

Using fractal analysis to assess how species perceive landscape structure

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Abstract

To develop a species-centered definition of 'landscapes,' I suggest using a fractal analysis of movement patterns to identify the scales at which organisms are interacting with the patch structure of the landscape. Significant differences in the fractal dimensions of movement patterns of two species indicate that the species may be interacting with the patch structure at different scales. Fractal analysis therefore permits comparisons of 'landscape perceptions' of different species within the same environment.

I tested the utility of this fractal application by analyzing the movement patterns of three species of acridid grasshoppers (Orthoptera) in a grassland mosaic. The largest species moved up to 6 times faster than the two smaller species, and species exhibited different responses to microlandscape structure within 25-m² plots. Further, the largest species exhibited different responses to microlandscape structure in two pastures subjected to different intensities of cattle grazing. This species thus is able to integrate information on landscape structure at broad spatial scales. Fractal analysis of movement patterns revealed that the two small species had significantly more tortuous patterns than the larger species, which suggests that these species are interacting with patch structure at a finer scale of resolution than the large species. Fractal analysis can be used to identify the perceptive resolution of a species; that is, the spatial grain and extent at which they are able to perceive and respond to heterogeneity. Analysis of movement patterns across a range of spatial scale may reveal shifts in fractal dimension that reflect transitions in how species respond to the patch structure of the landscape at different scales.

Introduction

With the recognition that the scale of 'landscapes' must be relevant to the organism or process under investigation (Risser 1987; Wiens and Milne 1989; Turner and Gardner 1991) has come the operational problem of identifying the pertinent range of scales that bounds a landscape in a given context. To adopt an organism-centered view of landscapes, one must define the perceptive resolution of the organism, the range of spatial scales across which an

organism views the landscape as heterogeneous. Perceptive resolution is constrained by the *grain*, the finest resolution at which an organism perceives spatial heterogeneity, and by an *extent*, the largest scale that an organism perceives (Kotliar and Wiens 1990; Wiens 1990; Kolasa and Rollo 1991; Turner and Gardner 1991). Because perceptual acuity (the ability of an organism to resolve spatial heterogeneity) is a function of the sensory abilities of the organism and is modified by physiological and behavioral constraints, it would be a daunting task to

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define all states that encompass the perceptive range of an organism. Further, the upper and lower thresholds defining grain and extent may shift during the development of the organism (With, *in review*), and may change as one alters the temporal resolution or duration of an investigation (*e.g.*, from a study of the daily movements to the lifetime home range of an organism).

Fortunately, perceptive resolutions may be assayed operationally by observing how an organism responds to the structural complexity of its environment. Animal movement patterns are ideal for assessing species' responses to heterogeneity because they provide a spatial record that documents how and at what scale(s) an organism interacts with patch structure (Wiens and Milne 1989; Crist *et al.* 1992; Johnson *et al.* 1992). Animal movement patterns provide a mechanistic link between a variety of ecological processes (*e.g.*, population dynamics, gene flow, predator-prey dynamics) and the spatial mosaic of the environment (Merriam *et al.* 1991; Johnson *et al.* 1992). Thus, inferences about the dynamics of broader scale processes might be made by extrapolating from easily manipulable, small-scale microlandscapes to the experimentally intractable broader-scale domain generally encompassing populations and trophic-level interactions (Turner *et al.* 1989; King 1991; Johnson *et al.* 1992).

Behavioral responses to landscape structure presumably integrate the sensory capabilities of the organism with the physical and biotic conditions of the environment (exogenous factors) that modify the 'motivational' state (endogenous factors) of the organism. In the present context, it is not important to understand *why* an organism interacts with landscape structure in a particular manner; rather, it is the result of this interaction that is of interest. Furthermore, it is not necessary to define the entire perceptive range to discern whether two organisms perceive landscape structure similarly. To illustrate, consider two species that move at different rates through a given landscape, perhaps as a function of body mass (*e.g.*, Swihart *et al.* 1988). The species that moves at a slower rate has the potential to discriminate landscape structure at a finer resolution than the more mobile species. The ability of an organism to process visual details varies as a function

of speed (Kareiva 1982; Gendron and Staddon 1983; Wiens 1985; Kolasa and Rollo 1991). Two species may have the same sensory capabilities, but their relative rates of movement will alter their abilities to resolve fine-scale details. As an analogy, consider one's relative ability to perceive minute details while sitting on a park bench versus sitting in a fast-moving vehicle. Rate of movement thus constrains the perceptive grain of an organism.

Although differences in movement rates may indicate that two species are operating at different scales within the landscape (the faster species has a greater extent per unit time than the slower species), this measure does not provide information on how species are interacting with the landscape structure across this range of scales. Do the species perceive landscape structure similarly? If a landscape is viewed as a hierarchical array of patchiness (*e.g.*, Kotliar and Wiens 1990), then one organism may ignore patch structure that occurs at certain scales, either because the level of heterogeneity at those scales falls outside its perceptual range, or because the patch structure within a particular range of scale is unimportant to the organism in a given context. In either case, the organism responds as if the landscape was homogeneous at these scales. Another organism may respond quite differently to landscape structure across this same range of scales.

My premise is that the response of an organism to heterogeneity will be reflected in the structure of its movement pattern. Departures of search patterns from either linear or random movement presumably reflect encounters with the physical structure of the vegetation or are in response to correlates of patch structure (*e.g.*, patch quality, potential for refugia, thermal properties of patches). Thus, if two species are interacting with the landscape mosaic across the same range of scale, similarities in the structure of their movement patterns suggest that they are responding similarly to (*i.e.*, perceiving) the patch structure of the landscape across this range of scales. In the example of the two species above, the faster species would exhibit greater net displacement in a given amount of time (a longer overall path length) relative to the slower species. Nevertheless, the movement pat-

terns may be similar in structure; the larger pattern may be a scaled-up version of the shorter one.

Fractal analysis offers a methodology for assessing pattern structure across a range of scales (Milne 1991); it affords a *scale-independent* measure of movement. The fractal dimension (D) indexes the overall complexity (tortuosity) of the pattern. If the same process (*i.e.*, response to landscape structure) influences movement patterns in different species, then differences in the values of D of movement patterns suggest that the species have different perceptions of landscape structure across the range of scales considered. Analysis of the fractal dimensions of movement patterns from different species within the same environment may therefore shed light on how different species perceive landscape structure.

To illustrate the utility of this approach, I analyzed the movement patterns of three grasshopper species (Orthoptera: Acrididae) in a grassland mosaic. I adopted a 'microlandscape' approach, which has been promoted as a means to increase the empirical rigor of tests of ideas normally considered at kilometers-wide scales (Wiens and Milne 1989; Johnson *et al.* 1992; Wiens 1992). In their own right, however, microlandscapes provide the template that dictates ecological and physical processes that occur at these small scales (cm to m). My objectives are to examine how microlandscape structure affects movement rates for these three grasshopper species and to determine whether species perceive landscape structure similarly in this system. I predict that large species of grasshoppers will move at faster rates than smaller species, as evidenced in another group of terrestrial arthropods, tenebrionid beetles (Coleoptera), within this same grassland system (Crist *et al.* 1992). It is not intuitive whether these three grasshopper species will share similar perceptions of the landscape; that is, whether they will interact with landscape structure in functionally similar ways across the range of scales encompassed by this microlandscape approach. Tenebrionid beetle species of different sizes move at rates commensurate to their size, but the different species nevertheless respond similarly to microlandscape structure (Crist *et al.* 1992).

Methods

Study area

I conducted this research at the Central Plains Experimental Range (CPER), a Long-Term Ecological Research site about 50 km NE of Fort Collins in Weld County, Colorado, USA (40° 49' N latitude, 107° 47' W longitude). At a broad scale, response of grasshoppers to large-scale patterns of heterogeneity was addressed by selecting two pastures that had been subjected to different intensities of cattle grazing since 1939. I established a 1.5 ha study site in each of these two pastures. The moderately grazed site had 40% of annual above-ground net primary production (ANPP) consumed by cattle, whereas 60% of the annual ANPP was consumed in the heavily grazed pasture. In general, the microlandscape structure within these pastures was represented by a perennial shortgrass matrix (*Bouteloua gracilis* and *Buchloe dactyloides*), which was disrupted to varying degrees by areas of bare ground and patches of other vegetation types such as shrubs (*Chrysothamnus nauseosus*, *Gutierrezia sarothae*), perennial midgrasses (*Aristida longiseta*), cactus (*Opuntia polyacantha*), and a number of forb species. The effect of intense cattle grazing was to produce a 'lawn-like' physiognomy (Milchunas and Lauenroth 1989), resulting in a more homogeneous landscape that was comprised of relatively few vegetation types.

The species

Two of the grasshopper species, *Psoloessa delicatula* (Scudder) and *Opeia obscura* (Thomas), belong to the subfamily Gomphocerinae, whereas the third species, *Xanthippus corallipes* (Haldeman), is in the subfamily Oedipodinae. These three species are numerically important in this grassland system (Van Horn 1972; Welch *et al.* 1991). *Psoloessa delicatula* and *X. corallipes* overlap temporally in that both are 'early season' species that overwinter as instars and are present as adults from early May to late June (Capinera and Sechrist 1982). *Opeia obscura* is a late-season species that overwinters as

eggs; nymphs emerge in mid June, and adults are present from August to October (Campbell *et al.* 1974). The two gomphocerines are relatively small (*P. delicatula* = 16–27 mm, *O. opeia* = 16–25 mm; Otte 1981; Capinera and Sechrist 1982) compared to *X. corallipes* (35–65 mm; Otte 1981). All three species are graminivorous; the perennial shortgrass *Bouteloua gracilis* is the major forage for all three species, comprising >90% of the adult diet in *P. delicatula* and *O. obscura*, and up to 60% in *X. corallipes* (Pfadt and Lavigne 1982).

Experimental design

In order to quantify the response of grasshoppers to microlandscape structure, I released individual grasshoppers within 5 × 5-m plots that had been selected to represent a continuum of heterogeneity found in this grassland system. Because the three grasshopper species forage primarily or exclusively on the shortgrass *Bouteloua gracilis* (Pfadt and Lavigne 1982), I assumed that the shortgrass matrix represented an important structural component of a grasshopper's landscape. I therefore classified microlandscape structure (heterogeneity) according to the degree to which the shortgrass matrix was disrupted by other types of vegetation (*e.g.*, cactus, shrubs). Heterogeneity was measured as the proportion of total cover that was shortgrass divided by the number of other major ($\geq 5\%$ total cover) vegetation types. Homogeneous (H) microlandscapes were nearly continuous shortgrass (% = $63.3 \pm 7.07(\text{SD})\%$ of total cover, $n = 36$ of 253 6.25 × 6.25-m cells sampled across the two pastures), which contained few vegetation types (\bar{x} number of vegetation types $\geq 5\%$ of total cover = 2.8 ± 0.38). At the other extreme, the shortgrass matrix within Very Heterogeneous (VH) microlandscapes was disrupted by more vegetation types ($\bar{x} = 4.2 \pm 0.43$, $n = 96$ cells), which reduced the cover of shortgrass in these areas to half that of H microlandscapes ($\bar{x} = 33.8 \pm 5.43\%$). Microlandscapes that were Moderately Heterogeneous (MH) were intermediate with respect to continuity of shortgrass cover ($\bar{x} = 50.5 \pm 5.20\%$, x vegetation types = 3.6 ± 0.51 , $n = 121$ cells).

The release plots were placed within randomly selected cells in each of the two pastures ($n = 5$ plots per pasture); the smaller size of the release grid (5 × 5 m) relative to the sampled area of the cell (6.25 × 6.25 m) ensured that a 'buffer zone' existed around the plot. In the event that an individual grasshopper left the plot during observations, it would still encounter the same degree of heterogeneity as within the plot. Because this study was conducted within the constraints of a larger research program, it was necessary to maximize sampling efficiency. I therefore stratified the placement of plots according to the composition of the different microlandscape types within each pasture. The microlandscape mosaic of the moderately grazed pasture was comprised primarily of MH (45.1%) and VH (48.4%) cells; H microlandscapes were a relatively minor component in this pasture (6.5%). Thus, two of the five (40%) release plots in this study area were placed in cells (selected at random) that were classified as MH, two in VH cells, and one in a H cell. The mosaic of the heavily grazed pasture was different from the moderately grazed pasture in that half of the area comprised equal numbers of H (21.4%) and VH (28.2%) cells, and the remainder of cells (50.4%) were MH. I therefore placed three of the five (60%) release plots in MH cells, and one plot each in a H and VH cell. This sampling scheme thus mimicked the spatial mosaic encountered by free-ranging grasshoppers in this system.

Analysis of movement patterns

I observed at least five individuals of each species in each of the five plots per pasture. Individual grasshoppers were released in approximately the middle of the plot and were observed for ca. 30 min each. I marked their location at 20 s intervals with consecutively numbered toothpick flags; flags were placed at a lagged time interval to keep from flushing the grasshopper. The movement patterns were electronically surveyed (Pentax PTS-II₀₅) in the field to provide coordinate data of the points (toothpick locations), from which movement parameters describing the pathway could be cal-

culated (Wiens *et al. in press*). Most individuals were observed between 20 and 30°C for all three species; these temperatures bracket the activity range of at least *P. delicatula* (Anderson *et al.* 1979), and my observations confirmed that the other two species were also active during this range of temperatures. I observed *O. obscura* only on the moderately grazed pasture. Thus, the response of grasshoppers to broad-scale landscape patterns (pasture effects) could only be assessed for the other two species.

Two movement parameters were used to assay how grasshoppers responded to microlandscape structure, Net displacement (cm), the straight-line distance between the starting and end points of the pathway, provided a scale-dependent measure that integrates other components of movement such as step length (distance moved between points) and turning angle (Crist *et al.* 1992; With *in review*). Besides the intuitive appeal of this measure, it has a foundation in theoretical models of animal movement (Kareiva and Shigesada 1983; McCulloch and Cain 1989). Net displacement was converted to a rate variable (cm/min) owing to the difficulty in obtaining complete patterns (*i.e.*, observation of movement for a total of 30 min) for *X. corallipes*, which had a high frequency of spontaneous (non-observer-induced) flushes.

The fractal dimension (D) of the movement pattern provided a scale-independent measure of how microlandscape structure affected movement in these three species. D was computed by the dividers method (Dicke and Burrough 1988; Milne 1991), which entails measuring the total length of the pathway (summation of distances between points) at different 'ruler' lengths. As the length of the ruler used to measure the pathway increases, the total length of the pathway decreases because more of the details of the pattern are being ignored. Minimum ruler length in this analysis was constrained by the average step length (mean distances between points) of the organism and by 1/3 the total path length at the other extreme (three points are required for a line in regression analysis); a total of 25 ruler lengths was used to measure the length of each movement pattern. The regression of the natural log of the total path length on the natural

log of the ruler length results in a slope, which is then subtracted from 1 to yield D (Fig. 1). This relationship may be summarized as:

$$L(\delta) = k\delta^{1-D}$$

where L is the length of the pathway, δ is the length of the ruler used to measure the pathway, k is the intercept of the regression line, and D is the fractal dimension. In the assessment of two-dimensional patterns, D can theoretically vary from 1, a straight line, to 2, a convoluted pattern that essentially fills a plane (Mandelbrot 1983). In practice, however, the value of D for a movement pattern falls between these extremes; D thus indexes the tortuosity of movement.

Analysis of variance (ANOVA; Type III sums of squares for unbalanced sampling designs) was performed on log-transformed data to assess the effects of various factors on these two movement parameters (rate of net displacement and fractal dimension). Separate analyses assessed whether large-scale landscape patterns affected the rate of net displacement or fractal dimension of movement patterns in *P. delicatula* and *X. corallipes* by using pasture (moderately grazed vs. heavily grazed) as a main effect with species and level of heterogeneity (H, MH, and VH) in a full-factorial model. Differences among the three grasshopper species were addressed in another series of analyses that employed a two-way model to test the effects of species and microlandscape structure (heterogeneity) on the two movement parameters. If no significant pasture effects (main or interaction) were found for *P. delicatula* and *X. corallipes* in the first group of analyses, then data across pastures were pooled for these two species in the latter analyses testing for differences among the three species. Tukey's Studentized Range was used to test for significant differences between groups.

Results

Grasshoppers interacted differently with microlandscape structure in the two pastures (Pasture \times Heterogeneity: $F = 5.30$, $df = 2, 136$, $p = 0.006$; Table 1, Fig. 2). Rate of net displacement

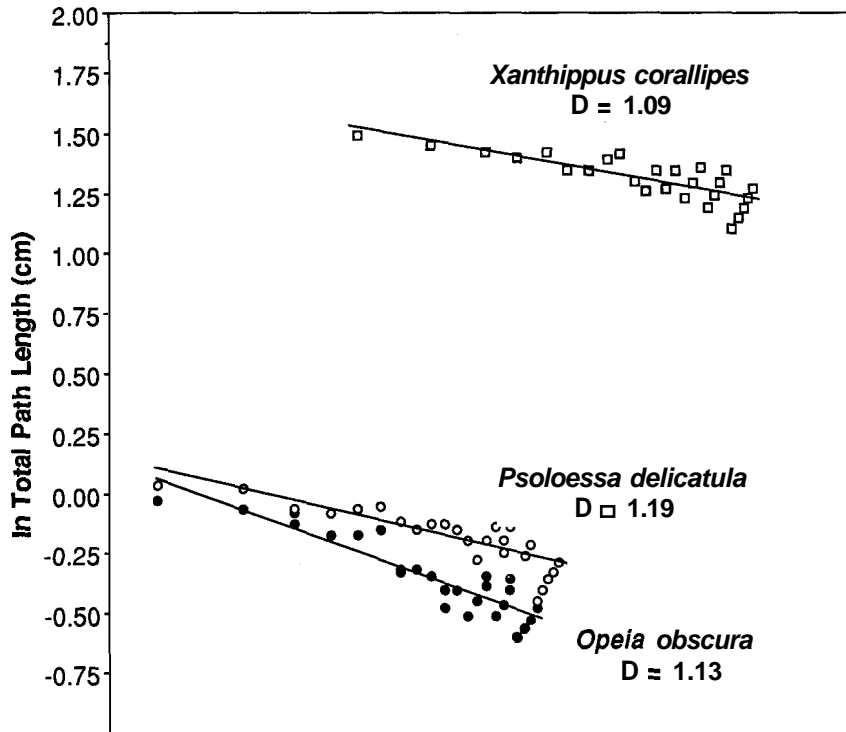


Fig. 1. Calculation of the fractal dimension (D) for movement patterns from representative individuals of three grasshopper species (Orthoptera: Acrididae) in a shortgrass prairie landscape. Regression of the natural log of the length of the 'ruler' used to measure the pattern against the natural log of the total path length generates a slope, which is subtracted from 1 to yield D . Each regression line in the figure thus corresponds to a single movement pattern from each of the three species.

decreased with increasing heterogeneity in the heavily grazed pasture; grasshoppers moved 2.5 times faster in the H plot than in MH and VH plots (all $p < 0.001$, Tukey's Studentized Range; Fig. 2, Pasture \times Heterogeneity). In the moderately grazed pasture, however, grasshoppers moved 3.5 times faster in MH plots than in the H plot, and 2.5 times faster than in the VH plots (all $p < 0.001$; Fig. 2, Pasture \times Heterogeneity). This interaction effect is strongly influenced by *X. corallipes*' response to heterogeneity in the different pastures (Fig. 2, Species \times Pasture \times Heterogeneity). Because of the differential responses by the two species to heterogeneity in the two pastures, there was no significant pasture effect on rate of net displacement (Table 1). Overall, *X. corallipes* moved almost 6 times faster than the smaller *P. delicatula* (Species effect: $F = 29.53$, $df = 1$, 136 , $p =$

0.0001 ; Table 1). *Xanthippus corallipes* moved at an average rate of 12.2 cm/min ($SD = 18.72$, $n = 59$), compared to the average rate of 2.1 cm/min ($SD = 3.07$, $n = 89$) travelled by *P. delicatula*. Because *X. corallipes* always moved faster than *P. delicatula* irrespective of microlandscape structure (Species \times Heterogeneity, Fig. 2) or pasture (Species \times Pasture, Fig. 2), there were no significant interactions between species and these factors (Table 1).

Xanthippus corallipes moved about 3 times faster than *O. obscura* and *P. delicatula* across the grassland mosaic of the moderately grazed pasture ($MS = 2.01$, $df = 2$, 74 , $F = 4.31$, $p = 0.017$; $p < 0.05$, Tukey's Studentized Range). In this pasture, *X. corallipes* moved at an average rate of 14.9 cm/min ($SD = 21.21$, $n = 33$), whereas the two smaller species both moved about 4 cm/min

Table 1. Analysis of variance (Type III sums of squares) for effects on rate of net displacement and fractal dimension of movement patterns of two acridid grasshoppers, *Xanthippus corallipes* ($n=59$) and *Psoloessa delicatula* ($n=89$).

Source of variation	DF	MS	F	P
Rate of Net Displacement				
Species	1	13.37	29.53	0.0001
Pasture	1	0.56	1.25	0.27
Heterogeneity	2	0.23	0.50	0.61
Species × Pasture	1	0.62	1.36	0.25
Species × Heterogeneity	2	0.41	0.91	0.41
Pasture × Heterogeneity	2	2.40	5.30	0.006-
Species × Pasture × Heterogeneity	2	0.18	0.40	0.67
Error	136	0.45		
Fractal Dimension				
Species	1	0.0155	14.29	0.0002
Pasture	1	0.0016	1.49	0.22
Heterogeneity	2	0.0008	0.83	0.44
Species × Pasture	1	0.0001	0.13	0.72
Species × Heterogeneity	2	0.0002	0.20	0.82
Pasture × Heterogeneity	2	0.0006	0.51	0.60
Species × Pasture × Heterogeneity	2	0.0015	1.39	0.25
Error	136	0.0011		

(*P. delicatula*: $\bar{X} = 4.64 \pm 5.07$, $n = 25$; *O. obscura*: $\bar{x} = 4.24 \pm 4.85$, $n = 25$). *Xanthippus corallipes* moved at faster rates than the other two species across all microlandscapes, although the difference was most pronounced in moderately heterogenous (MH) microlandscapes where *X. corallipes* moved about 5 times faster than the two smaller species (Fig. 3). As a consequence, there was a marginally significant effect attributable to heterogeneity (MS = 1.30, df = 2, 74, $F = 2.79$, $p = 0.068$), but no significant interaction effect (Species × Heterogeneity: MS = 0.73, df = 4, 74, $F = 1.57$, $p = 0.19$; Fig. 3).

Analysis of the rate of net displacement thus demonstrated that the largest species, *X. corallipes*, always moved at a faster rate across the landscape than did the two smaller species. Fractal analysis of the movement patterns revealed that the species were interacting with microlandscape structure in fundamentally different ways, however (Species effect: MS = 0.014, df = 2, 164, $F = 11.23$, $p = 0.0001$; data pooled across pastures because no significant pasture effects for Fractal Dimension, Table 1). The movement pathways of the two smaller species were significantly more tortuous than those of *X. corallipes* (*O. obscura*: $\bar{x} = 1.19 \pm 0.136$, n

= 25; *P. delicatula*: $\bar{X} = 1.16 \pm 0.108$, $n = 89$; *X. corallipes*: $\bar{x} = 1.09 \pm 0.05$, $n = 59$; $p < 0.05$, Tukey's Studentized Range). This was true irrespective of the structural complexity of the microlandscape and thus there were no significant effects attributable to heterogeneity (MS = 0.0008, df = 2, 164, $F = 0.72$, $p = 0.49$) or the interaction between the terms (Species × Heterogeneity: MS = 0.0005, df = 4, 164, $F = 0.45$, $p = 0.77$).

Discussion

Grasshopper species are scaling the landscape mosaic of the shortgrass prairie differently. The large species, *X. corallipes*, moved at a faster rate through the grassland mosaic than the two smaller species, *P. delicatula* and *O. obscura*. Rate of movement is presumably an allometric consequence of hind-leg length in grasshoppers (Gabriel 1985; Bennett-Clark 1990) and it is therefore not surprising that *X. corallipes*, which is some 5 times larger than *P. delicatula* and *O. obscura*, should move up to 6 times faster overall than the two smaller species. Nevertheless, these interspecific differences in mobility set the stage for how small

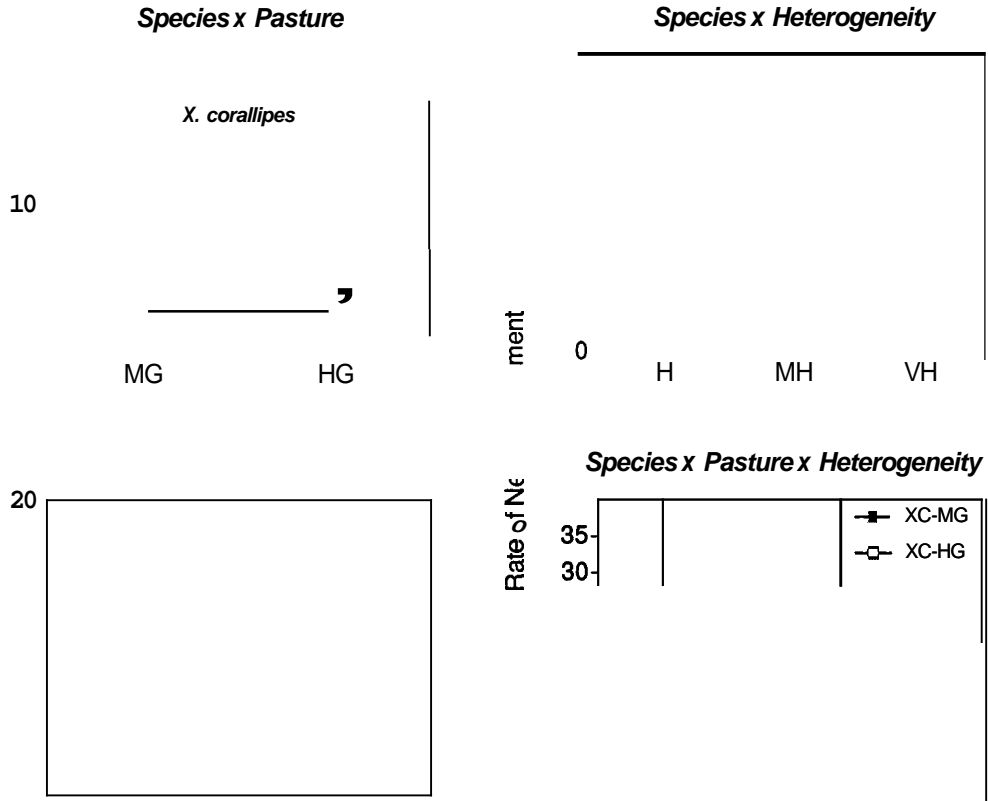


Fig. 2. Interaction plots for factors in the analysis of variance of effects on rate of net displacement (cf. Table 1) in the acridid grasshoppers *Xanthippus corallipes* ($n=59$) and *Psoloessadelicatula* ($n=89$). Levels of pasture: MG = moderately grazed, HG = heavily grazed. Levels of heterogeneity: H = homogeneous, MH = moderately heterogeneous, and VH = very heterogeneous. Abbreviations in legend for Species \times Pasture \times Heterogeneity interaction: XC-MG = movement rates for *X. corallipes* in the moderately grazed pasture, XC-HG = *X. corallipes*, heavily grazed pasture, PD-MG = *P. delicatula*, moderately grazed pasture, and PD-HG = *P. delicatula*, heavily grazed pasture. Sample sizes in MG pasture: *Psoloessadelicatula* = H: $n = 5$, MH: $n = 10$, VH: $n = 10$; *Xanthippus corallipes* = H: $n = 5$, MH: $n = 14$, VH: $n = 14$. Sample sizes in HG pasture: *P. delicatula* = H: $n = 12$, MH: $n = 41$, VH: $n = 11$; *X. corallipes* = H: $n = 5$, MH: $n = 16$, VH: $n = 5$. Error bars are ± 1 SE.

and large grasshoppers might perceive landscape structure differently in this system.

Large grasshoppers have a different perception of the shortgrass prairie than small ones. Fractal analysis revealed that the large species of grasshopper, *X. corallipes*, was interacting with landscape structure in a functionally different manner than the two smaller species, as evidenced by significant differences in the D values of their movement patterns. Movement in *X. corallipes* was nearly linear (D values < 1.1). The differential effect of heterogeneity on movement rates in this species may be attributable to broad-scale landscape effects (*i.e.*, pasture differences due to grazing intensity). The

high vagility of *X. corallipes* may enable it to integrate information on the patch structure of the landscape at scales exceeding the spatial extent of this study (*i.e.*, 25-m² plots). Movement in different species of tenebrionid beetles, which co-occur with these species of grasshoppers in the same grassland system, likewise was influenced by broad-scale landscape structure imposed by different grazing regimes (Crist *et al.* 1992). That arthropods are capable of visually perceiving vegetative structure at a distance is further evidenced by the 'bee-line' response of tenebrionid beetles to shrubs on their visual horizon when seeking shade at high temperatures (Parmenter *et al.* 1989). Grasshoppers also

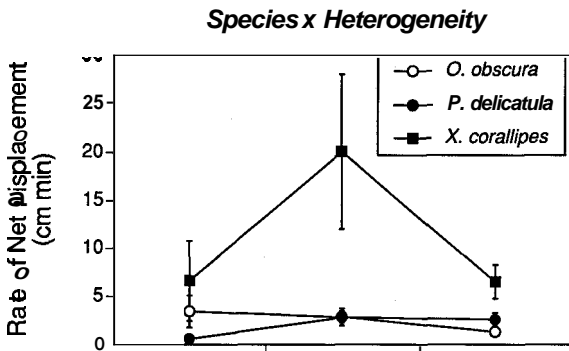


Fig. 3. Interaction plot of factors in the analysis of variance of effects of species and heterogeneity on rate of net displacement among three species of acridid grasshoppers in the moderately grazed pasture. Levels of heterogeneity: H = homogeneous, MH = moderately heterogeneous, and VH = very heterogeneous. Sample sizes: *Opeia obscura* = H: $n = 5$, MH: $n = 10$, VH: $n = 10$; *Psoloessa delicatula* = H: $n = 5$, MH: $n = 10$, VH: $n = 10$; *Xanthippus corallipes* = H: $n = 5$, MH: $n = 14$, VH: $n = 14$. Error bars are ± 1 SE.

have been documented to orient towards structural features of the environment in both field and laboratory arenas (Kennedy 1939; Wallace 1958; Mulhern 1967).

The two small species moved little compared to *X. corallipes*, and the effect of heterogeneity on their rate of movement through different micro-landscapes was marginal, although the two species did exhibit contrasting responses to heterogeneity (Fig. 3). The differential response of the two small species to microlandscape structure might be related to differences in microhabitat preference (Joern 1982) or to differences in forage quality (Chapman 1990). Although both species forage primarily on *B. gracilis*, forage quality might change throughout the season (*P. delicatula* is an early season species and *O. obscura* is a late-season species). Nevertheless, it is apparent from the fractal analysis of their movement patterns that the two species are interacting similarly with the patch structure of the microlandscape. The fractal dimensions of movement patterns did not differ significantly for these two species, and the higher values of D that describe their movement patterns imply a greater tortuosity to their movement than evidenced in *X. corallipes*.

The small species may be interacting with patch structure that perhaps exists at a finer resolution than that assessed across the 25-m² release grids.

The utility of any new application resides not just in its operational value, but in its heuristic value as well. What novel insights can be gained by applying fractal analysis to the movement patterns of animals? Apart from traditional measures of movement (e.g., rate of net displacement), the fractal dimension provides a scale-independent measure of the structural complexity of the movement pattern. Because the effect of scale (e.g., differences in net displacement) is removed, this permits the comparison of patterns among different species or in different habitats, which may bring about accord among investigators conducting research on similar questions at different scales (Wiens 1989).

What then is the biological significance of different landscape perceptions in these two groups of grasshoppers? Differences in the fractal geometry of their movement patterns suggest that these grasshoppers are interacting differently with heterogeneity that occurs across the same range of scales, and are perhaps capable of discriminating landscape structure across different ranges of spatial scale. The abundance and dispersion of a resource (e.g., host plant distribution) may vary with the scale at which animals are able to perceive landscape structure (Milne *et al.* 1992). As a consequence, the large species, *X. corallipes*, may be responding to a different pattern of resource distribution (or to some other resource altogether) that presumably exists at larger spatial scales (given the high vagility of this species) than that perceived by the two smaller species. These differences in how species scale the landscape and perceive resource distributions should ultimately be reflected in the spatial structure and dynamics of populations, competitive interactions, predator-prey relationships, and the like. For example, the different landscape perceptions of large and small species of grasshoppers may explain the differences in the distributional patterns of *X. corallipes*, which has a clumped distribution, and *P. delicatula*, which exhibits a random distribution, in this grassland mosaic (With, unpubl. data).

As a caveat, it is important to realize that this

approach to defining landscape perceptions *is* an operational one, which precludes scales of heterogeneity that an organism perceives but to which it does not respond. The primary assumption of this approach is that the structure of the movement pattern reflects encounters with the patch structure (or some correlate of patch structure) of the landscape. For a terrestrial arthropod like a grasshopper, in which the vegetative structure of the landscape primarily influences microhabitat selection (Anderson 1964; Joern 1982, 1983), such an assumption appears reasonable. The limitation of this approach is that it does not provide a mechanistic explanation for *why* an organism exhibits a particular response to heterogeneity. Reduced movement through an area may result because the microlandscape presents physical barriers to movement (increased patch ‘viscosity’) or because the patch structure of the microlandscape affords profitable patches or refugia from predators that increase retention time within these patches (*e.g.*, area-restricted foraging; Smith 1974). By assessing at what scales landscape structure affects movement, however, this approach permits the identification of ‘domains’ of scale (Wiens 1989). Ideally, fractal analysis could be employed to assay the perceptible resolution of species across a range of scales. The value of *D* for the movement pattern may exhibit abrupt shifts between ranges of scale; presumably, these shifts between spatial domains indicate a concomitant shift in the underlying process responsible for the pattern (*e.g.*, Krummel *et al.* 1987). In the present context, such shifts in the value of *D* suggest that the organism is bounded by patch structure that exists at different scales. An organism may resolve the differences between cactus pads and grass blades at a microscale, avoid clumps of cactus and move along bare ground corridors at a mesoscale, and be restricted in its wanderings by habitat type (grassland versus shrubsteppe) at a macroscale. The patch structure evidenced at these different scales are all expected to influence the overall movement of the organism. Thus, defining landscape perceptions provides information not only on whether species share similar perceptions of landscape structure within a range of scale, but also serves to identify transitions between spatial domains. This pro-

vides a focus for subsequent investigations of the mechanisms underling responses to heterogeneity, and thus serves to promote a unification of pattern and process in the study of the ecological consequences of spatial heterogeneity, which is the main tenet of landscape ecology.

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