

Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns

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Summary

1. Patterns of animal movement provide a spatial record of how organisms interact with landscape structure.
2. Although species may differ in absolute measures of movement (e.g. net displacement), they may nevertheless interact with landscape structure in similar ways. Fractal analysis affords a scale-independent measure that assesses pattern structure across a range of spatial scales. Similarities in the fractal geometry of movement pathways therefore indicate that species are interacting with landscape structure in similar ways.
3. Within a species, different life stages may possess different perceptions of landscape structure. To test this idea, I examined how developmental stages of a gomphocerine grasshopper (Orthoptera, Acrididae), *Opeia obscura*, interacted with microlandscape structure in a grassland mosaic.
4. Adults moved two to six times farther and were more strongly influenced by microlandscape structure than were nymphs. The fractal dimensions of movement pathways (an index of pattern complexity) differed significantly between life stages, indicating that adults and nymphs interacted with landscape structure in different ways.
5. Nymphs traverse the landscape in a different manner to adults: nymphs leap between discrete vegetative structures (e.g. grass blades), whereas adults move across the plane of the landscape. Nymphs thus possess a finer perceptual grain of landscape structure; nymphs move at slower rates and can resolve small-scale details. Adults move at faster rates across the mosaic, and may operate at a greater spatial extent than nymphs.

Key-words: Fractal analysis, heterogeneity, landscape ecology, scale

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Introduction

Movement patterns provide a spatial record of how organisms interact with environmental complexity. They therefore provide an operational means for identifying the scale(s) bounding individual movement (e.g. Wiens & Milne 1989; Crist *et al.* 1992; With 1994). Identification of these 'domains' of scale (*sensu* Wiens 1989) is not a trivial pursuit. If patterns at fine scales are essentially indicative of patterns at larger scales (i.e. they are either independent of scale or change linearly as a function of scale), then information gained about small-scale patterns may be employed to understand processes operating at broader scales (Gardner *et al.* 1989). Given the tractability of working at small scales, research on

animal movement patterns may provide mechanistic explanations for distributional patterns and dynamics of populations in spatially complex environments (e.g. Turchin 1991; Johnson *et al.* 1992).

Identification of what constitutes boundaries to individual movement is central to understanding how an organism views landscape structure—the vegetation or habitat mosaic through which an organism moves (Wiens, Crawford & Gosz 1985). Certain elements within a landscape may facilitate movement, whereas others may impede movement to varying degrees or may be impassable. In the two-phase landscape characteristic of a grassland system (grass interspersed with bare ground), for example, movement of tenebrionid beetles (*Eleodes* spp.) was enhanced along bare ground 'corridors' (Wiens & Milne 1989). Different species are likely to be constrained to different degrees by landscape structure. Nevertheless, similarities in responses to landscape structure might be

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clear once these differences in scale are taken into consideration. For example, a large species of tenebrionid beetle (*Eleodes hispilabris*) travelled farther in a grassland mosaic than smaller species of beetle (*E. obsoleta* and *E. extricata*), but the structure of its movement patterns was similar to those of the smaller species (Crist *et al.* 1992). Movement patterns of large beetles are essentially scaled-up versions of those of small beetles.

Such findings of similarities in landscape interactions among species occupying the same habitat are intriguing because they suggest that a general set of 'rules' may determine how different organisms respond to landscape structure across a range of scales. But does the manner in which an organism interacts with landscape structure remain constant throughout its lifetime, particularly for species that undergo ontogenetic changes within the same habitat? Ontogenetic shifts in habitat or resource use presumably reflect trade-offs in foraging, predator avoidance or reproduction that may be constrained by body size (Van Horne 1982; Werner & Gilliam 1984; Werner & Hall 1988). To document ontogenetic shifts in how a species interacts with landscape structure, one approach would be to compare the movement responses of different life stages to heterogeneity. As indicated previously, a scale-independent measure of movement is desired in order to factor out allometric effects attributable to differences in body size between developmental stages.

Similarity in response to landscape structure may be addressed by fractal analysis, which affords a scale-independent measure that can be used to assess movement pattern structure across a range of scales. The fractal dimension, D , is a standardized index of pattern complexity that permits comparisons of patterns occurring at different scales (e.g. Sugihara & May 1990; Milne 1991). Theoretically, animal movement patterns in two-dimensional space may have fractal dimensions ranging from 1, a straight line, to 2, a convoluted, tortuous pattern that essentially fills a plane (i.e. a random walk; Mandelbrot 1983). Linear movement patterns typify directed movement in landscapes that offer little resistance and which are viewed as homogeneous by the organism (With 1994). The value of D for movement pathways should increase as the environment becomes more heterogeneous; animals exhibit more convoluted patterns of movement in structurally complex environments (Wiens & Milne 1989; Crist *et al.* 1992).

Grasshoppers provide a model system with which to investigate organismal responses to heterogeneity because vegetation structure influences microhabitat choice (Anderson 1964; Joern 1982, 1983) and it is therefore reasonable to expect that landscape structure will influence movement patterns in grasshoppers. Furthermore, grasslands are essentially two-dimensional templates, which facilitate the study of how movement is affected by environmental com-

plexity. I therefore studied *Opeia obscura* (Thomas), a gomphocerine grasshopper (Orthoptera: Acrididae) that inhabits the shortgrass prairie of north-central Colorado. This species undergoes continuous development in the same habitat, which provided an ideal opportunity to explore how different life stages (nymphs vs adults) respond to microlandscape structure. I conducted field experiments to test the responses of nymphal and adult *O. obscura* to microlandscape structure, by analysing movement patterns across plots that collectively represented a continuum of heterogeneity found in this grassland mosaic. My objectives were (1) to determine how microlandscape structure affected movement in this species, and (2) to compare movement responses of different life stages to heterogeneity. Grasshopper movement should be reduced in areas with a high degree of structural complexity. Given their larger size, adults are expected to exhibit greater rates of movement than nymphs, but it is not clear whether adults and nymphs will interact with microlandscape structure in similar ways. I therefore employed fractal analysis of movement patterns to evaluate my third (3) objective as to whether different life stages within a species interact similarly with microlandscape structure.

Materials and methods

THE SPECIES

The gomphocerine grasshopper *O. obscura* is an abundant species of the shortgrass prairie, ranging from Alberta and Manitoba south to Mexico (Otte 1981; Capinera & Sechrist 1982). *Opeia obscura* is one of 10 acridids that together comprise >95% of the grasshopper biomass at the Central Plains Experimental Range (CPER), the study area for this research (Van Horn 1972; Welch, Redak & Kondratieff 1991). This species is a late-season grasshopper: it overwinters in the egg stage and emerges in mid- to late June in eastern Colorado (K. A. With, unpublished observation). There are five instars, and adults are present from late July into October (Campbell *et al.* 1974; K. A. With, unpublished observation). As in most acridids, this species is sexually dimorphic in size (females, 25 mm; males, 16 mm; Capinera & Sechrist 1982). *Opeia obscura* feeds almost exclusively on blue grama (*Bouteloua gracilis* [H.B.K.] Lag.): 99.6% of the nymphal diet and 94.3% of the adult diet was composed of this perennial shortgrass (Pfadt & Lavigne 1982).

STUDY AREA

This research was conducted at the CPER Long-Term Ecological Research site, 50 km north-east of Fort Collins in Weld County, Colorado, USA, at an elevation of 1640 m. The primary study area was a 1.5-ha

area within a pasture that had been subjected to moderate grazing intensity (40% annual above-ground net primary production consumed by cattle) since 1939. Vegetation on this site comprised a matrix of perennial shortgrasses (primarily *B. gracilis*), interspersed with perennial midgrasses (*Aristida longiseta* Nutt.), shrubs (*Chrysothamnus nauseosus* [Pall.] Britt., *Gutierrezia sarothae* [Pursh.] Britt. & Rusby), cactus (*Opuntia polyacantha* Haw.), a number of forb species, and areas of bare ground.

EXPERIMENTAL DESIGN

The movement responses of grasshoppers to microlandscape structure were assessed within five 5 × 5 m plots, which collectively represented a continuum in heterogeneity, and which were placed within the primary study site. The degree of heterogeneity was assessed by visually estimating the per cent cover of each of six vegetation types [shortgrass, midgrass (>10 cm high), shrub, cactus, forb, bare ground] within each plot. An 'index of heterogeneity' (HI) was obtained for each plot by dividing the percentage of the matrix cover type (shortgrass) by the number of other cover types that comprised at least 5% of the total vegetation cover of that plot. Given that *O. obscura* feeds almost exclusively on the shortgrass *B. gracilis*, it is reasonable to assume that the abundance and distribution of its host plant (i.e. the shortgrass matrix) is an important structural component of this grasshopper species' landscape. Describing landscape structure solely in terms of the total coverage of the host plant ignores the spatial complexity of the vegetation mosaic, however. The degree to which the distribution of the host plant is disrupted by other vegetation types (i.e. microlandscape structure) is predicted to affect movement responses in this species. Two plots may contain the same coverage of shortgrass (e.g. 55%), but differ in spatial complexity: one plot may contain 45% bare ground and thus be structurally more simple (homogeneous) than another containing 15% cactus, 10% midgrass and 20% bare ground (heterogeneous). My measure of heterogeneity therefore indexes the continuity of the shortgrass matrix; it is not sensitive to the specific types of vegetation that disrupt the matrix, however.

The grassland mosaic across the entire study area could be categorized by three types of heterogeneity, relative to the continuity of shortgrass cover: (1) homogeneous (H) (HI > 19; $\bar{x} \pm \text{SD} = 27.2 \pm 6.53$), (2) moderately heterogeneous (MH) (HI = 11–19; 14.6 ± 2.46), and (3) very heterogeneous (VH) (HI ≤ 10; 7.5 ± 1.35) ($F = 180.86$, $P < 0.001$, $df = 2, 119$, $n = 122$ 6.25 × 6.25-m² cells sampled throughout the 1.5-ha study area; ANOVA). The majority of the study area comprised very heterogeneous (48.4%) and moderately heterogeneous (45.1%) areas; only 6.6% of the area could be classified as homogeneous. To reflect the landscape mosaic

through which individual grasshoppers moved in this habitat, the number of release plots placed within each of these three categories of heterogeneity was stratified according to the mosaic composition of the study area. Thus, two plots were representative of very heterogeneous areas, two were moderately heterogeneous, and a single plot was homogeneous. The homogeneous plot represented nearly continuous ('lawn-like') coverage of shortgrass ($64.4 \pm 12.37\%$), with few patches of other vegetation types (number of other cover types > 5%, 2.6 ± 0.52). At the other extreme, coverage of shortgrass in very heterogeneous plots ($32.2 \pm 5.02\%$) was patchily distributed in a mosaic of other cover types (4.4 ± 0.48). Moderately heterogeneous plots were intermediate with respect to coverage and distribution of shortgrass ($49.1 \pm 5.37\%$, 3.4 ± 0.50 cover types). Because nymphs and adults were necessarily observed at different times in the season, vegetation stature within the plots may have changed in the interim. As my measure of heterogeneity indexes the complexity of microlandscape structure and is based on coverage, not height, of vegetation, the degree of heterogeneity remains unaffected by such phenological changes.

MEASUREMENT OF MOVEMENT PATTERNS

Nymphs (instars 3–5; size 14.4 ± 2.42 mm, range = 10–18 mm) were observed from 14 July to 10 August 1991. Adults were observed from 8 September to 29 September 1991. Individuals to be used in the experiments were captured carefully by hand within the study area and were stored in plastic bags (with tops folded but not zipped shut) for no more than 1 h prior to release; grasshoppers in bags had access to both sun and shade, and *B. gracilis* was added for forage. Grasshoppers were released in approximately the centre of a plot and allowed to settle for 2–3 min. Individuals were usually observed at 20–30 °C. The movement patterns of five grasshoppers were measured in each of the five plots for each life stage (nymphs, $n = 25$; adults, $n = 25$). To reduce potential intersexual biases in the analysis of movement patterns of adults, only females were observed.

I marked the positions of individual grasshoppers with sequentially numbered toothpick flags at 20-s intervals for a total of 30 min (e.g. Turchin, Odendaal & Rausher 1991). This time interval proved to be on a small-enough scale to encompass the details of movement in grasshoppers; smaller time intervals (e.g. 10 s) did not significantly increase the resolution of the movement pattern (K.A. With, unpublished observation). Placement of toothpick flags required some finesse to avoid flushing the grasshopper and invariably entailed placement of toothpicks at lagged time intervals. Movement patterns were measured in the field using an electronic surveying station (Pentax PTS-II₀₅, Tokyo, Japan), which enabled accurate recording of the distances and angles between points

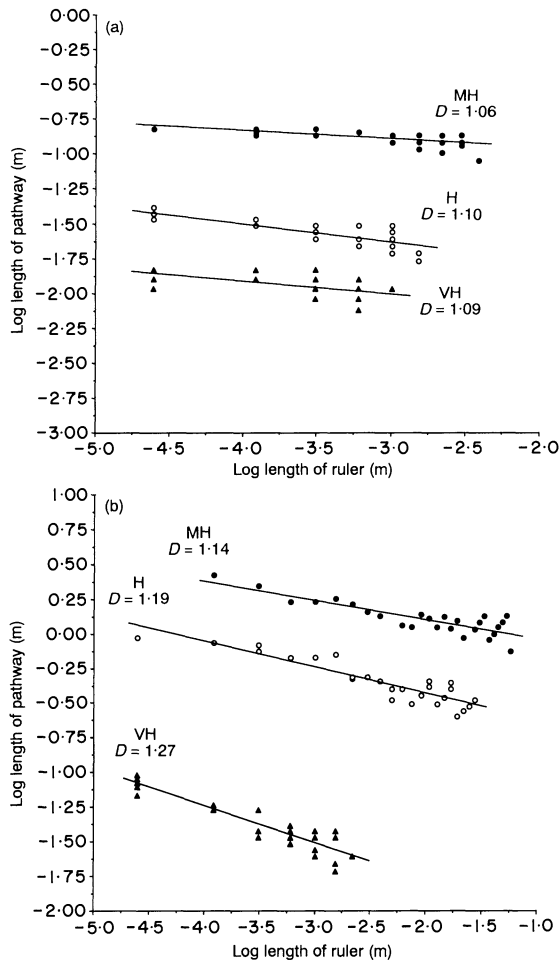


Fig. 1. Regression analysis used to obtain the fractal dimension of movement patterns for representative pathways of nymphal (a) and adult (b) *Opeia obscura* in different microlandscapes (H, homogeneous; MH, moderately heterogeneous; VH, very heterogeneous). Each line is for a single pathway that was measured at 25 different ruler lengths, which provided a corresponding overall path length. The fractal dimension, D , is obtained as 1 minus the slope of the regression line of the natural log of the path length against the natural log of the ruler length. Movement patterns that are essentially linear have D values close to 1 (e.g. nymphal *O. obscura*); more convoluted patterns of movement result in larger values of D (adult *O. obscura*).

from a fixed reference (corner stake of each plot). Data were converted to cartesian coordinates with surveying software (Maptech Inc., Colorado, USA) and were downloaded into a Pascal program to provide summary statistics on each movement pattern (Wiens, Crist & Milne 1993).

ANALYSIS OF MOVEMENT PATTERNS

Net displacement (cm), the straight-line distance between the starting and end points of the pattern, was obtained for each pattern of movement to serve as a scale-dependent measure of movement. Besides pro-

viding an intuitive interpretation (i.e. how far an animal has travelled in a given time period), this movement parameter also has a theoretical basis in models of animal movement (Kareiva & Shigesada 1983). The fractal dimension (D) provided a scale-independent measure of movement because pattern structure was assessed across a range of scales using the dividers method (Dicke & Burrough 1988; Milne 1991). This method entails measurement of the pathway of movement at different 'ruler' lengths; path length increases as the ruler length decreases because more details of the pattern are being measured at smaller ruler lengths (With 1994; Fig. 1). Programming the calculation of the fractal dimension of movement patterns actually requires the use of a circle with a fixed radius (owing to the difficulties of programming a line with a fixed length) and sliding the circle across the pathway and calculating the points at which it intersects the pathway (Fig. 2). A circle with a small radius (small ruler length) will intersect the pathway many times, whereas a circle with a relatively large radius will intersect the pathway fewer times (a small ruler is capable of measuring more of the details of the pattern than a larger one). The overall path length of the movement pattern is the sum total of measurements made at each scale (the different radii or ruler lengths); thus, path length will be greater at small scales (small ruler lengths) than at large scales (large ruler lengths).

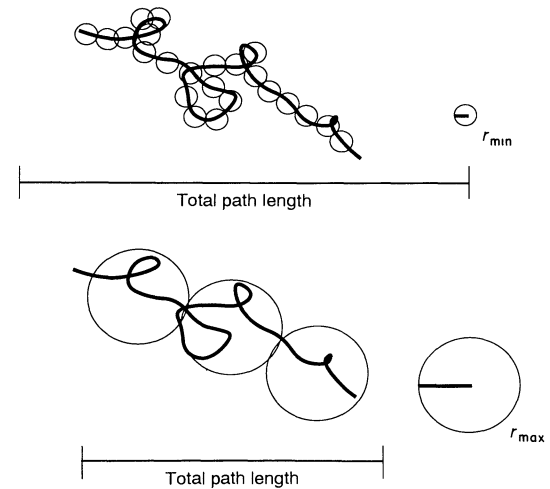


Fig. 2. Schematic representation of programming tool used to calculate fractal dimension. A circle with a fixed radius (owing to the difficulties of programming a line with a fixed length) is made to slide across the movement pattern and the points at which it intersects the pathway are calculated. The overall path length of the movement pattern is the sum total of measurements made with the circle at a given radius (ruler length). Other measurements are made with circles of varying radii to provide a relationship between the size of the ruler length used to measure the pattern and the corresponding path length of the movement pattern. Basically, as ruler length increases, the total path length decreases because fewer details of the pattern are being measured.

The fractal dimension is obtained from a regression of the natural log of the different ruler lengths against the natural log of the corresponding overall path lengths for each movement pattern (Fig. 1). Minimum ruler length was constrained by the average step length (mean distances between marked positions of the animal); maximum ruler length was obtained by one-third the total path length (three points required for a line in regression analysis). A total of 25 ruler lengths was used to measure each movement pattern (i.e. 25 points for each regression). The fractal dimension is acquired by subtracting the slope of this regression line from 1. Because the value of D is sensitive to the starting point within the pattern, D was calculated for four different starting points within the movement pattern (from each of the first four points of the pattern). The fractal dimension was thus derived as the average D from four regression analyses performed on each pattern. All patterns exhibited a linear relationship across the range of ruler lengths used to measure the pattern (Fig. 1). For a given phenomenon, a shift in the underlining process is likely to result in a change in D (Krummel *et al.* 1987). A significant difference in D for two movement patterns thus would indicate that the patterns are structurally dissimilar, presumably because of fundamental differences in the ways in which the organisms interact with microlandscape structure.

To assess the effects of microlandscape structure and life stage on movement patterns, I performed an analysis of variance (ANOVA, type III sums of squares for unbalanced sampling designs) with a mixed-effects model for each of the two dependent variables (net displacement and fractal dimension). Life stage and heterogeneity were classified as fixed effects, and plots were nested within heterogeneity and classified as a random effect (plots were randomly selected to

represent the three heterogeneity classes). A caveat of this type of ANOVA model is that potentially few degrees of freedom (relevant to the appropriate error term) are used to assess the significance of the F -statistic [e.g. plot \times stage(hetero), with 2 df, is the error term for the test of life-stage effects]. Therefore, analyses were also run using a pooled heterogeneity error term to increase the power of the test; the results from both sets of analyses are reported. Data were log transformed because graphs of residuals revealed departures from normality and homoscedasticity. Transformation of the data produced the desired distributions.

Results

Little of *O. obscura*'s activity period was spent in actual movement. Nymphs were stationary 90% of the time, whereas adults were slightly more mobile, remaining stationary 80% of the time. Adults moved three times farther (straight-line distance) than nymphs over the 30-min period (adults, $\bar{x} \pm SE$, 77.3 ± 14.98 cm; nymphs, 24.8 ± 5.07 cm, Table 1; mixed-model ANOVA with pooled heterogeneity error term: $F = 26.72$, $df = 1,4$, $P = 0.007$, $n = 50$). Adults exhibited greater displacement than nymphs in all three types of heterogeneity (Figs 3 and 4). This difference was most apparent in homogeneous areas, where adults moved 5.7 times farther than nymphs (Fig. 4). Heterogeneity had a small effect on nymphal displacement (nymphs moved only 50% farther in moderately heterogeneous plots as compared to homogeneous and very heterogeneous plots), whereas adults exhibited a significant decrease in net displacement as heterogeneity increased (Fig. 4, $F = 12.50$, $df = 2,2$, $P = 0.07$, $n = 25$; mixed-model ANOVA). Heterogeneity thus had a significant effect on overall net

Table 1. Effect of various factors on attributes of movement patterns for the gomphocerine grasshopper *Opeia obscura*. Effects attributable to individual plots (random effect) are nested within the type of plot (heterogeneity) for this mixed-effects ANOVA (type III sums of squares for unbalanced designs). Sample sizes are 25 nymphs and 25 adults (five from each life stage per release plot). NS, not significant at $P \leq 0.10$

Source of variation	df*	MS	F	P
<i>Net displacement</i>				
Heterogeneity	2,2 ^a	1.109	35.74	0.027
Plot(hetero)	2,2 ^b	0.031	0.40	NS
Life stage	1,2 ^b	2.660	33.99	0.028
Heterogeneity \times life stage	2,2 ^b	0.118	1.51	NS
Life stage \times plot(hetero)	2,40 ^c	0.078	0.26	NS
<i>Fractal dimension</i>				
Heterogeneity	2,2 ^a	0.001	0.45	NS
Plot(hetero)	2,2 ^b	0.002	2.09	NS
Life stage	1,2 ^b	0.013	13.17	0.068
Heterogeneity \times life stage	2,2 ^b	0.001	0.66	NS
Life stage \times plot(hetero)	2,40 ^c	0.002	0.58	NS

* Degrees of freedom used to test F -statistic. Error terms used in test were ^aplot(hetero) MS, ^bstage \times plot(hetero) MS, and ^ctotal error MS.

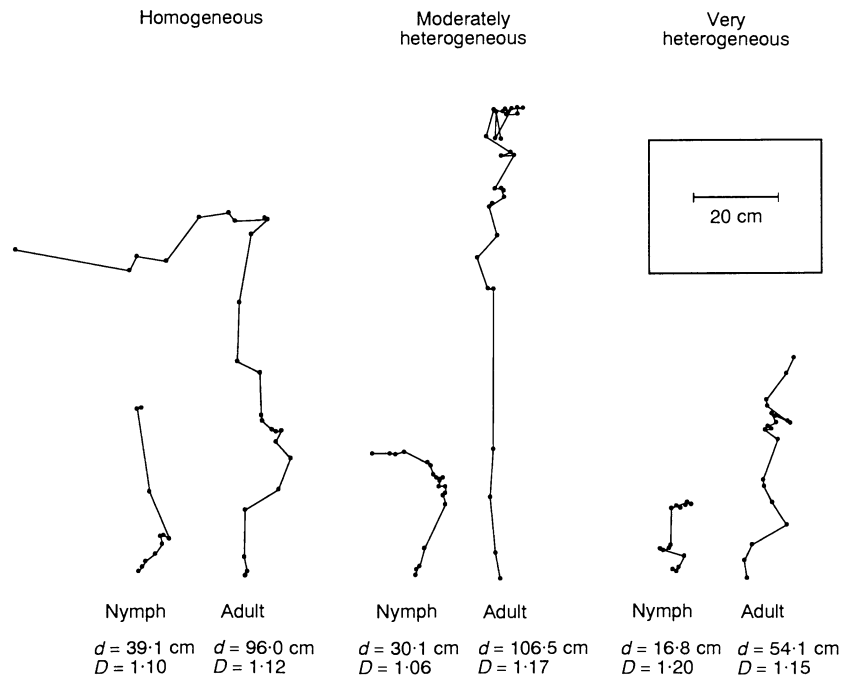


Fig. 3. Representative movement patterns of nymphal and adult *Opeia obscura*, a gomphocerine grasshopper, as a function of microlandscape structure in a shortgrass prairie. Each individual was observed for a total of 30 min and its location marked at 20-s intervals. Movement parameters for each pattern are net displacement (d), the straight-line distance between the starting and end points of the pattern, and fractal dimension (D), a measure that indexes pattern complexity across a range of scales.

displacement in this species (Table 1; H, 66.4 ± 30.07 cm; MH, 62.7 ± 12.93 cm; VH, 31.7 ± 8.43 cm).

Although *O. obscura* exhibits essentially linear patterns of movement ($D \rightarrow 1$; Fig. 3), adults produced more convoluted patterns than nymphs ($D_{adults} > D_{nymphs}$; Figs 1 and 4). The significant difference in the fractal geometry of nymphal and adult movement patterns indicates that pathways produced by these two life stages are structurally different (adults, 1.19 ± 0.03 ; nymphs, 1.10 ± 0.02 ; Table 1; mixed-model ANOVA with pooled heterogeneity error term: $F = 17.89$, $df = 1,4$, $P = 0.01$, $n = 50$). Adults and nymphs are thus interacting with microlandscape structure differently across the range of scales encompassed by the 25-m^2 release plots. The degree of heterogeneity had little effect on the fractal dimension of movement patterns, and there was no significant interaction between terms because adult movement patterns always had higher fractal dimensions whatever the microlandscape structure.

Discussion

Nymphal and adult *O. obscura* moved at different rates across this grassland mosaic and exhibited different responses to microlandscape structure. Adults travelled twice as far as nymphs in the heterogeneous plots and six times farther in the structurally simple

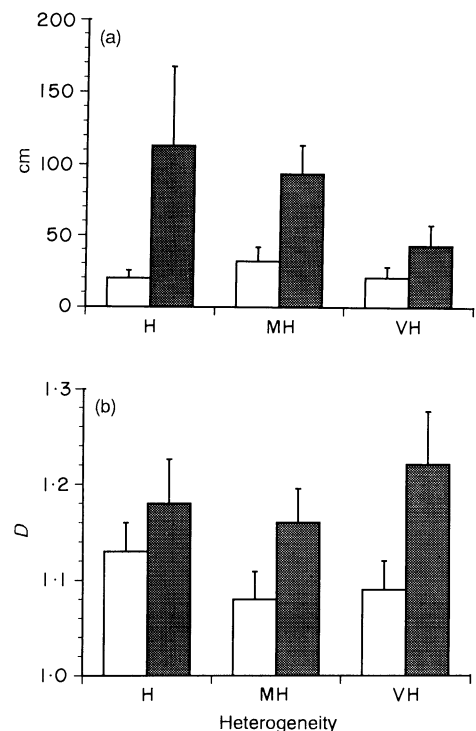


Fig. 4. Net displacement (a) and fractal dimension (b) ($\bar{x} \pm 1SE$) of movement patterns for the gomphocerine grasshopper, *Opeia obscura*, as a function of microlandscape structure (H, homogeneous; MH, moderately heterogeneous; VH, very heterogeneous) and life stage [nymphs (\square), $n = 25$; adults (\blacksquare), $n = 25$].

homogeneous plot. Given the differences in body size between life stages, it is perhaps not surprising that adults travelled farther than nymphs in a given amount of time. A scale-independent measure of movement pattern structure is therefore necessary to assess whether nymphs and adults are interacting with microlandscape structure in similar ways. Although this species of grasshopper produces essentially linear patterns of movement, the structure of adult movement patterns was significantly more complex than nymphal patterns (the fractal dimension of adult movement patterns was greater than that of nymphal movement patterns). Significant differences in the structural complexity of movement patterns (as indexed by D) suggest that nymphs and adults are interacting with the microlandscape structure of the shortgrass prairie in different ways. Fractal analysis thus revealed new insights into whether these two life stages interacted with landscape structure similarly, which was not apparent from the scale-dependent measure of net displacement alone.

How can we be certain that movement patterns actually reflect interactions with microlandscape structure, or that heterogeneity has been assessed at a scale relevant to grasshoppers? Heterogeneity is frequently defined in terms of the perceptions of the investigator rather than those of the organism under study. Kolasa & Rollo (1991) make the distinction between *measured heterogeneity*, which is a product of the observer's arbitrary perspective, and *functional heterogeneity*, which an organism actually perceives and to which it responds. In identifying how an organism perceives its landscape, the objective is to quantify the response of the organism to environmental complexity. In this study, response of grasshoppers to heterogeneity was assessed within a range of scale from centimetres to 25 m². Adults exhibited a differential response to heterogeneity within this range (an overlap in measured and functional heterogeneity), whereas nymphs did not.

The lack of a clear response to heterogeneity by nymphs over this range of spatial scales does not mean that nymphs are incapable of interacting with heterogeneity at this scale, however. There is evidence to suggest that nymphs are indeed capable of the range of movement exhibited by adults, but merely require longer time periods. I marked 30 nymphs on the pronotum with dots of enamel paint in unique colour combinations and then released each individual at the site of its initial capture. Of the nine nymphs found 2 days after release (23% recapture rate), the average \pm SD distance travelled was 165.1 \pm 67.00 cm. A single nymph that was located again 4 days after release had travelled 358.6 cm (almost twice as far as the location of this individual on day 2). Although nymphs may eventually interact with landscape structure across the same range of scales as encountered by adults, there is no way to assess from these data whether they are interacting

with landscape structure at larger scales in a manner similar to adults.

The differences in landscape interactions between developmental stages of *O. obscura* presumably reflect differences in the perceptive resolutions of the two life stages (With 1994). As a caveat, it is important to note that an analysis of movement patterns provides an *operational* definition of the perceptive resolution of an organism. The perceptive resolution of an organism is measured in this instance as the differential responses to landscape structure, which may integrate sensory perceptive abilities, physical constraints, behavioural preferences, and the like. Certainly, grasshoppers may perceive heterogeneity to which they do not respond. The perceptive resolution of an organism may comprise different levels of responses reflecting the hierarchical structure of heterogeneity existing at different scales (Kotliar & Wiens 1990). An organism's perceptive resolution is defined according to a spatial grain, the smallest scale at which an organism responds to environmental patterning, and an extent, the largest scale of heterogeneity to which an organism responds (Kotliar & Wiens 1990). The rate of movement across a landscape directly affects an organism's ability to perceive heterogeneity: as speed increases, the ability to perceive heterogeneity at smaller scales diminishes, whereas the spatial extent at which the organism operates may increase (Kolasa & Rollo 1991). Because adults moved more rapidly across the landscape (greater net displacement in the same time period as opposed to nymphs), they encountered more landscape elements and thus were more affected by heterogeneity (at least at the scale heterogeneity was measured in this study) than nymphs. Thus, vagile organisms (e.g. adult *O. obscura*) may perceive environmental patterns at small scales as being homogeneous (Kareiva 1982; Gendron & Staddon 1983; Wiens 1985; Kolasa & Rollo 1991).

Because of their sedentary nature, nymphs are capable of perceiving smaller scales of heterogeneity that perhaps lie outside the scope of adults; that is, the spatial grain of nymphs occurs at smaller scales than for adults. Adults, however, might be expected to operate at a larger spatial extent than nymphs, given their propensity for movement across the landscape. This would be true unless adults are bounded by some constraint other than landscape structure (e.g. territoriality or home range size). Acridids have been documented to exhibit a degree of 'site tenacity' within an area. In another arid grassland dominated by *Bouteloua*, four acridid species demonstrated average displacements of 60–80 m over a 6-week period (Joern 1983). Movement greater than 200 m from the initial release point was not detected for an Australian grasshopper (*Phaulacridium vittatum*; Clark 1962). Thus, adult acridids do not exhibit unbounded directional movement across the landscape. Data are not available on the long-term dispersal of *O. obscura* to

permit an assessment of the entire spatial range encompassing the landscape perception of this species.

Ontogeny may thus shift the perceptive resolution of a species toward broader scales. The notion that different developmental stages might possess different landscape perceptions has been based on the premise that statistically significant differences in the fractal geometry of movement pathways have a biological basis in how different life stages interact with landscape structure. A mechanistic explanation for this ontogenetic shift may be provided by comparing the way in which nymphs and adults move through the landscape and by considering the functional role each developmental stage plays in the life history of this species. The nymphal stage is a period of growth, in which the primary concerns of the organism revolve around finding food in favourable thermal environments and avoiding predation. Because this species forages on the abundant and widely available host plant, *B. gracilis*, *O. obscura* is immersed in its food resource. Searching for food is probably a minor consideration in comparison to locating a favourable thermal environment or avoiding predators. Nevertheless, nymphal *O. obscura* do not traverse the landscape as adults do, but leap between vegetative structures such as grass blades. This type of locomotory behaviour may increase convective cooling because it minimizes contact with the ground, which radiates more heat than vegetation (Whitman 1987). Clinging to vegetation may also serve as an anti-predation strategy, as the elongate and cream-coloured nymphs are cryptic when perched on a grass blade and tend to orient their bodies on the grass stem away from potential predators (K. A. With, personal observation). The functional role of adults, on the other hand, is reproduction. In addition to the above concerns for nymphs, adults are attempting to encounter mates and, in the case of females, locate favourable oviposition sites. Adults rarely fly: movement in adults, although not continuous, occurs either by walking or occasionally by short jumps.

The differences in landscape interactions between developmental stages in *O. obscura* may therefore result from differences in the way nymphs and adults move through the landscape, which in turn may be related to the functional roles played by each life stage. The implications of such ontogenetic shifts in landscape interactions extend to the study of the spatial dynamics of populations. My results suggest that the age-class characteristics of a population (e.g. vagility of different life stages) may be fundamentally important in understanding the distribution and dynamics of populations in a given habitat. Because grasshoppers are an important prey base in this grassland system, the spatial dynamics of different life stages (or species) may ultimately influence the foraging decisions and patterns of space use of predators (K. A. With, in preparation). Assessing how different

organisms interact with landscape structure may therefore provide a mechanistic foundation for the development of spatially explicit models of patterns occurring at broader scales.

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