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The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands

Sharon K. Collinge[1,2,3,*] and Todd M. Palmer[2]
[1]*Department of Environmental Design, University of California, One Shields Avenue, Davis, CA 95616, USA;* [2]*Graduate Group in Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA;* [3]*Current address: Department of EPO Biology and Environmental Studies Program, University of Colorado, 334 UCB, Boulder, CO 80309-0334, USA; *Author for correspondence*

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Abstract

Landscape ecologists typically identify boundaries to demarcate habitat patches. The boundary between two habitat types may be abrupt, such as the transition between a grassland and a parking lot, or more gradual, such as the shift between successional forest stages. Two key aspects of landscape boundaries, their shape and contrast, are predicted to influence movement of materials, plants, and animals. Ecological theory suggests that a patch's perimeter-to-area ratio should strongly influence animal emigration when patch boundaries are relatively permeable, but not when boundaries are more severe. We investigated the interactive effects of patch shape and boundary contrast on movement of ground-dwelling beetles (Carabidae and Tenebrionidae) in native grassland habitat at Jepson Prairie, Solano County, California, USA. We conducted a field experiment with two patch shape treatments, square and rectangle, that held patch area constant, and two boundary contrast treatments created by mowing grass surrounding each plot at two different heights. We monitored the number of beetles leaving each patch over a three-week period following treatment establishment. We observed a significant effect of boundary contrast on net movement of beetles, with low contrast boundaries exhibiting net immigration and high contrast boundaries experiencing net emigration. Moreover, the importance of patch shape appeared to be greater for low contrast versus high contrast boundaries, consistent with theoretical expectations. Our combined observations indicate that these ground-dwelling beetles were more likely to move into patches that were rectangular and surrounded by a low contrast matrix than patches that were square or surrounded by a high contrast matrix. We conclude that net movement of beetles across patch boundaries is strongly influenced by boundary contrast and may be affected by patch shape when boundary contrast is low.

Introduction

As human activities continue to cause loss and fragmentation of native habitats, ecologists are increasingly concerned with two pressing questions: First, how do habitat loss and fragmentation influence animal and plant populations? Second, what spatial characteristics of fragments are important determinants of population responses? The ecological impacts of habitat loss and fragmentation have been intensively studied in many different habitat types (reviewed in Collinge (1996) and Harrison and Bruna (1999)), and a general consensus is of negative consequences for native species. Our understanding of how specific spatial characteristics of habitat patches and boundaries (e.g., connectivity, shape, spatial arrangement, context) influence plant and animal populations remains incomplete, however (Wiens et al. 1993; Mazerolle and Villard 1999; Collinge (2000, 2001); Tischendorf and Fahrig 2000; Laurance et al. 2001; Tischendorf 2001).

As ecologists, we typically identify boundaries to demarcate habitat patches. These boundaries define patch shapes and mark the transition from patch into non-patch habitat. The boundary between two habitat types may be abrupt, such as the transition between a grassland and a parking lot, or more gradual, such as the shift between old growth and early successional forest types. Despite their importance in landscape ecology and conservation biology, relatively little is known about the ecological dynamics of boundaries, especially as they influence animal movement (Wiens et al. (1985, 1993); Hansen and di Castri 1992; Forman 1995; Ims 1995; Lima and Zollner 1996; McIntyre and Wiens (1999a, 1999b); Laurance et al. 2001).

Two key aspects of landscape boundaries, their shape and contrast, are predicted to influence movement of materials, plants, and animals (Stamps et al. 1987; Wiens et al. 1993; Forman 1995). Of the various descriptors of shape, patch perimeter-to-area ratios (also termed "edge-to-interior ratios") have received the most attention regarding their effect on animal movement into and out of habitat patches. Generally, theory holds that as the perimeter-to-area ratio increases, emigration increases as well (Okubo 1980; Kareiva 1985; Turchin 1998), based on simple diffusion. Boundary contrast refers to the degree to which habitat types on either side of the boundary differ from one another, and may be described as abrupt, sharp, and hard (e.g., Forman (1995)) or as soft and gradual. Boundary contrast may also fall anywhere in between these two extremes. The adjectives "sharp" and "gradual" clearly reflect human perception of the structural differences across boundaries. It remains unclear how these structural attributes (boundary *contrast*) translate into functional aspects (boundary *permeability*) of animal movement (Holmquist 1998). As landscape ecologists we suspect that soft boundaries are more permeable to movement and hard boundaries are more impermeable, yet few data exist to confirm our suspicions.

Stamps et al. (1987) suggested that boundary shape and permeability interact to determine animal movement patterns. They defined boundary permeability as the tendency of an animal to cross over a boundary when it is encountered; thus, the same boundary may be differentially permeable to different species, age classes, or sexes. When a hard boundary separates two habitats, it is assumed to be relatively impermeable. Hence, the proportion of animals that encounter the boundary and cross it is low, and patch shape may have little or no effect on movement rates. Conversely, when boundaries are soft and assumed to be permeable, animals move readily across them, and emigration is a function of the number of individuals encountering the boundary. When perimeter to area ratios are high, boundaries are encountered more often, resulting in higher emigration from patches. In summary, Stamps et al. (1987) concluded that patch shape would affect emigration when boundaries are permeable but not when they are relatively impermeable.

The model simulations of Stamps et al. (1987) are intriguing because they suggest that the importance of boundary shape to animal movement is context dependent, relying on the structural and functional relationships between patches and their surrounding matrix, and the behavior of the particular individual animal or species in question. Numerous empirical studies (Thiollay 1993; Hamazaki 1996; Hawrot and Niemi 1996; Usher and Keiller 1998; Helzer and Jelinski 1999; Grez and Prado 2000) suggest that patch shape may determine a species' response to fragmentation, whereas other studies have detected no effect of shape on species distribution or movement patterns (Gutzwiller and Anderson 1992; Harper et al. 1993; Hawrot and Niemi 1996; Virolainen et al. 1998). These contrasting results may not be surprising if the importance of patch shape to organisms depends critically on boundary permeability (Stamps et al. 1987; Holmquist 1998). Whether boundary permeability may modify the importance of patch shape to animal movement is a crucial link in our understanding of the ecological consequences of fragmentation and in our recommendations for reserve design (Game 1980; Kunin 1997; Siegfried et al. 1998).

Our research goal was to examine the interactive effects of two patch characteristics, shape and boundary contrast, on the localized distribution of ground-dwelling carabid (Coleoptera: Carabidae) and tenebrionid (Coleoptera: Tenebrionidae) beetles. We studied beetles in native grassland habitat in northern California for several reasons. First, we could readily alter the spatial structure of the grassland habitat by mowing specified areas of grassland vegetation (Collinge (1998, 2000); Collinge and Forman 1998). Second, beetles have been shown to respond significantly to landscape structure (Duelli et al. 1990; Halffter et al. 1992), and strongly influence the distribution and abundance of organisms at both higher and lower trophic levels. Finally, North American grasslands have suffered loss and isolation to a greater extent than most other ecosystems (Herkert 1994) yet have received comparatively little attention in the context of ecological responses to habitat loss and fragmentation.

We asked two questions: first, do patch shape and boundary contrast influence beetle movement from patches? Second, do beetle species vary in their response to patch boundaries? Based on the predictions of Stamps et al. (1987), we hypothesized that patch shape and boundary contrast would produce interactive effects, with shape influencing beetle movement only when boundaries were relatively permeable. Conversely, we expected that patch shape would not significantly affect movement when boundaries were relatively impermeable. We also expected that different species would respond in different ways to patch shape and contrast.

Methods

Study area

We conducted our study in 1998 at the Jepson Prairie, Solano County, California, USA (38°15′00″ N, 121°45′00″ W), which is a 640-ha grassland preserve associated with the University of California Natural Reserve System (NRS). Jepson Prairie Preserve was established in 1983 to protect relatively undisturbed prairie typical of pre-European settlement California grasslands. The preserve contains primarily California perennial bunchgrass prairie and associated vernal pool habitats, is periodically grazed by sheep and subjected to prescribed burning to prevent encroachment by exotic plant species (Pollak and Kan 1998). We avoided vernal pool habitat and selected a relatively flat, 3-ha study area located at the southern end of the preserve. Our site was dominated by native grasses and forbs *Pleuropogon californicus* (semaphore grass, Poaceae), *Eryngium vaseyii* (button celery, Apiaceae), *Lupinus bicolor* (lupine, Fabaceae), *Lasthenia californica* (goldfields, Asteraceae), and exotic annual grasses including *Lolium multiflorum* (Italian ryegrass, Poaceae) and *Hordeum marinum* (Mediterranean barley, Poaceae).

We studied carabid and tenebrionid beetles, which are conspicuous, species-rich and abundant groups at the study site. These two beetle families have been used extensively in studies of insect movement in relation to landscape structure (e.g., Burel (1989) and Duelli et al. (1990), Johnson et al. (1992), Vermeulen (1994), Crist and Wiens (1995), Wiens et al. (1997), McIntyre and Wiens (1999a, 1999b)) and their primary movement mode is walking rather than flying. Little is known about feeding habitats of particular species, but carabid adults are typically omnivorous or predatory, and tenebrionid adults are typically scavengers or herbivores (White 1983).

Experimental design

We performed a field experiment to examine beetle movement in relation to patch shape and boundary contrast. Our experiment was a split-split-plot design, arranged in three blocks (Figure 1). We designated blocks as the whole plot factor, patch shape (rectangle or square) as the split-plot factor, and boundary contrast (high or low) as the split-split-plot factor (Figure 1) (Keppel 1982). Each block was divided in half, with one half assigned rectangular plots and the other assigned square plots. Rectangular and square plots were equal in area but differed in perimeter and in perimeter/area ratio. Rectangular plots were 2.25 m by 22 m (area = 49 m^2, perimeter = 48.5 m) and square plots were 7 m by 7 m (area = 49 m^2, perimeter = 28 m). Each plot was 4 m from adjacent plots.

Within each split plot, we randomly assigned boundary contrast treatments. Vegetation height within plots averaged 34.88 cm (SE ± 0.87, n = 30), so to apply low boundary contrast treatments to designated plots, we mowed the vegetation surrounding each plot to an average height of 19.08 cm (SE ± 0.70, n = 30), representing a reduction in plant height of 45%. For high boundary contrast treatments, we mowed vegetation surrounding each plot to an average height of 4.7 cm (SE ± 0.26, n = 30), a reduction in plant height of 87%.

Because our study area was relatively small (30 m × 80 m) and homogeneous, we did not expect systematic gradients in moisture or species composition to influence our results. Thus the choice of our block placements was arbitrary, and we considered an interaction between our blocks and our treatment effects unlikely (Newman et al. 1997). Our statistical models described below reflect this assumption of no block*treatment interaction effect.

Insect sampling and deposition of voucher specimens

We used directional pitfall traps to capture beetles (Duelli et al. 1990), which consisted of plastic trays 53 cm long by 27 cm wide by 6 cm deep, divided

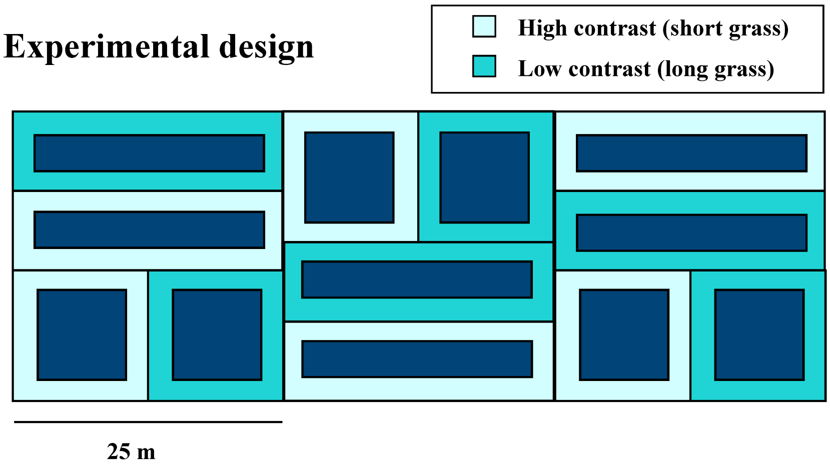

Figure 1. Split-split plot experimental design of field study. Vertical lines delineate the three blocks. Square and rectangular plots were randomly assigned to short grass (high contrast boundary) or long grass (low contrast boundary) treatments. The entire study area was approximately 30 m × 80 m.

lengthwise into two, parallel, equal-sized compartments (Figure 2). We chose this trapping technique because Duelli et al. (1990) developed it to quantify movement of carabids and other arthropods across field borders in an agricultural landscape. We placed trays into the ground flush with the soil surface, and we dug small trenches on either end of the traps to prevent beetles from entering traps from the short sides. Beetles were unable to cross the center partition of the traps. Traps were placed 5 cm from plot edges. We designated the trap compartment near the patch as the inner trap and assumed that this side of the trap captured beetles as they left the grassland patches (Figure 2). We designated the other compartment as the outer trap and we assumed that it captured beetles destined to enter the patches or moving in the mowed grassland matrix (Figure 2).

To achieve equal sampling effort for beetles near rectangular and square plots, we placed traps along 7.5% of the perimeter of each plot (7 traps for each rectangular plot, 4 traps for each square plot). We also placed nine control traps in the unmowed grassland surrounding the experimental plot to record ambient levels of beetle abundance throughout the experiment. We sampled beetles in all traps before we applied the mowing treatments, and then every 2–3 days over a three-week period following the mowing treatments, for a total of eleven sampling dates. We collected beetles from each side of each trap, placed them in labeled collection vials, and stored them in a freezer until we counted and recorded each individual per vial to compare the number of beetles of each species leaving and entering patches.

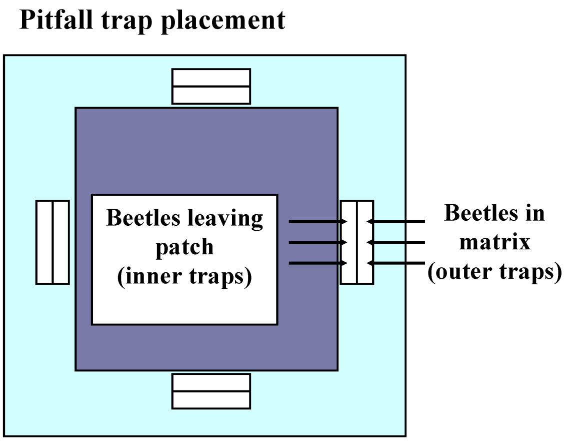

Figure 2. Directional pitfall trap placement adjacent to grassland patches. Diagram shows square, high contrast plot as an example. The inner traps were designed to capture beetles as they left the patches, while the outer traps were designed to capture beetles moving in the grassland matrix. Traps were placed 5 cm from the edge of the grassland patches.

Dr Fred Andrews, a tenebrionid and carabid beetle specialist at the California Department of Food and Agriculture, Sacramento, California, USA, identified all beetles to species. We deposited voucher collections at the Bohart Museum, University of California-Davis and in the first author's laboratory at the University of Colorado at Boulder.

Data analyses

To ensure that there were no systematic differences in beetle abundance among plots prior to our manipulation of patch shape and boundary contrast, we compared beetle abundance in all plots prior to the mowing treatment using split-split-plot Analysis of Variance (ANOVA), with block, patch shape, and boundary contrast as the main effects. Abundance data were square root transformed to achieve normality (Sokal and Rohlf 1995). Because we assumed no block*treatment interaction, we tested the effect of the patch shape*boundary contrast interaction using the residual mean square as the error term (Newman et al. 1997).

We examined effects of patch shape and boundary contrast on beetle abundance in two ways. First, we performed within-subjects ANOVA on total beetle abundance in each side of the directional pitfall traps (inner and outer), and on the difference in abundance between inner and outer traps, over the ten sampling dates according to the split-split-plot experimental design (Figure 1). We calculated the difference between inner and outer traps to estimate net flux of beetles across patch boundaries. Abundance data for inner and outer traps analyzed separately were square root transformed to achieve normality (Sokal and Rohlf 1995), but values of the difference between inner and outer traps were normally distributed and were not transformed. The three blocks were treated as the subjects in which beetle abundance was sampled at each level of patch shape (factor A, two levels), boundary contrast (factor B, two levels), and time (factor C, ten levels) (Keppel 1982). Because we assumed no block*treatment interaction, we tested the effect of the patch shape*boundary contrast interaction using the residual mean square as the error term (Newman et al. 1997). We interpreted the sphericity test on orthogonally transformed variables to determine the covariance structure of the data set and used the results to determine whether to interpret unadjusted univariate results or MANOVA results (SAS Institute 1990).

Second, we performed split-split plot ANOVA on beetle abundance in inner traps, outer traps, and the difference in abundance between inner and outer traps, averaged over the ten sampling dates with block, patch shape, and boundary contrast as the main effects. Because we assumed no block*treatment interaction, we tested the effect of the patch shape*boundary contrast interaction using the residual mean square as the error term (Newman et al. 1997). Similarly, for single species we summed the number of individuals observed in each plot over the entire sampling period and performed ANOVA using the split-split-plot experimental design. We conducted all data analyses using SAS Version 6.0 or JMP Version 3.2 (SAS Institute (1990, 1997)).

Results

We observed twenty species of tenebrionid and carabid beetles in pitfall traps over the three-week period of our experiment. We captured over 100 individuals each of the four most common species, *Apsena rupifes* (Tenebrionidae, 111 individuals), *Blapstinus discolor* (Tenebrionidae, 455), *Dicheirus dilatatus* (Carabidae, 533), and *Pterostichus subcordatus* (Carabidae, 220). For the 16 other species, the number of individuals captured ranged from 1 to 79. The four dominant species differ slightly in body size; *A. rufipes* (4–7 mm) and *B. discolor* (5–6 mm) are slightly smaller than *D. dilatatus* (9–12 mm), and *P. subcordatus* (10–12 mm).

Beetle abundance was similar in all sample plots prior to the mowing treatment (Table 1, Fig. 3a, 3c, “PT”) in both inner and outer traps. As stated above, for the ten post-treatment sampling dates, we assumed that beetles captured in inner traps reflected those leaving patches, and beetles in outer traps were either destined to enter the patches or moving in the mowed grassland matrix surrounding each patch (Figure 2). Beetle abundance in inner traps varied significantly among sampling dates (Table 2, Fig. 3a). Contrary to our prediction, however, the numbers of beetles in inner traps was independent of patch shape and boundary contrast (Table 2, Fig. 3a, 3b). Similarly, we observed significant variation in beetle abundance in outer traps among sampling dates (Table 2, Fig. 3c). However, the effect of patch shape on the number of beetles in outer traps was significantly influenced by boundary contrast (Table 2, time*shape*boundary effect, $F_{9,54} = 2.36$, $P < 0.05$; Fig. 3c). We observed significantly more beetles in outer traps within the matrix surrounding rectangular compared to square patches, and more beetles in low contrast, long grass compared to the high contrast, short grass matrix (Fig. 3d).

Net flux of beetles across patch boundaries, estimated by calculating the difference between inner and outer traps for each sampling plot, varied significantly in both magnitude and direction for different patch

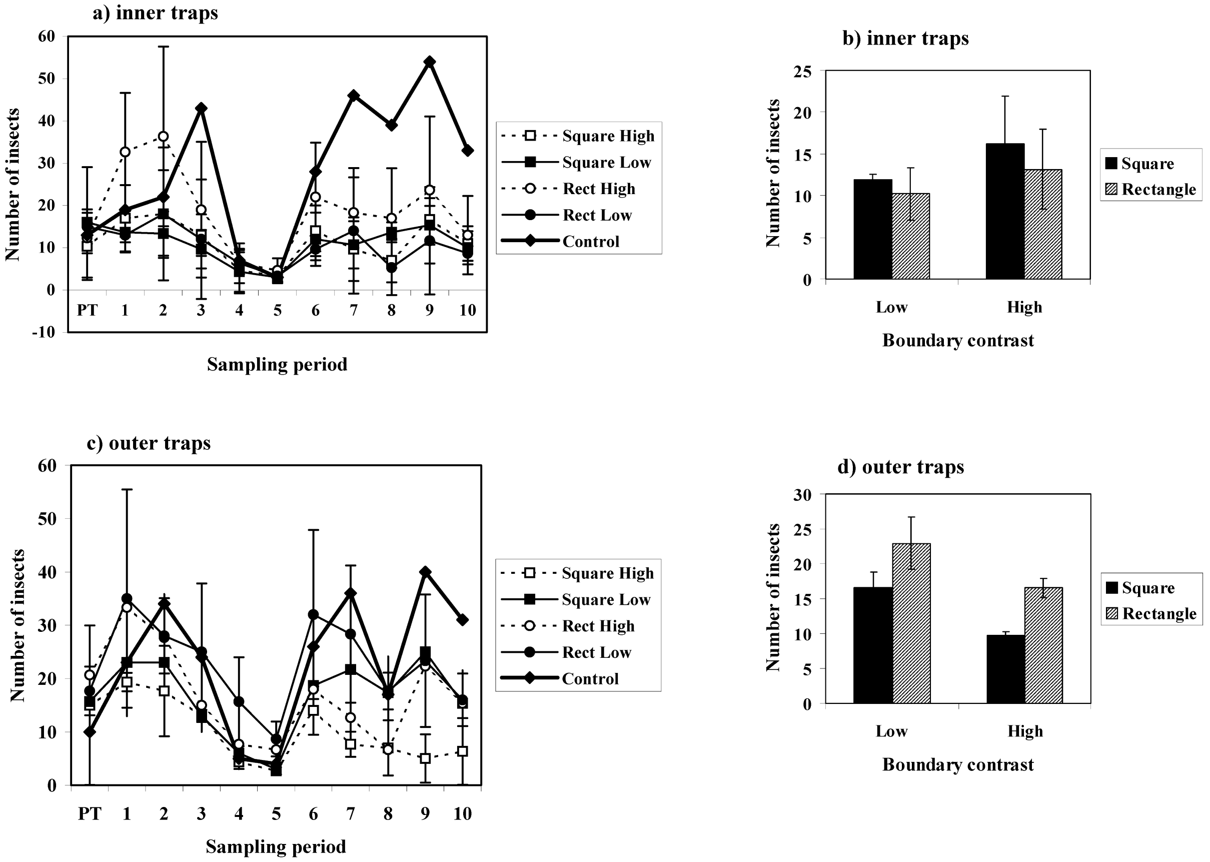

Figure 3. Beetle abundance in a, b) inner and c, d) outer traps over the ten sampling dates. For a) and c), abundance was calculated as the sum of the number of beetles observed in all traps per plot. PT refers to the pre-treatment sample. Means and 95% confidence limits are shown for each experimental treatment (n = 3) as well as for the control traps placed in unmowed grassland on each sampling date. For b) and d), we present average beetle abundance in inner and outer traps for all ten post-treatment sampling dates. Means and standard errors are shown for each treatment (n = 3). Sampling interval was 2–3 days.

types (Figure 4, Table 1). Net movement was negative for low contrast boundaries, indicating a net flow of beetles into patches surrounded by long grass compared to short grass. In contrast, net movement was positive for high contrast boundaries, indicating a net flow of beetles out of patches surrounded by short grass compared to long grass (Figure 4). Additionally, differences in beetle abundance between square and rectangular patches (effect of patch shape) were greater for low contrast versus high contrast boundaries (Figure 4).

For the four individual species for which sufficient data were available to perform statistical analyses, we observed no significant effects of patch shape or boundary contrast on beetle abundance in inner traps ($P > 0.05$ for all four species). For *Blapstinus discolor*, we observed significantly greater numbers of individuals in outer traps adjacent to rectangular plots than near square plots ($F_{1,11} = 10.56$, $P < 0.05$). For *Dicheirus dilatatus*, we observed significantly more beetles in outer traps in long (low contrast) versus short (high contrast) grass ($F_{1,11} = 10.19$, $P < 0.05$).

Discussion

Patch shape and boundary contrast affected beetle distribution and abundance in our field experiment, but in unanticipated ways. Stamps et al. (1987) predicted that patch shape should influence animal emigration from patches when boundary contrast is low but not when boundary contrast is high. Our results for inner traps, which measured insects leaving patches, are therefore inconsistent with the predictions of Stamps et al. (1987). Our outer traps were designed to capture beetles moving in the grassland matrix, and we

Table 1. Results of factorial ANOVA (F-ratios) on the numbers of beetles in inner traps, outer traps, and the difference between inner and outer traps, in relation to grassland patch shape and boundary contrast. “Pre-treatment” samples were collected before mowing to establish patch shape and boundary contrast treatments; “Post-treatment” results are the average of samples collected on ten sampling dates after the mowing treatments were established.

Source of variation	df	Inner	Outer	Inner – Outer
Pre-treatment				
Block	2, 6	1.40	1.47	0.32
Shape	1, 6	0.59	1.11	2.59
Boundary	1, 6	0.06	0.01	0.12
Shape*Boundary	1, 6	0.01	0.30	0.04
Post-treatment				
Block	2, 6	0.21	1.10	3.66
Shape	1, 6	0.95	8.38^{*}	1.89
Boundary	1, 6	1.67	8.55^{*}	29.88^{**}
Shape*Boundary	1, 6	1.14	0.01	3.23

* P < 0.05
**P < 0.01

Table 2. Results of repeated measures ANOVA (F-ratios) on the number of beetles in inner traps, outer traps, and the difference between inner and outer traps, on ten sampling dates following mowing to establish patch shape and boundary contrast treatments.

Source of variation	df	Inner	Outer	Inner – Outer
Time	9, 54	14.32^{**}	22.06^{**}	1.06
Time*Block	18, 54	0.76	0.71	0.82
Time*Shape	9, 54	1.05	0.73	0.62
Time*Boundary	9, 54	0.83	2.30^{*}	1.42
Time*Shape*Boundary	9, 54	1.07	2.36^{*}	1.11

* P < 0.05
**P < 0.01

observed strong effects of patch shape and boundary contrast on beetle abundance in outer traps. Beetles were more abundant near rectangular patches than square patches, and more abundant in long grass than in short grass.

The net flux of beetles across patch boundaries, however, estimated by calculating the difference between inner and outer traps for each sampling plot, was consistent with Stamps et al. (1987) theoretical predictions. The sign of the difference between inner and outer traps indicates whether net movement of beetles was into patches (immigration) or out of patches (emigration). We observed a significant effect of boundary contrast on net movement of beetles, with low contrast boundaries exhibiting net immigration and high contrast boundaries experiencing net emigration. Moreover, the difference between square and rectangular patches (effect of patch shape) was greater for low contrast versus high contrast boundaries (Figure 4), as predicted by Stamps et al. (1987) theoretical models. This latter result was not statistically significant (P = 0.12), given our low statistical power, but the pattern is suggestive.

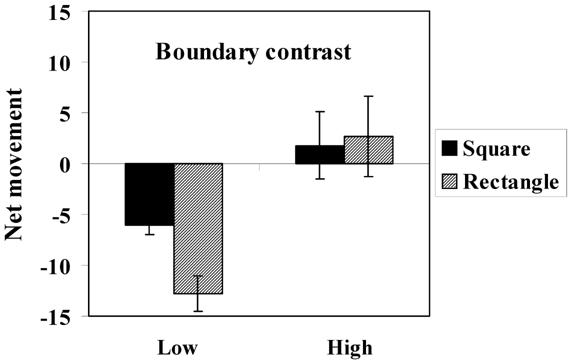

Figure 4. Net movement (number of beetles in inner – outer traps) of beetles from grassland patches, averaged over all ten sampling dates. Means and standard errors are shown for each treatment (n = 3).

Our combined observations indicate that these ground-dwelling beetles were more likely to move into patches that were rectangular and surrounded by a low contrast matrix than patches that were square or surrounded by a high contrast matrix. In fact, high contrast patches experienced net emigration, while low contrast patches experienced net immigration. The lower abundance of beetles in short grass versus long grass was probably because of the relative lack of cover in short grass and the elevated surface temperature compared to long grass. Further, we suspect that our observations of net emigration in high contrast patches may be due to edge effects caused by mowing the grassland matrix. The short grass treatment may have altered the microclimate significantly not only in the matrix, but these microclimatic changes may have permeated the unmowed grassland patches as well. If so, then we would expect high contrast patches to experience greater edge effects and that may explain why beetles emigrated from these patches. Moreover, the effect of patch shape on beetle movement was more pronounced in low contrast versus high contrast patches. These results are consistent with theoretical expectations that animal movement should be affected by patch shape when boundary contrast is low, but not when boundary contrast is high. The most parsimonious explanation for the increased movement of beetles into rectangular versus square patches under these conditions is simple diffusion. Alternatively, beetles may have moved in response to other cues, such as resource abundance or predator avoidance (McIntyre and Wiens 1999b).

For two of the most abundant beetle species in our experiment, we observed similar, significant effects of patch shape and boundary contrast in outer traps. *Blapstinus discolor* was more abundant in outer traps near rectangular compared to square patches, and *Dicheirus dilatatus* was more abundant in outer traps placed in long grass than in short grass. At least for *D. dilatatus* individually, it appears that the short grass was inferior habitat compared to the long grass, possibly due to the microclimatic effects discussed above.

Our equivocal results for inner traps may have been due to our indirect method of measuring beetle movement from patches. Although we did not mark and recapture individual beetles, we used a method (directional pitfall traps) that was developed to assess insect emigration and immigration across boundaries between cultivated fields and semi-natural habitats in Switzerland (Duelli et al. 1990). While we did not place pitfall traps directly in grassland patches in addition to patch edges, we assumed that insects were more or less homogeneously distributed prior to our mowing treatments. Our pre-treatment sample (Figure 3) confirms that there was no systematic variation in beetle abundance among grassland patches prior to the experimental manipulation.

Our observations are comparable to some other studies that have examined the influence of patch shape or boundary conditions on animal movement from patches. For example, Grez and Prado (2000) found that ladybird beetle emigration from *Brassica oleracea* patches was significantly affected by both patch shape and the composition of the surrounding vegetation. Similarly, Hamazaki (1996) observed greater numbers of millipedes in patches with elongated shapes compared to those with more compact shapes. Conversely, Harper et al. (1993) noted that patch shape did not significantly affect dispersal patterns of meadow voles and suggested that this may be due to edge-tolerance by this rodent species.

Our study highlights the importance of distinguishing structural versus functional aspects of habitat boundaries (e.g., Duelli et al. (1990) and Wiens et al. (1993), Holmquist (1998)). Our human perception of patches and boundaries, based on structural landscape features and contrast among adjacent habitat types, may not always parallel the perception of boundaries by different organisms that inhabit the landscape. This underscores the importance of defining landscape structural features, such as connectivity, based on how organisms perceive and use the landscape (e.g., Ferreras (2001)). Few ecological studies have directly compared the movement responses of different animals to similar landscape conditions. Those studies that include such a comparison generally find differences among species, likely due to differences in boundary encounter rates or perception of boundaries (Holmquist 1998; Haddad 1999). We suggest that ascribing functional attributes to structural landscape features such as patches and boundaries must be based on an understanding of how organisms perceive and respond to landscape structure.

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