With et al. 1997). When $p > p_{crit}$, habitat destruction results in habitat loss but does not create a *fragmented* landscape (Andrén 1994, With 1997); when $p < p_{crit}$, however, habitat isolation disrupts overall landscape connectivity. The value of p_{crit} is determined by a variety of factors, including the number, size, and shape of habitat patches (Gardner et al. 1992) and the movement "rules" followed by an organism (i.e., whether an organism can "leapfrog" over impermeable areas or is confined to move to only adjacent habitat patches, and whether an organism can move in any direction or is constrained to move in only certain directions; Pearson et al. 1996). For a landscape with habitat distributed at random and animal movement limited to only the four "nearest-neighbor" habitat patches (i.e., patches adjacent in the four primary cardinal directions), $p_{crit} = 0.5928$ (Stauffer and Aharony 1985). In other words, if a landscape is composed of at least 59.28% habitat (on average), it is functionally connected. More liberal movement rules (representing greater organism vagility; With 1997) decrease p_{crit} .

Recent research by With et al. (1997) has explored the relationship between the spatial structure of a landscape and percolation. With and colleagues compared population

dispersion and landscape functionality in random and fractal neutral landscape models. These models predicted that the value of p_{crit} would depend upon the spatial arrangement of habitat in a landscape. In a series of simulation experiments, With and colleagues compared the movement of organisms in landscapes with habitat arranged at random ($p_{crit} = 0.5928$) to movement in landscapes where the habitat was arranged with varying degrees of spatial dependence (i.e., contagion; $p_{crit} = 0.29-0.50$). By varying the proportions of three habitat types in their models, they were able to assess landscape carrying capacities, population distributions, and spatially dependent habitat affinities. Their simulation results predicted that (1) the amount of habitat present will have a greater effect when habitat patches are situated at random than when they are aggregated, and (2) the influence of the amount of habitat will be particularly evident when habitat is very rare.

In a similar series of simulation experiments, Fahrig (1997) predicted that the amount of habitat present would exert a stronger influence in enhancing long-term population survival than would habitat pattern. Because Fahrig's model was population-parameter-based rather than individual-response-based as is percolation theory, we could not test its predictions per se; we can, however, provide evidence at a different hierarchical level (that of the individual) to support or refute its predictions.

I empirically tested the predictions from percolation theory in With et al. (1997) in a set of field experiments. Modeling proposes mechanisms that account for biological patterns. Without experimentation, however, the proposed relationship between cause and pattern remains hypothetical. Progress in ecology depends upon combining empiricism with theory by testing predictions generated from models (Weiner 1995) in a spatially realistic fashion (Fahrig and Merriam 1994, Wiens 1995). Making this progress requires that theory be synthesized with experimentation (Wiens 1996, 1997b), as in this paper and the only other experimental test of percolation theory (Wiens et al. 1997).

The ultimate goal of such a theoretical-empirical synthesis is to predict how landscape heterogeneity affects the structuring of populations by affecting how individuals respond to spatial patterning. Knowledge of this sort is a critically important component of effective biodiversity conservation in the face of anthropogenic landscape fragmentation (Harrison 1994, Lidicker 1995, Harrison and Taylor 1997). Because real landscapes exhibit more contagious habitat patterns than random patterns (Gardner et al. 1987), results from this research should provide a better understanding of how natural landscape heterogeneity influences, proximally, the behavior of organisms and, ultimately, landscape function.

METHODS

My field experiments were conducted from 30 June through 2 August 1997 on the shortgrass prairie of northern Colorado. I used a 5x5-m experimental outdoor arena in which I could manipulate the amount and configuration of habitat patches. This arena consisted of a sand matrix, surrounded by a 4-cm-high wooden fence, in which buffalograss sod (*Buchloë dactyloides*) habitat patches were arrayed (following the design in Wiens et al. 1997). This experimental system mimicked the surrounding shortgrass prairie environment by using patches of a native prairie grass species (Lauenroth and Milchunas 1991). This physiognomically simple experimental design also provided a field representation of the two-dimensional, binary landscapes of percolation theory.

Previous work with a similar experimental design that compared movement patterns in landscapes composed of 0, 20, 40, 60, and 80% grass revealed that simple grass-sand landscapes containing $\geq 20\%$ grass were functionally equivalent with respect to movement and significantly different from a homogeneous sand landscape (Wiens et al. 1997). Therefore, I created treatments with habitat coverage no greater than this 20% threshold even though this amount of coverage is well below previously derived values of p_{crit} .

Four treatments were created by manipulating the ratio of grass to sand as either 10%:90% (grass:sand) or 20%:80% and the configuration of the grass patches as either randomly distributed or contagious (Fig. 6.1). I divided the 25-m² arena into 400 0.25x0.25-m squares. The two treatments with 10% grass coverage consisted of 40 grass squares and 360 sand squares; for the two treatments with 20% grass coverage, 80 squares contained grass and 320 contained sand. For the two treatments with randomly distributed grass coverage, I used a random-number generator to assign squares to be filled with grass sod. For the two treatments with contagious habitat coverage, I randomly selected squares to represent "seeds" from which further habitat coverage would grow. For the 10% coverage treatment, I used 4 seeds (10% of 40 grass squares, selected at random); for the 20% coverage treatment, 16 seeds were used (20% of 80 grass squares, selected at random). I then assigned sod coverage to squares adjacent to these seeds in a spatially constrained manner (fractal growth; Mandelbrot 1983). Habitat clusters "grew" from each seed in a stepwise fashion: "growth" proceeded from each seed in a randomly selected direction to one of the four "nearest-neighbor" adjacent squares, then from that square, and so on until the total landscape proportion of grass coverage was achieved. This design thus comprised a 2x2 factorial array in which the two random-coverage treatments could be considered collectively for comparison with the two contagious-coverage treatments or the two 10%-coverage treatments could be combined for comparison with the two 20%-coverage treatments.

The buffalograss sod was sunk into the sand until the sod surface was flush with the sand so as to keep the sod from showing raised edges that could have impeded movement into and out of grass patches. The presentation order of the four landscape treatments was selected at random, although all pathways for a treatment were completed before a new treatment was constructed. Treatments were presented in this sequential-block manner to ensure exact spatial replication of the landscape treatments; this critically

important source of variation would not have been controlled if the pathway-replicate/landscape treatment presentation had been completely randomized. Since it took only ca. 7 d to complete all the pathways for a treatment, any possible temporal block effect was minimized.

Eleodes obsoleta beetles (Coleoptera: Tenebrionidae) were then allowed to percolate through these landscapes. *E. obsoleta* is one of the most abundant animal species of the shortgrass prairie (Whicker 1983, Lauenroth and Milchunas 1991, Crist et al. 1992). Although incapable of flight, these beetles are highly vagile and possess no true home ranges, wandering over hundreds of meters in a single day (Calkins and Kirk 1973, Doyen and Tschinkel 1974, Crist et al. 1992). Because these beetles are detritivorous, feeding primarily on grass and forbs (Young 1971, Rogers et al. 1988), the buffalograss sod used in the experiments provided resources that the sand did not.

I used wild-caught adult beetles in the experiments. These beetles were obtained within 0.5 km of the grass-and-sand arena immediately prior to experimental trials. To start a trial, an individual was placed in the center of the arena underneath an inverted opaque plastic cup for ca. 1 min. Upon removal of the cup, the trial began. The beetle's location was marked at 5-s intervals with small, consecutively numbered flags. The trial ceased when the beetle encountered the arena wall (which occurred after 60-230 s). Each beetle was used only once and then marked with a dot of paint on the elytra before being released in the vicinity of capture; marking individuals in this manner prevented "experienced" individuals from being used again in the experiments. All beetles were thus naïve with respect to the experimental arena, effectively mimicking the nomadic nature of these animals.

I took several precautions to minimize contact with the beetles. First, beetles were handled as briefly as possible. Second, I crouched at least 0.5 m away from individuals during movement trials. Third, I ensured that my shadow did not fall across an

individual's movement trajectory. Fourth, I swept the experimental arena after each trial to remove footprints and any other obstacles or cues. Finally, I delayed placing the numbered flags that marked beetle locations for ca. 1 s to prevent pursuing or herding the beetle. A 5-s movement interval was used because it provided a fine temporal scale of assessing movement responses to spatial structure while minimizing pursuit or herding of beetles.

Trials were conducted when soil surface temperatures were 17-29 °C, the thermal activity window for this species (Whicker 1983, Whicker and Tracy 1987). All trials were conducted between 0700 and 1100 MDT. Each pathway was electronically surveyed with a Pentax PTS-II05 electronic distance-measuring device (Tokyo, Japan). Locational data were translated into distance and angle measurements with software created by the Maptech Corporation (Loveland, Colorado). Twelve replicate pathways (one pathway per individual beetle) were surveyed for each of the four landscape treatments.

I used seven response variables to characterize the beetles' respond to the amount and configuration of grass habitat patches. *Path length* was the total distance travelled by an individual during one trial. *Net displacement* was the linear distance between the first and last points of a pathway. *Displacement rate* was the velocity of a beetle, calculated by dividing the net displacement by the total time of movement. *Fractal dimension (D)* quantified path tortuosity (with $D = 1.0$ being a perfectly straight line and $D = 2.0$ being a convoluted pathway that fills a plane; Mandelbrot 1983); this unitless metric is assumed to be scale-independent over the extent (*sensu* Kotliar and Wiens 1990) of measurements (Turchin 1996). *The number of time-steps* was the number of 5-s locational measurements made before the arena boundary was encountered. *The number of stops* was the number of pauses made during a pathway (i.e., the number of time-steps that were at the same location as the previous time-step). *The proportion of time-steps made on grass* assessed habitat selection. These seven variables were chosen because they represent multiple aspects of how an organism may respond to spatial heterogeneity, including turning

mechanics, distance travelled, speed of travel, and habitat selection (Crist et al. 1992, Wiens et al. 1997).

Statistical analyses used a balanced design of $N = 12$ replicated pathways for each of the four treatment landscape types. Each of the seven response variables was analyzed with separate analyses of covariance (ANCOVA, with soil-surface temperature and beetle sex as covariates, and the amount and pattern of grass as main effects). If temperature and sex were not significant covariates, the data were reanalyzed in simple analyses of variance (ANOVA). Variables with significant ANOVA models were then compared between the two amounts of grass cover (10% vs. 20%) and the two grass-patch configurations (random vs. contagious) with Fisher's Protected Least Significant Difference (LSD) post-hoc multiple-comparison test.

RESULTS

Neither the sex of a beetle nor the soil-surface temperature at the time of experimental trials significantly influenced any movement pathway characteristics (P -values ranged between 0.3833 and 0.9942 for the seven response variables).

The question of whether a landscape with less but contiguous habitat was functionally equivalent to one with greater but randomly arrayed habitat was clearly answered affirmatively for only one of the seven variables measured (fractal dimension; Fig. 6.2d). Four other variables displayed interactions between habitat amount and configuration (net displacement, number of time-steps, proportion of time-steps made on grass, and number of stops; Fig. 6.2c, e, f, and g, respectively). For the remaining two variables (path length and displacement rate; Fig. 6.2a, b), the amount of habitat elicited stronger responses than did the pattern of habitat configuration. Movement path length was longer when there was relatively little habitat (10% grass), regardless of its configuration (Fig. 6.2a). The shortest pathways were seen in the treatment with 20% contagious

habitat. These relationships were also evident in examining the other variable that assessed distance travelled, net linear displacement (Fig. 6.2b), although significance was not as clearly segregated by habitat amount. Beetles travelled more quickly when there was relatively little habitat present, regardless of its configuration (Fig. 6.2c). Beetle pathways were the most convoluted in the treatment with 20% contagious habitat (Fig. 6.2d). With regard to habitat selection, beetles spent the longest time in movement (before encountering the arena wall) in the 20% random treatment (Fig. 6.2e), and most of this time was spent in the grass patches (Fig. 6.2f). Beetles also paused during movement the most in the 20% random treatment (Fig. 6.2g).

DISCUSSION

The patterns of significance in Fig. 6.2 show that, for the most part, the amount of habitat present elicited stronger responses than did the configuration of habitat. In other words, the comparison between 10% and 20% grass coverage exhibited more differences than did the comparison between the random and contagious treatments. Thus, *Eleodes obsoleta* beetles appear to be more responsive to habitat amount than to habitat pattern, at least at the scale and for the amounts of habitat in my experiments, although there were also significant interactions between these two factors. Given the nomadic nature of these insects, their insensitivity to spatial pattern is biologically logical because vagile animals encounter environmental heterogeneity in their wanderings, and sensitivity to such heterogeneity and habitat boundaries would repeatedly inconvenience them in their travels. Being responsive to the abundance of habitat, however, means that these beetles may respond negatively to the loss of habitat through conversion of prairie to agricultural fields or urbanized areas, although there are currently no data to evaluate this claim. A similar sort of difference between the importance of habitat area versus habitat isolation on population structuring and territory size has been shown for other species (Rolstad and

Wegge 1989).

Some of the seven response variables assessed slightly different aspects of the same overall movement behavior. For example, both path length and net displacement assessed distance travelled, whereas the number of time-steps, proportion of time-steps taken on grass, and number of stops assessed time spent in movement. There was concordance within these groups of related variables, as shown by similar patterns of significance. This concordance suggests that the observed responses were robust; the validity of any conclusions drawn would have been suspect if similar variables exhibited opposite trends.

It is perhaps not surprising that beetles moved more quickly when there was relatively little grass present to impede them (see also Chapter V). Similarly, it comes as no surprise that the most convoluted pathways were present in the 20% contagious habitat treatment. The fractal dimension assessed path-site selection by determining the degree of turns taken. Because the most tortuous pathways were found in the 20% contagious habitat treatment, it follows that the path length and net displacement values in this treatment were low. There is not necessarily a direct relationship between these variables and the number of time-steps taken (and, indeed, no such concordance is seen in Fig. 6.2) because a beetle may move only a short distance between successive 5-s points.

These results were largely consistent with the predictions of With et al. (1997) in that the amount of habitat present had a greater influence than did habitat configuration, particularly when habitat patches were situated at random. My results also support the simulation results of Fahrig (1997), whose model predicted that habitat loss is more critical to long-term population persistence than is habitat configuration. My study, however, also revealed interactions between the amount of habitat and the pattern of habitat for five of the seven pathway variables measured (Fig. 6.2b and d-g), indicating that a land-cover map, considered alone, may not predict whether a landscape is functional (i.e., connected, as opposed to fragmented).

This conclusion has important implications for conservation biology, as the primary objective of most conservation efforts is to preserve landscape function indirectly by directly maintaining some minimum amount of habitat coverage. Previous studies of how organisms are affected by landscape pattern have measured variables such as percent coverage of a given habitat type, average size of habitat patches, spacing between patches, and the like; predictions about the abundance and distribution of organisms on the landscape have then followed, given knowledge about the habitat requirements and life histories of the organisms under consideration. My results indicate that this endeavor may be short-sighted or perhaps incomplete because interactions between the amount and pattern of habitat will complicate how landscapes are used by organisms and how that use is detected and defined.

This conclusion should not be interpreted as criticizing the ability to make general predictions about organism-landscape relationships, however, particularly since it is logistically unfeasible to develop individual-based experiments or models for every species in every landscape (With 1997). Rather, my results reaffirm the need for generalizable spatially explicit models, and these models require empirical assessment before they can be usefully applied. Some specific areas of future research in applying percolation theory to conservation biology include identifying how species perceive and respond to spatial structure, explicitly including spatial heterogeneity in population models, evaluating consequences of habitat fragmentation, identifying domains of population dynamics, predicting extinction thresholds of fragmentation, incorporating spatial heterogeneity in reserve designs, and determining landscape connectivity (With 1997).

Percolation theory provides a neutral model against which to test alternative hypotheses about how landscape structure affects the abundance, distribution, and behavior of organisms. Like any such model, it contains several simplistic assumptions. The foremost of these is that the spatial characteristics, configurations, and interactions of

patches do not influence the movement of organisms, other than by stipulating in which patches movement is permissible. This is clearly an unrealistic assumption. In addition, percolation assumes that organisms move like inorganic particles, according to specified and fixed directional rules (Pearson et al. 1996). Because almost nothing is known about movement dynamics across habitat boundaries, however (Wiens et al. 1993), more research is needed on how organisms respond to environmental heterogeneity (Gardner et al. 1987).

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LITERATURE CITED

- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos* 71:355-366.
- Calkins, C.O., and V.M. Kirk. 1973. Distribution and movement of adult false wireworms in a wheat field. *Annals of the Entomological Society of America* 66:527-532.
- 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* 6:536-544.
- Doyen, J.T., and W.F. Tschinkel. 1974. Population size, microgeographic distribution, and habitat separation in some tenebrionid beetles. *Annals of the Entomological Society of America* 67:617-626.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61:603-610.

- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50-59.
- 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 models for landscape analysis. Pp. 289-307 *in: Quantitative Methods in Landscape Ecology* (M.G. Turner and R.H. Gardner, eds.). Springer-Verlag, New York, NY.
- Gardner, R.H., R.V. O'Neill, M.G. Turner, and V.H. Dale. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecology* 3:217-227.
- Gardner, R.H., M.G. Turner, V.H. Dale, and R.V. O'Neill. 1992. A percolation model of ecological flows. Pp. 259-269 *in: Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows* (A.J. Hansen and F. diCastri, eds.). Springer-Verlag, New York, NY.
- Harrison, S. 1994. Metapopulations and conservation. Pp. 111-128 *in: Large-scale Ecology and Conservation Biology* (P.J. Edwards, N.R. Webb, and R.M. May, eds.). Blackwell Scientific Publishers, Oxford.
- Harrison, S., and A.D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pp. 27-42 *in: Metapopulation Biology: Ecology, Genetics, and Evolution* (I.A. Hanski and M.E. Gilpin, eds.). Academic Press, San Diego, CA.
- Keitt, T.H., D.L. Urban, and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* [online] 1:4. Internet URL: <http://www.consecol.org/vol1/iss1/art4>
- Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* 59:321-324.
- Lauenroth, W.K., and D.G. Milchunas. 1991. Short-grass steppe. Pp. 183-226 *in: Ecosystems of the World 8A: Natural Grasslands* (R.T. Coupland, ed.). Elsevier, Amsterdam.
- Li, B.-L., and S. Archer. 1997. Weighted mean patch size: A robust index for

- quantifying landscape structure. *Ecological Modeling* 102:353-361.
- Lidicker, W.Z. 1995. The landscape concept: Something old, something new. Pp. 3-19 *in: Landscape Approaches in Mammalian Ecology and Conservation* (W.Z. Lidicker, ed.). University of Minnesota Press, Minneapolis, MN.
- Loehle, C., B.-L. Li, and R.C. Sundell. 1996. Forest spread and phase transitions at forest-prairie ecotones in Kansas, U.S.A. *Landscape Ecology* 11:225-235.
- Mandelbrot, B.B. 1983. *The Fractal Geometry of Nature*. W.H. Freeman and Co., New York, NY.
- Orbach, R. 1986. Dynamics of fractal networks. *Science* 231:814-819.
- Pearson, S.M., M.G. Turner, R.H. Gardner, and R.V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. Pp. 77-95 *in: Biodiversity in Managed Landscapes: Theory and Practice* (R.C. Szaro, ed.). Oxford University Press, New York, NY.
- Rogers, L.E., N.E. Woodley, J.K. Sheldon, and P.A. Beedlow. 1988. Diets of darkling beetles (Coleoptera: Tenebrionidae) within a shrub-steppe ecosystem. *Annals of the Entomological Society of America* 81:782-791.
- Rolstad, J., and P. Wegge. 1989. Capercaillie *Tetrao urogallus* populations and modern forestry - a case for landscape ecological studies. *Finnish Game Research* 46:43-52.
- Stauffer, D., and A. Aharony 1985. *Introduction to Percolation Theory*. Taylor and Francis, London.
- 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. 1996. Fractal analyses of animal movement: A critique. *Ecology* 77:2086-2090.
- Turner, M.G., R.H. Gardner, V.H. Dale, and R.V. O'Neill. 1989. Predicting the spread of disturbance across heterogeneous landscapes. *Oikos* 55:121-129.
- Weiner, J. 1995. On the practice of ecology. *Journal of Ecology* 83:153-158.

- Whicker, A.D. 1983. Spatial and temporal distributions of tenebrionid beetles, genus *Eleodes*, in a grassland community. Ph.D. Dissertation, Colorado State University, Fort Collins, CO.
- Whicker, A.D., and C.R. Tracy. 1987. Tenebrionid beetles in the shortgrass prairie: Daily and seasonal patterns of activity and temperature. *Ecological Entomology* 12:97-108.
- Wiens, J.A. 1995. Landscape mosaics and ecological theory. Pp. 1-26 *in*: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- Wiens, J.A. 1996. Wildlife in patchy environments: Metapopulations, mosaics, and management. Pp. 53-84 *in*: *Metapopulations and Wildlife Conservation* (D.R. McCullough, ed.). Island Press, Washington, D.C.
- Wiens, J.A. 1997a. The emerging role of patchiness in conservation biology. Pp. 93-107 *in*: *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity* (S.T.A. Pickett, R.S. Ostfeld, M. Shachak, and G.E. Likens, eds.). Chapman and Hall, New York, NY.
- Wiens, J.A. 1997b. Metapopulation dynamics and landscape ecology. Pp. 43-62 *in*: *Metapopulation Biology: Ecology, Genetics, and Evolution* (I.A. Hanski and M.E. Gilpin, eds.). Academic Press, San Diego, CA.
- Wiens, J.A., R.L. Schooley, and R.D. Weeks. 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. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9:25-36.
- With, K.A. 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 A.W. King. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79:219-229.

With, K.A., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151-169.

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

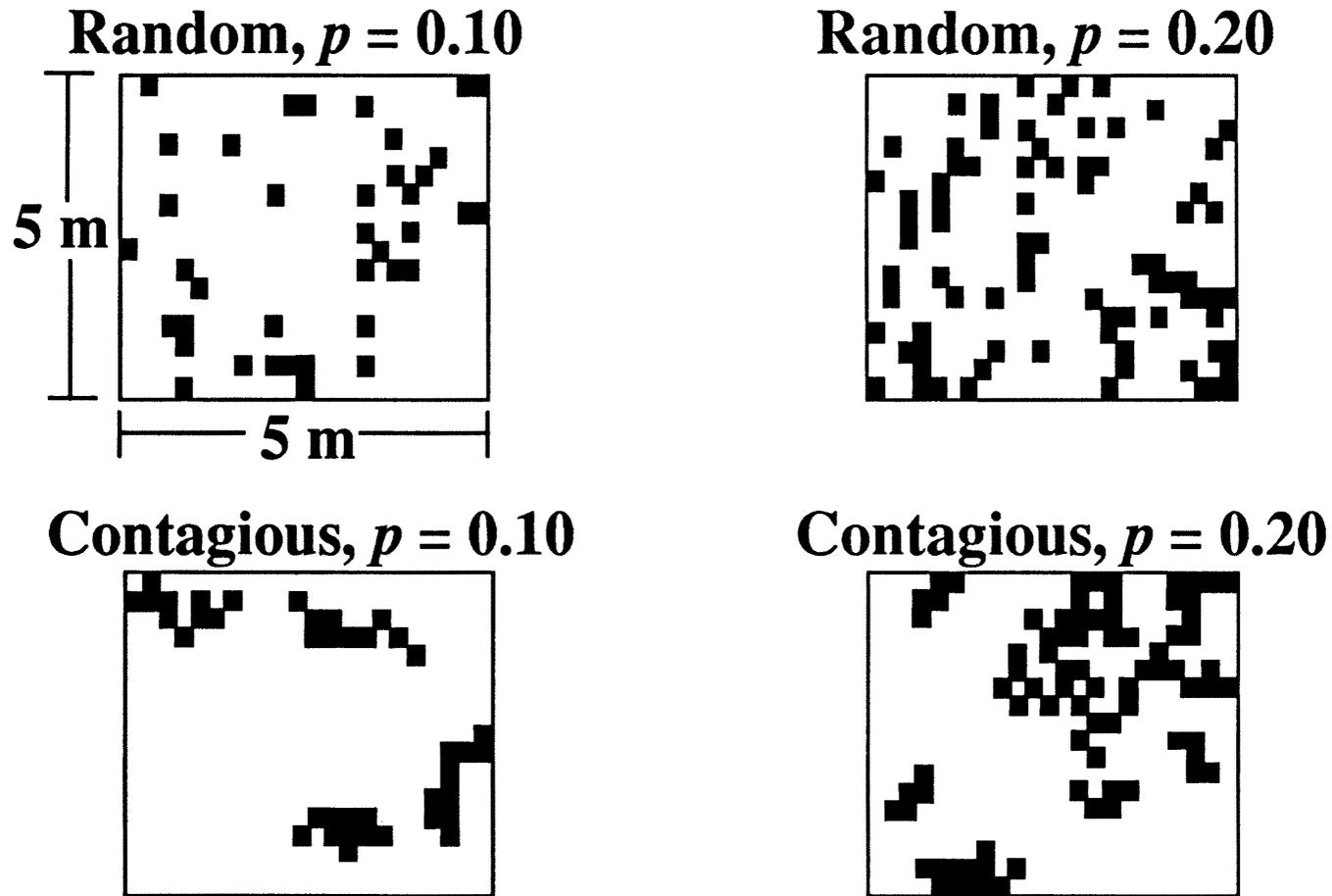


Fig. 6.1. The four landscape treatments used in the experiments. The proportion p of grass (shaded squares) within a sand (white background) matrix was varied as 10% or 20% and arranged at random (Random) or with some spatial autocorrelation (Contagious).

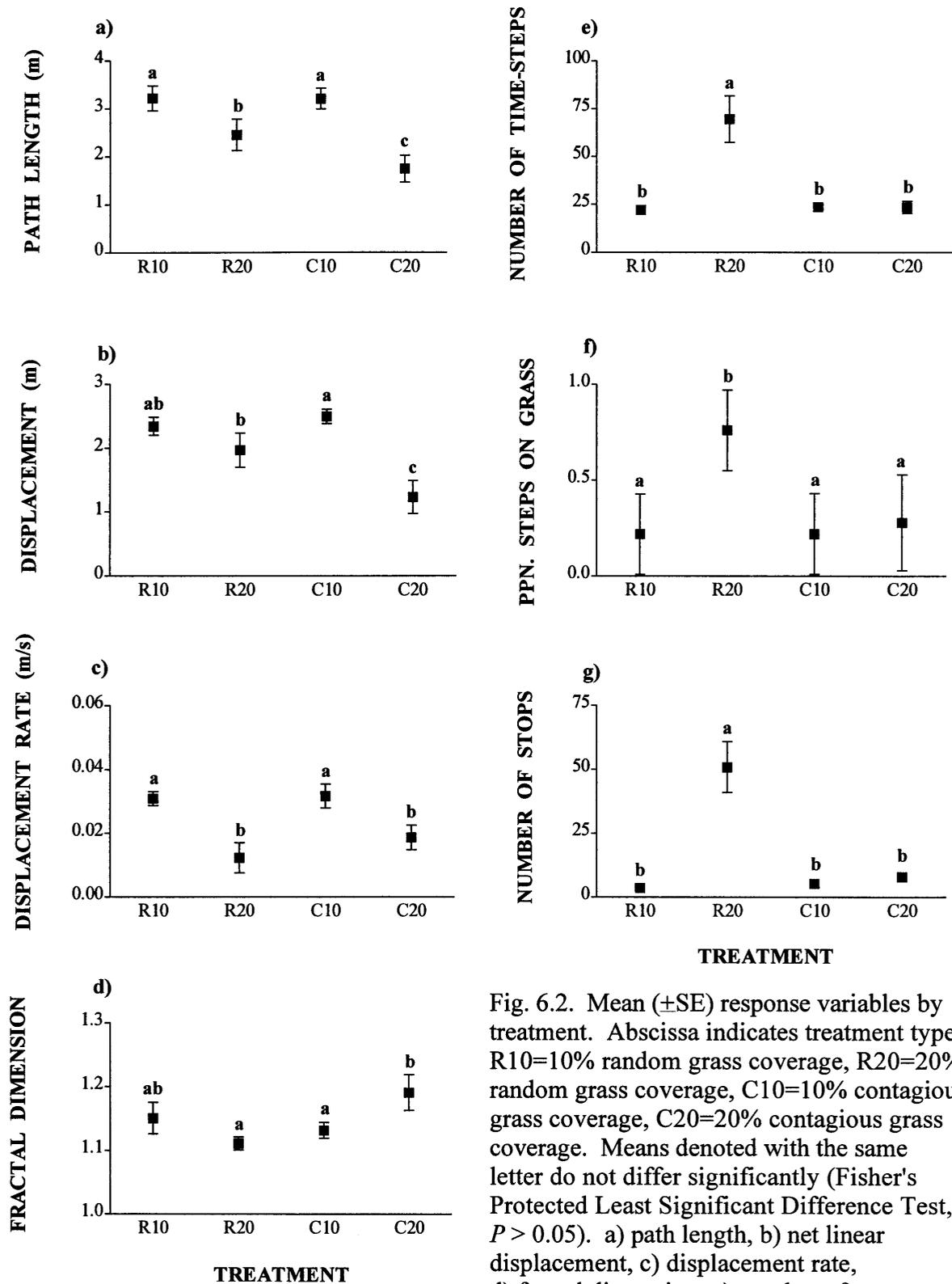


Fig. 6.2. Mean (\pm SE) response variables by treatment. Abscissa indicates treatment type: R10=10% random grass coverage, R20=20% random grass coverage, C10=10% contagious grass coverage, C20=20% contagious grass coverage. Means denoted with the same letter do not differ significantly (Fisher's Protected Least Significant Difference Test, $P > 0.05$). a) path length, b) net linear displacement, c) displacement rate, d) fractal dimension, e) number of time-steps, f) proportion of time-steps taken on grass, g) number of stops.

"I like to think of landscape not as a fixed place but as a path that is unwinding before my eyes, under my feet."

Gretel Ehrlich

"Landscape," *Legacy of Light* (1987, C. Sullivan, ed.)

Knopf, New York, NY

CHAPTER VII

OVERALL CONCLUSIONS

Movement is the process by which animals occupy elements of a heterogeneous environment, and a movement pathway is a record of how an animal responds to environmental structure (With 1994). It is difficult to imagine an ecological process that is not influenced by (or even dependent upon) the movement of organisms (Ims 1995). Landscape spatial patterns influence the movement patterns of organisms. These movement patterns are one of the determinants of patterns of habitat occupancy. Detailed knowledge of this two-tiered relationship is crucial for maintaining ecosystem functioning and biodiversity (Wiens 1995, With 1997).

In exploring this pattern-process relationship, I examined correlations in patterns of community and population structure in eleodid beetles with various spatio-temporal features (Chapter II) and speculated that some patterns of habitat occupancy may be determined by landscape "viscosity," which would affect movement parameters. I then combined these observations with results from field experiments in which I manipulated features that determine the viscosity of small-scale model landscapes and examined how those features affect the movements of small-scale model organisms (eleodid beetles). The spatial arrangement of landscape elements influenced how animals use a landscape (Chapter IV), with this relationship being complicated by scale-specific responses. The data presented in Chapter III, for example, demonstrated how microhabitat preferences may not accurately predict macrohabitat preferences because of different habitat-selection mechanisms acting at

different spatial scales. The scale of spatial heterogeneity within a landscape (Chapter V) and the interaction between the amount of habitat and habitat configuration (Chapter VI) also influenced animal behaviors, illustrating how different landscapes may be structurally different and yet functionally equivalent.

This experimental approach to landscape ecology provided some mechanistic knowledge about organism-environment relationships, showing that there is an interaction between habitat configuration and some movement characteristics and that this response is scale-dependent. Although directly extrapolating the results of these studies on eleodid beetles to other organisms may not be possible, experiments in landscape ecology can provide general insights into how animals respond to spatial heterogeneity (Johnson et al. 1992).

LITERATURE CITED

- Ims, R.A. 1995. Movement patterns related to spatial structures. Pp. 85-109 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- Johnson, A.R., J.A. Wiens, B.T. Milne, and T.O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* 7:63-75.
- Wiens, J.A. 1995. Landscape mosaics and ecological theory. Pp. 1-26 in: *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, eds.). Chapman and Hall, London.
- With, K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9:25-36.
- With, K.A. 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* 11:1069-1080.

"My days and nights, as I travel here--what an exhilaration!--not the air alone, and the
send of vastness, but every local sight and feature. Everywhere something
characteristic--the cactuses, pinks, buffalograss, wild sage--the receding perspective...the
prairie dogs and the herds of antelope--the curious 'dry rivers'...While I know the standard
claim is that Yosemite, Niagara Falls, and Upper Yellowstone and the like afford the
greatest natural shows, I am not sure that the prairie and plains, while less stunning at
first sight, last longer, fill the esthetic sense fuller, precede all the rest, and make North
America's characteristic landscape. Indeed, through the whole of this journey, with all its
shows and varieties, what impress'd me, and will longest remain with me, are these same
prairies. Day after day, night after night, o my eyes, to all my senses--the esthetic one
most of all--they silently and broadly unfolded."

Walt Whitman

Specimen Days (1882; 1949 ed.)

Simon and Schuster, Inc., New York, NY