Movement behavior in response to landscape structure: the role of functional grain

Susan Romero · James F. Campbell · James R. Nechols · Kimberly A. With

Abstract Landscape structure can influence the fine-scale movement behavior of dispersing animals, which ultimately may influence ecological patterns and processes at broader scales. Functional grain refers to the finest scale at which an organism responds to spatial heterogeneity among patches and extends to the limits of its perceptual range. To determine the functional grain of a model insect, red flour beetle (*Tribolium castaneum*), we examined its movement behavior in response to experimental flour landscapes. Landscape structure was varied by manipulating habitat abundance (0%, 10%, 30%, and 100%) and grain size of patches (fine-2 × 2 cm, intermediate-5 × 5 cm, and coarse-10 × 10 cm) in 50 × 50 cm landscapes. Pathway metrics indicated that beetles used a similar proportion of all landscape types. Several pathway metrics indicated a graded response from the fine to the coarse grain landscape. Lacunarity analysis of beetle pathways indicated a non-linear change in space use between the fine and intermediate landscapes and the coarse-grained landscape. Beetles moved more slowly and tortuously (with many turns), and remained longer in both the overall landscape and individual patches, in fine-grained compared to coarse-grained landscapes. Our research demonstrates how detailed examination of movement pathways and measures of lacunarity can be useful in determining functional grain. Spatially explicit, organism-centered studies focusing on behavioral responses to different habitat configurations can serve as an important first step to identify behavioral rules of movement that may ultimately lead to more accurate predictions of space use in landscapes.

Keywords Search strategy · Grain size · Perceptive resolution · Space use · Red flour beetle · *Tribolium castaneum*

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Introduction

Fine-scale movement behavior of dispersing animals may affect ecological patterns and processes at broader scales, ultimately influencing population

dynamics (Wiens et al. 1993; With and Crist 1996; Russell et al. 2003; Heinz et al. 2006). Theoretical and empirical ecological research has emphasized the need for understanding how animals perceive and respond to spatial heterogeneity (Ives 1995; Zollner and Lima 1997; With et al. 2002) and the importance of integrating both behavioral and landscape approaches when studying searching behavior (Lima and Zollner 1996; Morales and Ellner 2002; Schooley and Wiens 2003; Heinz et al. 2006). Because population dynamics may be influenced by behavioral decisions of individuals in response to landscape structure, there has been much emphasis on integration of movement behavior into individual dispersal models which simulate dispersal on real and virtual landscapes (Conradt et al. 2003; Russell et al. 2003; Zollner and Lima 2005). Integration of movement behavior into models of dispersal is based on the premise that population viability is dependent on the dispersal success of organisms, and that this success may depend on an individual's ability to change search strategy depending on the abundance and configuration of habitat (Zollner and Lima 2005; Heinz and Strand 2006). The ability of insects to employ different search strategies in relation to landscape structure has been an active area of research in empirical studies (Bond 1980; Stamps et al. 1987; Bell 1991; Goodwin and Fahrig 2002; Olden et al. 2004; Conradt and Roper 2006) and several studies have highlighted the impact of landscape structure on search success (With and Crist 1995; With and King 1999; With et al. 2002).

Searching behavior, coupled with perceptual range (the minimum distance from which a resource may be detected), is a basic determinant of functional connectivity, or the degree to which resources are connected by movement (Taylor et al. 1993; Wiens et al. 1997; Moilanen and Hanski 2001) and searching success (Heinz and Strand 2006). Baguette and Van Dyck (2007) recently proposed that the grain of resource configuration in the landscape is a crucial factor shaping adaptive behavioral changes during dispersal that enhance landscape connectivity. Functional grain refers to the finest scale at which an organism responds to spatial heterogeneity among patches and extends to the limits of its perceptual range (Kotliar and Wiens 1990; Lima and Zollner 1996; Baguette and Van Dyck 2007). Awareness of functional grain may greatly enhance the ability to

predict the distribution of particular organisms and to assess functional connectivity of a landscape.

In this study we investigated the relationship of functional grain to movement behavior in a model insect (*Tribolium castaneum*) by manipulating landscape structure. Although most species of *Tribolium* are capable of flight, these beetles usually disperse by walking making them suitable for studies of fine-scale movement on landscapes (Morales and Ellner 2002; Campbell and Runnion 2003). Our objectives were to: (1) determine if variation in landscape structure results in changes in fine-scale search strategy (or movement rules), (2) understand how landscape structure influences movement rules, and (3) use this information to identify the functional grain at which this insect interacts with resources. To address our objectives, we created landscapes that differed in structure by varying the abundance and grain size of habitat (flour) and by recording movement pathways of searching beetles on these landscapes. We then evaluated how a variety of metrics of beetle movement behavior changed with landscape structure.

Methods

We used beetles taken from a lab colony founded with ~40 individuals collected from a flour mill ~22 months before the experiment was conducted. Sub-cultures were maintained by placing ~50 beetles (mixed sex) in pint jars containing 0.25 l of wheat/brewers yeast mixture (95:5). We reared colonies in an environmental chamber ($26 \pm 2°C$, $75 \pm 5\%$ RH) and conducted the experiment in a walk-in environmental chamber under the same environmental conditions. Age of beetles was standardized to 3 weeks $\pm$ 4 days and females only were used in this study because responses to resources used for reproduction (flour patches) are relatively more important for females than for males. Sex was determined based on the presence or absence of the setaceous patch present on the first femur of males (Good 1936). One day prior to use in the experiment we removed a group of beetles (36) from a colony jar and held them in a container with food under the environmental conditions described above.

We created experimental landscapes with three grain size treatments (2×2, 5×5, and 10×10 cm)

within two levels of habitat abundance (10% and 30%). Holding the extent of the landscape constant (50 × 50 cm) while varying grain size produced landscapes with varying degrees of habitat aggregation and heterogeneity of gap sizes (inter-patch distances) (Fig. 1). In his review, Andrén (1994) found that negative effects of habitat fragmentation increased for many species as suitable habitat abundance fell below 30%. Previous work with lady beetles indicated a threshold response to landscape structure when habitat abundance fell below 20% (With et al. 2002). Wiens et al. (1997) also documented threshold effects in movement parameters of tenebrionid beetles when habitat abundance was between 0% and 20%. We thus chose habitat abundance treatments that bracketed this critical 20% abundance level and that would most likely result in interesting and comparable differences in movement. We also included two control treatments: a 100% and a 0% flour landscape. We chose the landscape extent based on the largest size that was tractable for landscape creation, adequate replication, and accurate visual observation of beetle movement.

We generated experimental landscape patterns using the freely available RULE software program (Gardner 1999), creating four different random maps for each abundance × grain size combination. Habitat cells were comprised of unbleached, white flour and matrix cells that did not contain flour. RULE outputs binary maps of habitat and matrix cells,

which were transferred onto a piece of heavy cardstock marked with a grid of cells corresponding to the appropriate grain size treatment. Cells designated as habitat were then cut out creating a template for each landscape treatment. We placed the templates on a new sheet of white paper, marked with a grid, within a 58 × 58 cm arena, and a fine layer of flour was sifted over the template. Flour was applied at a depth shallow enough (<1 mm) to allow observation of the grids and beetles in habitat cells. We surrounded the arena on all four sides by meter-high white foam-core walls designed to reduce air movement and visual cues from the surroundings. Three light fixtures with 40-W incandescent bulbs were suspended ∼1.75 m over the arena, providing a relatively low light level ranging from 260 to 290 lux for all replicates.

We released one female beetle into the center of the landscape after a 3-min acclimation period under an inverted 14.8-ml glass vial (each beetle was observed only once and flour was discarded after each experimental run). Landscapes were chosen so that the center was a matrix cell and not a habitat cell. After release, we recorded which cells on the landscape grid the beetle occupied at 2-s intervals (i.e., each 2-s interval was treated as one time step of a beetle movement pathway) for a maximum of 3 min or until she crossed the boundary of the landscape. Each day an experiment was run, one of 4 maps corresponding to each treatment was used for all replicates. The

Fig. 1 Experimental landscapes (each 50 × 50 cm) showing heterogeneity of landscape structure (pattern and size of habitat cells and gaps between habitat cells): 10% fine-grained (**a**), 10% intermediate-grained (**b**), 10% coarse-grained (**c**), 30% fine-grained (**d**), 30% intermediate-grained (**e**), and 30% coarse-grained (**f**)
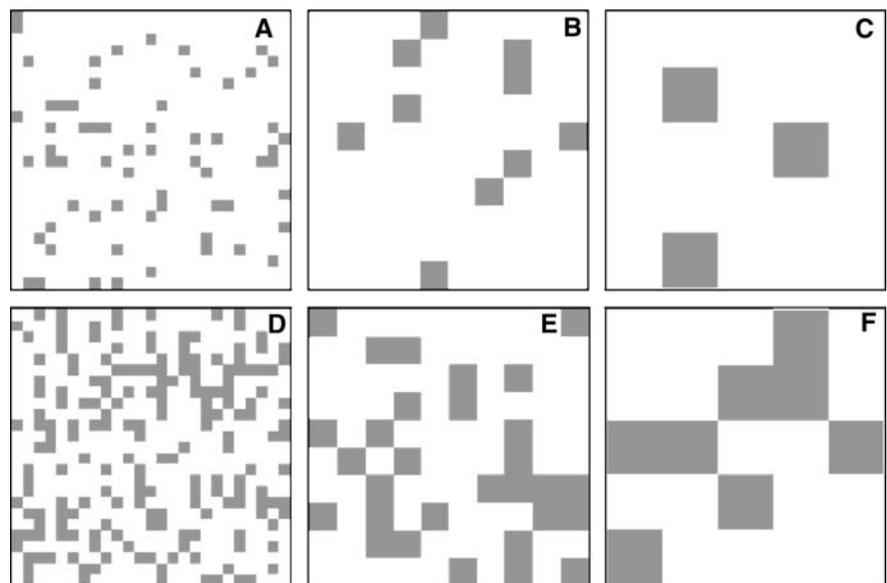
experiment was repeated sequentially over 8 days (blocks) with each of the 4 maps being used twice over the course of the experiment. Maps 1–4 were used in order for the first 4 blocks and then repeated sequentially in the four remaining blocks. Scheduling of the six abundance × grain size treatments and two controls was randomized and all treatments were replicated three times per day. This design resulted in each treatment being replicated 24 times.

To provide patch measures for relative comparisons of landscape structure and movement behavior, we quantified the following metrics for each landscape: total number of habitat patches (all adjacent habitat cells, including diagonals), total edges (sum of lengths of all habitat edge segments), nearest neighbor distance (distance to nearest habitat cell), and largest patch index (percent of total area composed of largest habitat patch). Another useful metric for comparing the spatial pattern of habitat and beetle movement pathways is the lacunarity index (Mandelbrot 1983; Plotnick et al. 1993; With and King 1999; McIntyre and Wiens 2000), which can be calculated for both landscape and movement patterns over multiple scales. Lacunarity describes landscape texture, or the variability of gap sizes. Therefore, this metric is especially useful for understanding how gap structure or, conversely, how habitat contagion or dispersion can influence movement behavior and space use. We characterized the spatial distribution of habitat cells by calculating lacunarity indices for the six landscape patterns. For landscape pattern, a high lacunarity value indicates large and more variable gaps between patches, whereas a low lacunarity value results when habitat cells are more widely dispersed and gap sizes are smaller and more uniform. Lacunarity index values can be calculated over a range of measurement scales (box sizes) based on grain size. We compared three lacunarity values per landscape calculated at equivalent scales of measurement across all landscapes; the first was at the scale of the largest grain size, 10 × 10 cm (scale 1), the second was at 20 × 20 cm (scale 2), and the third was at 30 × 30 cm (scale 3). Due to the design of the experiment, it was not possible to calculate lacunarity index values at scales finer than the size of the largest habitat cell.

Lacunarity values for beetle movement pathways were calculated as described above for landscape pattern and were based on the cells visited on each landscape. For movement pathways, a high lacunarity value indicates that cells through which beetles have moved are restricted to a localized area (aggregated) and there are large or irregular gaps in the pattern; while a low value occurs when cells through which beetles have moved are scattered over a wider area of the landscape and gaps are more regularly spaced. Beetle movement patterns were also quantified using a variety of other measures. We quantified immigration into all cells, both matrix and habitat, as a measure of landscape connectivity, and immigration into just the habitat cells as a measure of habitat connectivity. Since the area of large and medium cells were greater than small cells by factors of 5 and 2.5, respectively, we multiplied cell counts for large and medium cells by these factors in order to standardize the area of habitat cells so that metrics for immigration and time steps within habitat cells would not be biased due to size differences among habitat cells. We calculated three metrics for each beetle movement pathway: (1) the mean step length, i.e., distance moved during each 2 s time step; (2) the displacement ratio, i.e., computed as the net displacement (a straight-line measure of the pathway) divided by total path length (this ratio is a measure of pathway complexity standardized for different observation times [completely linear pathway = 1]); and (3) displacement rate, i.e., the net displacement divided by time step (2-s interval). The amount of time spent within landscapes and in individual habitat and matrix cells can also indicate how beetles respond to landscape structure. Therefore, we calculated the number of time steps in the overall landscape, in habitat cells, and in matrix cells, as well as the number of time steps within individual habitat and matrix cells. We recorded the time that beetles remained in the landscape as a measure of how habitat structure influenced retention time in the landscape. We used analysis of variance (ANOVA) (mixed-model procedure, SAS Institute, Inc. 2002) to test for differences in metrics describing the landscape using the treatment combination of habitat abundance and habitat grain size modeled as the main effect. To compare lacunarity of beetle movement versus that of the landscape, we used ANOVA (mixed-model procedure) with scale, abundance, and grain size modeled as main effects, and maps and blocks as random effects. Lacunarity values were log-transformed before analysis to normalize data. To test the effects of grain size and abundance on movement behavior, we performed an ANOVA (mixed-model procedure)

on beetle movement pathway metrics with habitat grain and abundance modeled as main effects and maps and blocks as random effects. Effects of habitat abundance on pathway metrics were analyzed separately from grain size effects because pathway data for controls were recorded only at one grain size (2 × 2 cm) and calculation of several metrics (e.g., time steps in habitat) were not possible for habitat abundance controls. The Residual Maximum Likelihood (REML) method was used to estimate the variance components of the mixed models. Tukey HSD was used for separation of means. Time that beetles remained on the landscape was analyzed using survival analysis (Proc Lifetest; SAS Institute, Inc. 2002) for censored data with a Bonferroni correction for multiple comparisons.

Results

Landscape metrics

Analysis of variance revealed significant differences among treatments for all landscape metrics: number of patches ($F = 305.02$; df = 5,127; $P < 0.0001$); largest patch index ($F = 210.62$; df = 5,127; $P < 0.0001$); total edges (4482.25; df = 5,127; $P < 0.0001$); and nearest neighbor distance ($F = 12.28$; df = 5,127; $P < 0.0001$) (Fig. 2a–d). Changes in landscape structure due to habitat abundance and grain size did not impact all patch metrics in the same manner. For example, the effect of habitat abundance on landscape structure was most apparent for the largest patch index and total edges within each grain size treatment. There was a 6- and 20-fold increase in the number of habitat patches in fine-grained landscapes compared to the intermediate and coarse-grained landscapes, respectively. As grain decreased and abundance increased, landscapes had significantly more habitat patches and, thus, more edges, while nearest neighbor distance decreased. The greatest difference in total edges occurred between the 10% coarse-grained and the 30% fine-grained landscapes.

Lacunarity of landscape patterns and movement pathways

The wide range of lacunarity values associated with landscapes indicated differences in distributions of
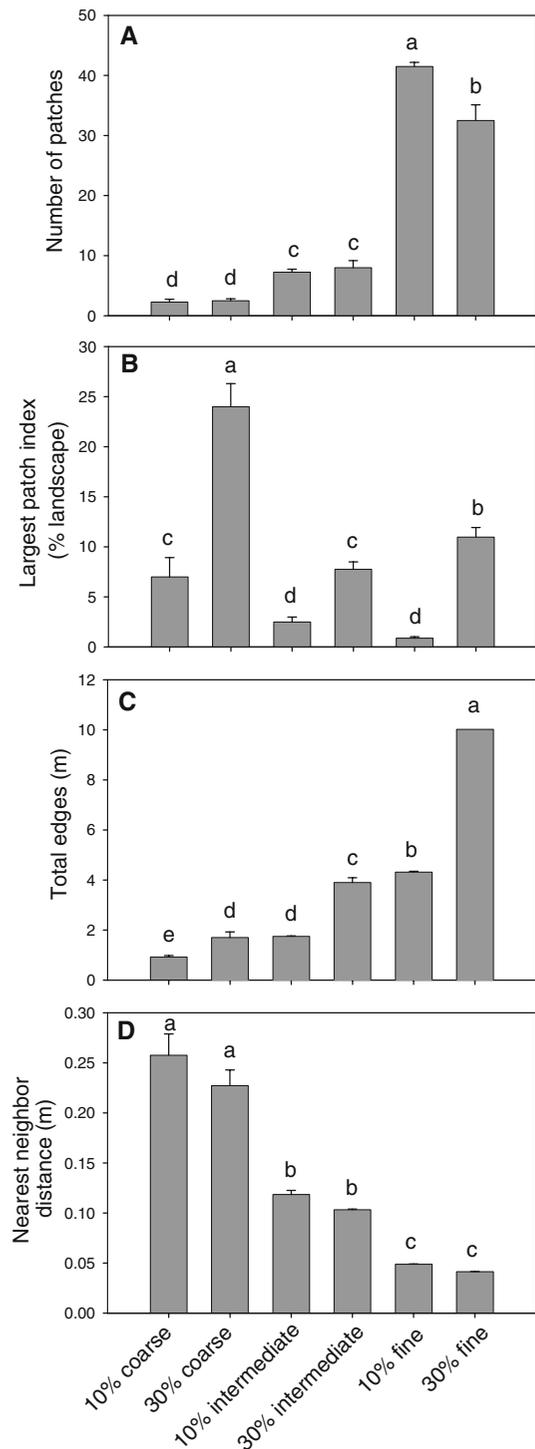
Fig. 2 Landscape metrics including: number of patches (**a**), largest patch index (**b**), total edges (**c**), and nearest neighbor distance (**d**) as functions of habitat abundance and grain size. Bars with the same letters within a plot are not statistically different (ANOVA, mixed procedure, α = 0.05)

habitat cells and heterogeneity in gap sizes (Fig. 3a). A full-factorial analysis of both landscape pattern and movement path lacunarity revealed significant differences between lacunarity of movement paths and landscape patterns ($F = 40.65$; df = 1,16; $P < 0.0001$) (Fig. 3). To examine sources of variation, lacunarity of landscape pattern and beetle movement paths were analyzed separately. The separate analysis of landscape lacunarity again showed significant differences between abundance levels ($F = 64.70$; df = 1,4; $P = 0.0013$); among scales ($F = 123.56$; df = 2,4; $P = 0.0003$); and among grain sizes ($F = 199.45$; df = 2,4; $P < 0.0001$) (Fig. 3a). Lacunarity values for landscape pattern were higher and there was more variation among treatments, especially among both coarse-grained and the
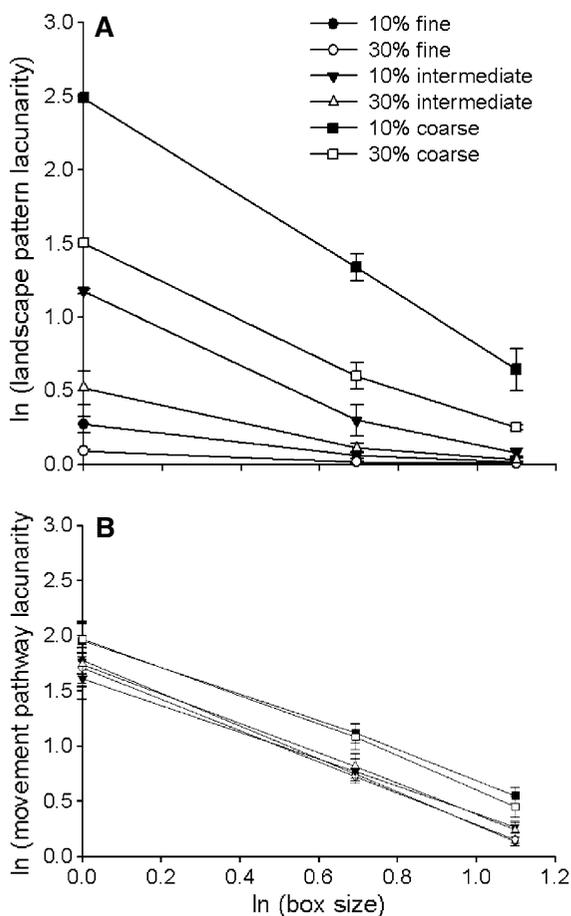
Fig. 3 Landscape pattern (**a**) and movement pathway (**b**) lacunarity plotted across three measurement scales (box sizes) showing relationship of habitat abundance and grain size to landscape structure and movement behavior of red flour beetle (*Tribolium castaneum*). Values on axes are log transformed

intermediate-grained 10% habitat landscapes. Lacunarity values were lower and less variable for the fine-grained and the 30% intermediate-grained landscapes. Higher lacunarity values in one group of landscapes (coarse and 10% intermediate-grained) indicate that habitat cells were more aggregated and inter-patch distances were larger and more variable in size than in the other landscape group (fine and 30% intermediate-grained) where habitat cells were more evenly dispersed and inter-patch distances were smaller and more regularly spaced (Fig. 3a).

Space use at the landscape scale

Lacunarity analysis revealed that grain size ($F = 96.56$; df = 2,4; $P = 0.0004$) significantly impacted the space use of beetles in the different landscapes, but habitat abundance did not ($F = 0.01$; df = 1,4; $P = 0.9123$) (Fig. 3b). Because there was no effect of habitat abundance, nor interaction between abundance and grain size, data were pooled and a reduced model examined the influence of grain size and scale of measurement on lacunarity of beetle movement pathways. As expected, lacunarity significantly decreased in all landscapes because, as box size increased, variation among locations was reduced ($F = 1703.64$; df = 2,9; $P < 0.0001$) (Fig. 3). There were no significant differences between lacunarity of beetle movement pathways in landscapes with 0% habitat and those with 100% ($F = 0.00$; df = 1,2; $P = 0.9931$) (data not shown). There was an abrupt non-linear response in beetles' use of space between the coarse-grained landscapes and the fine-grained and intermediate landscapes at the finest measurement scale (scale 1, 10×10 cm) ($F = 86.63$; df = 2,9; $P < 0.0001$) (Fig. 4a). In coarse-grained landscapes, lacunarity values were higher; thus there were large and irregular gaps among cells through which beetles moved, indicating that beetle movement was more linear. This pattern held even at the two larger scales of measurement (scales 2 & 3) although the change between the coarse-grained and the other landscapes is less abrupt (Fig. 4b, c).

Movement pathway response

Connectivity of overall landscape cells (number of unique landscape cells in which beetles moved) was similar among all grain size treatments ($F = 2.38$;
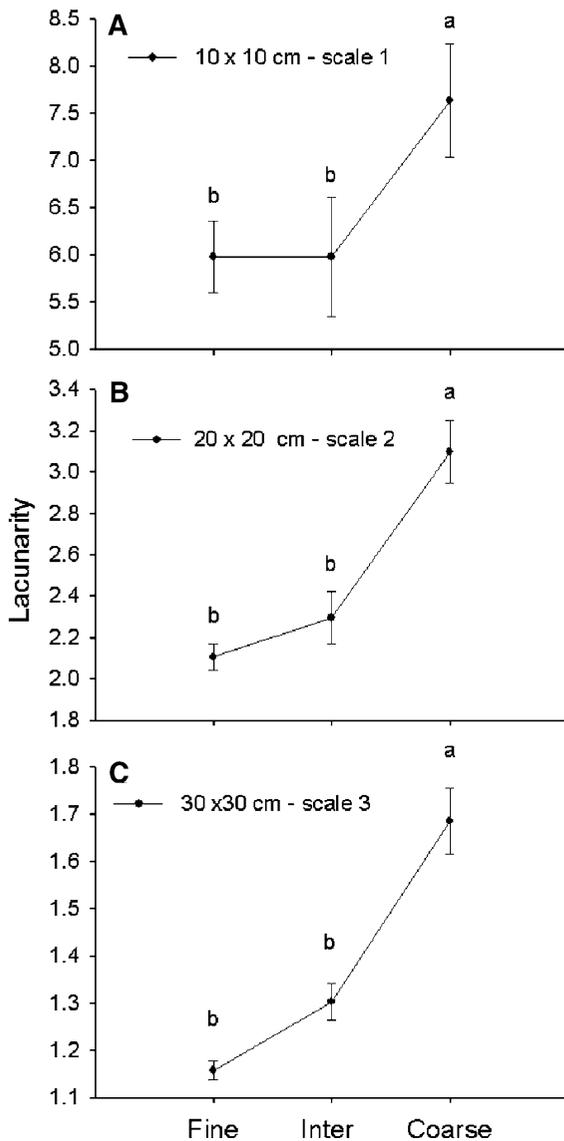
Fig. 4 Lacunarity of red flour beetle movement pathways as a function of habitat grain size over three scales of lacunarity (box size) including: scale 1–10 × 10 cm (**a**), scale 2–20 × 20 cm (**b**), and scale 3–30 × 30 cm (**c**). Symbols with same letters are not significantly different (ANOVA, mixed procedure, $\alpha = 0.05$)

df = 2,126; $P = 0.096$) (Table 1), as well as between abundance levels ($F = 0.01$; df = 1,126; $P = 0.943$) (Table 2). Connectivity of habitat cells (number of unique habitat cells into which beetles moved), while significantly higher in landscapes with 30% than in 10% habitat ($F = 69.00$; df = 1,126; $P < 0.0001$) (Table 2), followed the proportional difference of habitat abundance between the two

treatments. Unexpectedly, grain size was not a significant factor in connectivity of habitat cells ($F = 0.04$; df = 2,126; $P = 0.961$) (Table 1). Beetles spent 36% more time in fine-grained and 23% more time in intermediate-grained landscapes than in coarse-grained landscapes (time steps, $F = 9.36$; df = 2,126; $P < 0.0001$) (Table 1). Beetles spent less than half the amount of time in landscapes with no habitat (0%) than in landscapes with habitat, and significantly less than those with 30% or higher (time steps, $F = 8.75$; df = 3,169; $P < 0.0001$) (Table 2). Beetles moved in a significantly more tortuous manner in fine and intermediate-grained landscapes than in coarse-grained landscapes (displacement ratio, $F = 7.22$; df = 1,126; $P = 0.001$) (Table 1). This result agrees with that of the lacunarity analysis, showing that the movement pattern was more linear in the coarse-grained landscapes. Habitat abundance did not impact the tortuosity of movement pathways in landscapes ($F = 0.70$; df = 1,169; $P = 0.554$) (Table 2). Beetles' displacement rate was 2 times faster in coarse-grained and 1.2 times faster in intermediate-grained than on small-grained landscapes ($F = 4.61$; df = 2,126; $P = 0.012$). There were no significant differences in displacement rate between fine and intermediate-grained landscapes ($P = 0.216$) (Table 1). Beetles' displacement rate in landscapes where there was no habitat present (0%) was 1.7 times higher than in landscapes with 10% habitat, 2.8 times higher than in landscapes with 30% habitat, and 14 times faster than on landscapes with 100% habitat ($F = 12.60$; df = 3,169; $P < 0.0001$) (Table 2). Displacement rate was 1.6 times faster on landscapes with 10% habitat compared to those with 30% ($P = 0.028$) (Table 2). Grain size had no impact on the distance moved (i.e., number of cells visited) during a time step ($F = 1.12$; df = 2,126; $P = 0.330$). Distance beetles moved during a time step was 1.6 times greater in landscapes with no habitat present (0%) compared to those with 10% and was ~ 1.3 times greater in landscapes with 10% habitat compared to those with 30 % and 100% ($F = 14.11$; df = 3,169; $P < 0.0001$) (Table 2). Beetles spent roughly twice as much time in habitat in landscapes with 30% habitat abundance relative to those with 10% ($F = 23.48$; df = 1,126; $P < 0.0001$) (Table 2). This difference represented a 70% increase (18.53 steps) in addition to the 20% (4.13 steps) increase that was expected due to the increase in habitat

Table 1 Effects of grain size on movement behavior of female red flour beetle (*T. castaneum*) at various scales in experimental landscapes

Scale, pathway, and behavior measures	Grain size		
	Fine	Intermediate	Coarse
Overall landscape			
Landscape cells connected	28.16 ± 2.47 a	32.37 ± 2.48 a	26.66 ± 2.47 a
Habitat cells connected	6.63 ± 0.71 a	6.66 ± 0.71 a	6.88 ± 0.71 a
Time steps on landscape (2 s/step)	71.21 ± 4.23 a	59.44 ± 4.27 a b	45.52 ± 4.23 b
Displacement ratio	0.29 ± 0.04 b	0.36 ± 0.04 b	0.49 ± 0.04 a
Displacement rate (m/s)	0.004 ± 0.000 b	0.006 ± 0.000 a b	0.008 ± 0.000 a
Among cells			
Mean step length (m)	0.015 ± 0.002 a	0.017 ± 0.002 a	0.017 ± 0.002 a
Time steps in habitat (2 s/step)	35.42 ± 4.96 a	28.49 ± 4.99 a	25.54 ± 4.96 a
Time steps in matrix (2 s/step)	35.85 ± 3.05 a	30.72 ± 3.07 a	19.75 ± 3.05 b
Within cell			
Time steps per habitat cell (2 s/step)	7.55 ± 1.36 a	5.28 ± 1.37 a b	3.19 ± 1.36 b
Time steps per matrix cell (2 s/step)	1.82 ± 0.15 a	1.40 ± 0.15 a b	1.21 ± 0.15 b

Means ± SE with same letters within rows are not significantly different (ANOVA, mixed procedure, $\alpha = 0.05$, $n = 24$)

Table 2 Effects of habitat abundance on movement behavior of female red flour beetle (*T. castaneum*) at various scales in experimental landscapes

Scale, pathway, and behavior measures	Habitat abundance			
	0%	10%	30%	100%
Overall landscape				
Landscape cells connected	21.75 ± 2.86 a	29.17 ± 1.66 a	28.97 ± 1.67 a	28.17 ± 2.87 a
Habitat cells connected	–	3.45 ± 0.59 b	9.99 ± 0.59 a	–
Time steps on landscape (2 s/step)	24.75 ± 10.97 b	52.90 ± 3.45 a b	64.51 ± 3.47 a	58.54 ± 10.97 a
Displacement ratio	0.53 ± 0.84 a	0.40 ± 0.04 a	0.37 ± 0.04 a	0.40 ± 0.08 a
Displacement rate (m/s)	0.014 ± 0.001 a	0.008 ± 0.001 b	0.005 ± 0.001 c	0.006 ± 0.001 b c
Among cells				
Mean step length (m)	0.028 ± 0.003 a	0.018 ± 0.001 b	0.014 ± 0.001c	0.015 ± 0.003 b c
Time steps in habitat (2 s/step)	–	20.67 ± 4.09 b	39.20 ± 4.10 a	–
Time steps in matrix (2 s/step)	–	32.19 ± 2.46 a	25.35 ± 2.47 b	–
Within cell				
Time steps per habitat cell (2 s/step)	–	5.58 ± 1.14 a	5.12 ± 1.15 a	–
Time steps per matrix cell (2 s/step)	–	1.39 ± 0.12 a	1.56 ± 0.12 a	–

Means ± SE with same letters within rows are not significantly different (ANOVA, mixed procedure, $\alpha = 0.05$, $n = 24$)

abundance. The reciprocal was also true, with time spent in the matrix also being influenced by the amount of habitat, with beetles spending more time in matrix in landscapes with 10% relative to 30% habitat ($F = 5.99$; df = 1,126; $P = 0.016$) (Table 2). Interestingly, grain size played no role in the amount of time spent in habitat ($F = 1.40$; df = 2,126; $P = 0.250$) (Table 1), but did have a significant influence on time in the matrix ($F = 8.71$; df =

2,126; $P = 0.0003$). Beetles spent similar amounts of time in the matrix in fine and intermediate-grained landscapes, but at least 1.5 times longer than in coarse-grained landscapes ($P = 0.406$) (Table 1).

Grain size influenced time spent in individual habitat cells, with beetles spending 58% more time in individual habitat cells in fine-grained relative to coarse-grained landscapes ($F = 3.19$; df = 2,126; $P = 0.034$) (Table 1). Time spent in individual

habitat cells on intermediate-grained landscapes was not significantly different from that in either fine or coarse-grained landscapes (intermediate vs. fine, $P = 0.397$; intermediate vs. coarse, $P = 0.450$). Beetles spent 33% more time in individual matrix cells in fine-grained compared to coarse-grained landscapes ($F = 4.41$; df = 2,126; $P = 0.014$) and the amount of time beetles spent in matrix cells of intermediate-grained landscapes was intermediate between the two (Table 1). Habitat abundance did not have a significant effect on amount of time spent per individual habitat cell ($F = 0.13$; df = 1,126; $P = 0.724$) nor individual matrix cells ($F = 0.95$; df = 1,126; $P = 0.331$) (Table 2).

Landscape retention time

Time that beetles remained in landscapes varied significantly with landscape structure (Fig. 5, Table 3). Beetles remained longer in the 30% fine-grained landscapes relative to the other landscapes. In fine- and intermediate-grained landscapes with 30% habitat, beetles remained longer than in landscapes with 100% habitat. Retention time in landscapes with no habitat (0% control) was significantly lower than

for all other landscapes with habitat present with the exception that the 10% coarse-grained landscape had a similar low retention time (Table 3).

Discussion

Movement behavior of red flour beetle revealed the functional grain, or the scale of interaction between landscape structure and the organism. As landscape structure changed with the grain size of resources, beetles modified their search strategies. These modifications occurred as a result of behavioral mechanisms employed in response to the scale of the habitat pattern. At the extent of landscapes in this study, beetles accessed a similar proportion of habitat, but fine-scale responses indicated that beetles were searching these landscapes very differently depending on patch and gap structure of the landscape. Differences in movement behavior between coarse-grained, intermediate, and fine-grained landscapes, supported by both movement lacunarity and pathway metric analyses, show that beetles employed different behavioral strategies, especially at the two extremes of grain size in this study. Several metrics

Fig. 5 Curves of mean retention time for number of beetles (*T. castaneum*) remaining in landscapes as a function of landscape structure. Observations were censored after 180 s
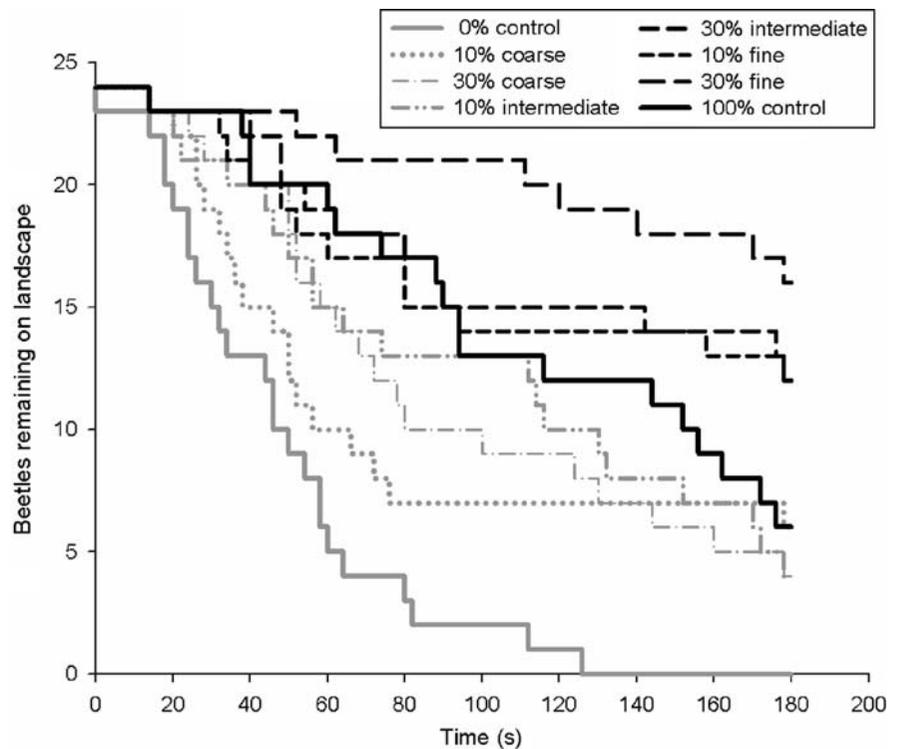
Table 3 Pair-wise comparisons of times until female red flour beetles (*T. castaneum*) leave experimental landscapes

Landscape comparisons	Time (s) Mean ± S.E.	*P*-value						
		10% coarse	10% inter.	10% fine	30% coarse	30% inter.	30% fine	100%
0%	49.5 ± 6.2	0.0235	**0.0001**	**<0.0001**	0.0004	**<0.0001**	**<0.0001**	**<0.0001**
10% coarse	54.4 ± 4.4	–	0.7167	0.0318	0.6724	0.0261	**0.0005**	0.3186
10% intermediate	104.7 ± 12.2	–	–	0.0441	0.8242	0.0366	**0.0003**	0.5878
10% fine	116. 9 ± 11.4	–	–	–	0.0347	0.9841	0.1633	0.1228
30% coarse	94.2 ± 10.5	–	–	–	–	0.0273	**0.0002**	0.3795
30% intermediate	131.2 ± 12.5	–	–	–	–	–	0.1602	0.1147
30% fine	151.3 ± 8.9	–	–	–	–	–	–	**0.0015**
100%	116.1 ± 11.4	–	–	–	–	–	–	–

Means ± SE reported are for biased mean leaving time (s). Comparisons of retention curves (Kaplan–Meier method) are significantly different at $P \leq 0.0017$ after Bonferroni correction for multiple comparisons. Significance level between pairs in rows and columns are indicated by *P*-values in bold type

such as habitat and landscape connectivity, mean step length, and time steps in habitat indicated no difference in response to grain size of habitat. Metrics such as displacement rate, time in habitat, and the landscape as a whole show a graded response across grain size. Lacunarity, displacement ratio, and time in matrix show a significant difference in space use between fine and intermediately-grained landscapes and the coarse-grained landscapes. Retention time on the landscape corroborates the results of the previously mentioned metrics, showing a distinction between the fine-grain (both high and low abundance) and high abundance, intermediate-grain landscapes and the coarse-grain landscape. Retention time on the low abundance, intermediate-grain landscape was similar to that of the coarse-grain landscapes, indicating an interaction between abundance and grain at the intermediate scale.

Discernment of the functional grain of an organism may depend on which movement metrics are considered. If the scale at which movement behavior changes in response to landscape structure is indicative of the functional grain (Baguette and Van Dyck 2007), then differences in lacunarity, displacement ratio, time in the matrix, and retention time on the landscape suggest that the fine- and intermediate-grain landscapes encompass the functional grain of red flour beetle. However, as grain size increased in the coarse-grain landscapes, with a concurrent increase in gap size and decrease in number of edges, beetles appeared unable to detect habitat that was not in close proximity; they thus engaged in a generalized

search strategy, employing increased velocity and a linear trajectory. In coarse-grained landscapes, movement pathways indicate that beetles may have perceived themselves as "out of patch". In fine and intermediately-grained landscapes, pathways were more tortuous and displacement rate lower than in coarse-grained landscapes even though mean step length was similar among landscapes. Beetles in these landscapes appeared to have perceived themselves as still in a patch even though part of their pathway was in matrix. Movement in fine and intermediately-grained landscapes appear to be associated with resource exploration, or routine foraging. In contrast, fast, directed movements on coarse-grained landscapes suggest specialized movements aimed at net displacement. These results corroborate other studies showing that individuals exhibit different behavioral components depending on landscape structure (see review by Van Dyck and Baguette 2005).

Results of this work, and that of others, indicate that variation in landscape resistance to movement may be a useful indicator of an organism's perception of being in acceptable or less acceptable habitat. With (1994) examined movement of large and small species of grasshoppers in relation to landscape heterogeneity and found significant differences in rate of movement and pathway tortuosity among the species. She proposed that differences in perceptual resolution affected movement behavior in response to patch structure, and this impacted relative permeabilities of the landscapes. The fine and intermediately-grained landscapes in the present study could be

described as being relatively resistant to movement while coarse-grain landscapes could be considered relatively more permeable.

Differences in resistance to movement between habitat and non-habitat have also been described in other insect systems. Goodwin and Fahrig (2002) reported that a specialist goldenrod beetle, *Trirhabda borealis*, moved infrequently and meandered slowly in goldenrod patches compared to cut patches (non-habitat) where beetles moved more frequently with sustained directionality. Haynes and Cronin (2006) reported that planthoppers exhibited greater step lengths, shorter residence times, higher displacement rates, and lower fractal dimension of movement paths (lower tortuosity) in non-habitat mudflat areas. In another study, the net displacement rate of various damselfly species increased in areas with a higher amount of non-habitat pasture compared to landscapes composed of only forest and stream habitat (Jonsen and Taylor 2000). A recent study by Schtickzelle et al. (2007) revealed that move lengths and turning angles of butterflies inside and outside of habitat patches were quantitatively different with movements in matrix much straighter than in habitat.

The data suggest that edge effects and small inter-patch distances most likely impacted behavioral responses of red flour beetles in fine and intermediate-grain landscapes. Beetles moving in fine-grained landscapes encountered a high number of edges and did not have far to travel before encountering another edge, thus traveling at a much slower rate and in a more complex manner. For instance, results show that beetles spent disproportionately more time (70% more than expected due to increase in habitat) in overall habitat on landscapes with 30% vs. 10% habitat. Survival analysis showed that beetles remained longest in the 30% fine-grained landscape, which had the smallest inter-patch distances and the highest number of edges. In contrast, the 10% coarse-grained landscape, with the largest inter-patch distances and the least number of edges, had the lowest retention time of all landscapes, not including the 0% control landscapes where beetles, predictably, left quite quickly.

The increased time spent on landscapes with a high number of edges may be explained by the observation that beetles often moved along edges of habitat cells both inside and outside the cell. Once

entering a habitat cell, beetles followed along interior edges of cells rather than transition immediately back out into the matrix. Beetles also spent more time in fine-grained habitat cells versus coarse-grained habitat cells. Beetles appear to be making fewer transitions out of fine-grain habitat cells than out of coarse-grain habitat cells. This behavior could be explained by increased edge encounters in the fine-grain cells that reflect beetles back into interior. Fine-scale response to edges is likely to be responsible, at least in part, for the decreased dispersal rate and increased retention time on fine-grained landscapes. These observations add to and further corroborate previous studies showing that differences in patch viscosity and edge permeabilities may be contingent on the structure of the surrounding landscape. For example, in a study of tenebrionid beetles moving in experimental landscapes of grass and bare ground, Wiens et al. (1997) implied that viscosity (degree of resistance to movement) of grass patches may not be constant, but may vary with the overall coverage of grass. They attributed this difference in viscosity to alteration of behavior at patch edges (e.g., stopping at patch edges) because these effects will accumulate in landscapes with a high edge-to area ratio of habitat patches (e.g., fragmented). In a similar manner, crickets moving among grass patches imbedded in sand used habitat significantly more than expected in 20% patchy landscapes compared to clumped landscapes (With et al. 1999).

Landscapes have been described as cost-benefit surfaces (Wiens 2001) whereby dispersers may incur costs from mortality or loss of fitness as they travel between suitable patches of habitat. Dispersal costs are likely to increase as inter-patch distances increase because of habitat loss and fragmentation. Zollner and Lima (1999) predicted that movement should be more linear when animals are facing greater risks, such as searching in an inhospitable matrix for suitable habitat, than when moving through a benign matrix. Variation in dispersal success in patchy landscapes may be mitigated if individuals have the ability to respond to habitat structure by changing their search strategy (Roitberg and Mangel 1997). The ability of an animal to modify its searching behavior is related to the information the individual receives concerning the distribution of resources as it is moving on the landscape and the amount of information received is determined by its perceptual

range. On fine- and intermediate-grain landscapes habitat fragmentation intensified edge effects, resulting in reduced displacement. On the coarse-grain landscape beetles utilized behaviors which increased displacement and thus the probability of locating suitable habitat. Fine scale movement behaviors such as these may influence colonization patterns at broader landscape scales by increasing aggregation or dispersal propensities of individuals (Turchin 1989; With and Crist 1996).

A behavioral-based approach for investigating a species' distribution in real landscapes (Lima and Zollner 1996) requires knowledge of how functional grain, or the scale at which an organism interacts with landscape structure, may influence search strategies. Our research demonstrated how detailed examination of movement pathways and measures of lacunarity in response to landscape structure can be useful in determining the scale at which an organism interacts with landscape structure. Spatially-explicit, organism-centered studies focusing on behavioral responses to different habitat configurations can serve as an important first step to identify behavioral rules of movement that may ultimately lead to more accurate predictions of space use in landscapes.

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