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Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix

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Animal interpatch movement and spatial distribution are known to be influenced substantially by the composition of the landscape matrix, but little is known about the underlying mechanisms. In previous mark–recapture experiments we have found that the rates of emigration and immigration for the planthopper *Prokelisia crocea* are greater within a matrix composed of the introduced grass smooth brome (*Bromus inermis*) than a mudflat matrix. Additionally, census data indicated that individuals aggregate near the edge of host-plant patches (prairie cordgrass; *Spartina pectinata*) bordered by mudflat, but not in patches bordered by nonhost grasses such as brome. Here, we investigate the mechanistic basis of these matrix effects by tracking the individual movements of planthoppers released at the edge of brome- and mudflat-bordered cordgrass patches, and within homogeneous habitats of each type (cordgrass, brome, and mudflat). We found that patch edges bordered by brome were three times more permeable to emigration than mudflat-bordered edges. Also, planthoppers exhibited no tendency to avoid edges by moving away (i.e. towards the patch interior). Within homogeneous habitats, comparison of the fractal dimension of movement paths revealed that movement was more linear in mudflat than in brome or cordgrass. In addition, planthoppers exhibited greater step lengths (distance moved per 10-min interval), shorter residency times (duration of pauses between movements), and greater rates of net linear displacement in mudflat than brome and cordgrass. We attribute the planthopper's distributional patterns within patches to the lower permeability of mudflat than nonhost grass edges and the absence of edge–avoidance behavior. Contrary to conventional wisdom that low-resistance matrix types (e.g. those that promote high displacement rates) enhance interpatch dispersal rates, dispersal success may be higher in brome matrix because tortuous movement through this matrix increases the planthopper's rate of encounter with cordgrass patches.

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Along with loss and fragmentation of habitats, human modifications to the surrounding landscape (e.g. through introduction of exotic plants, urbanization) may significantly influence the persistence of native species (Drake et al. 1989, Noss 1991, Debinski and Holt 2000, Cronin and Haynes 2004). For herbivorous insects distributed among host-plant patches, the composition of the intervening matrix often has substantial effects on connectivity, i.e. the rate of interpatch movement (Kareiva 1985, Jonsen et al. 2001, Ricketts 2001, Haynes and Cronin 2003). Some matrix types may be resistant to individual movement and favor low connectivity, whereas other less resistant matrix types may favor greater connectivity (Ricketts 2001). By influencing connectivity, the composition of the matrix can affect patch occupancy, local extinction risk and regional

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persistence (Gustafson and Gardner 1996, Cantrell et al. 1998, Moilanen and Hanski 1998, Vandermeer and Carvajal 2001, Cronin and Haynes 2004). Furthermore, recent studies have shown that certain matrix types can promote edge effects in animal density, such that herbivores or their natural enemies amass near the perimeter or interior of host-plant patches (Tscharntke et al. 2002, Cronin 2003a, Haynes and Cronin 2003). To date, however, there has been little empirical exploration of the mechanistic basis of matrix effects on either connectivity or density edge effects (but see Jonsen and Taylor 2000, Goodwin and Fahrig 2002a, Schooley and Wiens 2003, Revilla et al. 2004).

Upon encountering a patch edge, the type of bordering matrix may influence an organism's willingness to approach, move away, or cross the edge (Lidicker 1999). These matrix dependent-changes in behavior can influence the distribution of organisms within a patch. Matrix types resulting in a hard edge (i.e. the edge is relatively impermeable to emigration; Stamps et al. 1987) may encourage a buildup of individuals near the patch edge (Cantrell and Cosner 1998). In contrast, these edge aggregations might not occur if the matrix causes a softer edge and individuals readily move out of the patch. Density edge effects can play a significant role in the dynamics of fragmented populations by altering interactions with competitors or natural enemies (Fagan et al. 1999). Edge effects have been found in many insect populations (Cappuccino and Martin 1997, Davies and Margules 1998, Rothman and Roland 1998); however, the underlying mechanisms are often unclear (McGeoch and Gaston 2000). Our understanding of these mechanisms should benefit from detailed study of individual movement behavior near patch-matrix edges (Ries and Debinski 2001, Schultz and Crone 2001, Schtickzelle and Baguette 2003).

In addition to its effect on animal responses to the patch edge, the composition of the matrix can also affect patterns of movement while in transit between patches (Jonsen and Taylor 2000, Goodwin and Fahrig 2002b). Movement behaviors that allow individuals to quickly colonize a patch may be critical because of mortality risks associated with time spent in the matrix (e.g. starvation, dehydration, predators; Zollner and Lima 1999, Berggren et al. 2002). The tortuosity of the movement path can in theory be a particularly important behavioral parameter. Highly tortuous movement likely increases the probability that a searching individual will encounter patches if they are spatially aggregated (Lima and Zollner 1996, Zollner and Lima 1999, Baum and Grant 2001). If this is a significant factor influencing dispersal success, effects of matrix composition on tortuosity (Crist et al. 1992, Jonsen and Taylor 2000, Goodwin and Fahrig 2002b) may be important mechanisms underlying matrix effects on connectivity. To date, very few studies have examined how changes in movement behavior due to matrix composition ultimately affect dispersal success (but see Jonsen and Taylor 2000). As an example, calopterygid damselflies colonize riparian habitat at a higher rate in a partially, as compared to a fully, forested landscape (Pither and Taylor 1998). Directed movement through pastures apparently underlies the higher colonization rate in the former landscape (Jonsen and Taylor 2000).

Matrix composition is known to influence the interpatch movement rate and within-patch distribution of the planthopper *Prokelisia crocea* (Van Duzee) (Hemiptera, Delphacidae; Haynes and Cronin 2003, Cronin and Haynes 2004), but we do not yet understand the behavioral basis for these matrix effects. Previous mark–recapture experiments revealed that connectivity among prairie cordgrass patches (*Spartina pectinata* Link; Poaceae) is 3–10 times higher for patches embedded in a matrix composed of the exotic grass smooth brome (*Bromus inermis* Leyss) than in a matrix composed of mudflat. This difference in connectivity is attributed to higher emigration and dispersal success in the former matrix (Haynes and Cronin 2003), suggesting that the effect of matrix composition may occur both at the patch edge and within the matrix itself. In addition, field census data show that planthoppers tend to accumulate against the edges of mudflat-bordered cordgrass patches but not in patches bordering nonhost grasses (native grasses or brome; Haynes and Cronin 2003).

Here, we examine movement behaviours of individual planthoppers within patches, within different matrix types (brome and mudflat) and at the patch-matrix edge. Given the lower rates of emigration and interpatch dispersal in mudflat than brome matrix (Haynes and Cronin 2003), we predicted that the permeability of patch edges would be lower in the presence of the former matrix. We also tested whether planthoppers avoided or were attracted to patch edges. Finally, we tracked individual planthoppers within two different matrix habitats (brome and mudflat) and cordgrass patches (as a control) to investigate the possibility that the matrix affects connectivity via its influence on movement behavior while in transit between patches. For the planthopper, it has been hypothesized that crooked (or tortuous) movement paths through matrix habitats would promote connectivity (Kareiva and Odell 1987, McIntyre and Wiens 1999, Haynes and Cronin 2003, Cronin and Haynes 2004). In contrast, linear pathways would likely increase the tendency for planthoppers to pass by neighboring patches without encountering them. Given the planthopper's higher rate of immigration into cordgrass patches within brome than mudflat, planthopper movement was predicted to be more tortuous through brome than mudflat.

Methods

Study system

Prairie cordgrass is a native perennial species associated with hydric grasslands and marshes of North America (Mobberly 1956, Hitchcock 1963). In North Dakota, cordgrass grows in discrete patches ranging in size from 0.1 m^2 to 4 ha and nearest neighbor patches are separated from one another by <50 m (Cronin 2003a, 2003b, 2003c, Cronin and Haynes 2004). Cordgrass patches are embedded within three main types of matrix habitat: 1) mudflats sometimes dominated by saltwort (*Salicornia rubra* Nels.), 2) mixtures of predominantly native grass species (primarily foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb., and little bluestem *Schizachyrium scoparium* Michx.), and 3) stands of exotic smooth brome (*B. inermis*). Brome and cordgrass are approximately equal in height and are considerably taller than the two native matrix types (especially mudflat; Haynes and Cronin 2003). Within our study areas, the three matrix types occur in approximately equal proportions (Haynes and Cronin 2003).

The monophagous sap-feeder *Prokelisia crocea* is the most common herbivore of prairie cordgrass (Holder and Wilson 1992, Cronin 2003a, 2003b, 2003c). The planthopper is bivoltine in North Dakota, with peaks in adult abundance in mid June and early August. Adults are wing-dimorphic, but populations are primarily composed of macropterous individuals ($>$ 90%). Recently, Cronin (2003b, 2004) characterized planthopper populations within prairie remnants as having mainland–island metapopulation structure with frequent extinction–recolonization events and moderately high connectivity among cordgrass patches.

Movement at the patch-matrix edge

The planthopper's behavioral response to patch-matrix edges was examined within experimental microlandscapes in a common garden (located at The Univ. of North Dakota, Grand Forks, North Dakota, USA). Each microlandscape (1.1×1.1 m) contained cordgrass habitat bordering a matrix composed of brome or mudflat. The native grass matrix (above) was not included in the study because planthoppers exhibit nearly identical rates of emigration from cordgrass patches bordering native grass and brome matrix (Haynes and Cronin 2003). Cordgrass or brome habitats were created by planting individual stems in 5.1 cm diameter pots using ProMix BX potting soil (Premier Horticulture Limited, Riviere-du-Loup, Quebec, Canada). To minimize variation in the nutritional quality of cordgrass plants and height of vegetation (cordgrass and brome), plants were obtained as small shoots from a single source patch of each grass. Each microlandscape consisted of potted plants, or mudflat (a flat surface of bare potting soil), arranged in a 20×20 grid (Fig. 1a). The density of stems established within experimental cordgrass and brome habitat (165.3 m^{-2}) was within the range of densities found in natural cordgrass patches (80 – 1072 m^{-2}; 408.7 ± 16.1 m^2, mean $\pm$ SE, $n = 133$). This low density, relative to natural patches, was necessary to allow accurate tracking of very small planthoppers ($\sim$2 mm).

Adult female planthoppers were collected from nearby cordgrass habitat with sweep nets and chilled during transport. Individuals were then marked with Dayglo fluorescent powder to make them more visible to observers (Dayglo Corporation, Cleveland, Ohio, USA). The marker has no significant effect on the dispersal ability or survivorship of the planthopper (Cronin 2003b). Males were not used because population spread occurs primarily through the dispersal of mated females (Cronin 2003b, Haynes and Cronin 2003).

Individuals were released on relatively calm (wind $<$ 12.6 km h^{-1}) and sunny days between 09:00 and 13:00 and then tracked until dusk, provided that the weather conditions remained unchanged. Because we terminated movement trials if winds or cloudiness increased, the length of observation varied from 5 to 13 h. Marked individuals were released into the center of the microlandscape on one of the edge-most cordgrass plants, and their locations were recorded at 10-min intervals as the grid cell above which an individual was located (Turchin et al. 1991).

We tested whether edge permeability, measured as the frequency with which individuals emigrated into the matrix in their first movement from the release location, differed between the brome and mudflat edges with Fisher's exact test (Sokal and Rohlf 1995). Among individuals that did not emigrate on their first move, we tested for edge avoidance behavior by examining the direction of their first movement (i.e. did they move further into the interior or along the patch edge?). Movements from the edge were divided into one of three directional categories (of absolute angles with respect to the edge), each with equal probability of occurrence if movement was random: movement near the edge (0–30°), away from the edge (60–90°), or between these two extremes (30–60°). We examined whether movement was biased towards any of these directions by performing separate chi-square goodness-of-fit tests (Batschelet 1981) for each type of bordering matrix. In the analyses described above, there was one potential source of magnified type I error: non-independence between edge-crossing (permeability) and edge-avoidance behaviors. To protect against finding spurious effects of edge composition on movement, the error rate for the tests of permeability and edge-avoidance was set to $\alpha' = 0.025$.

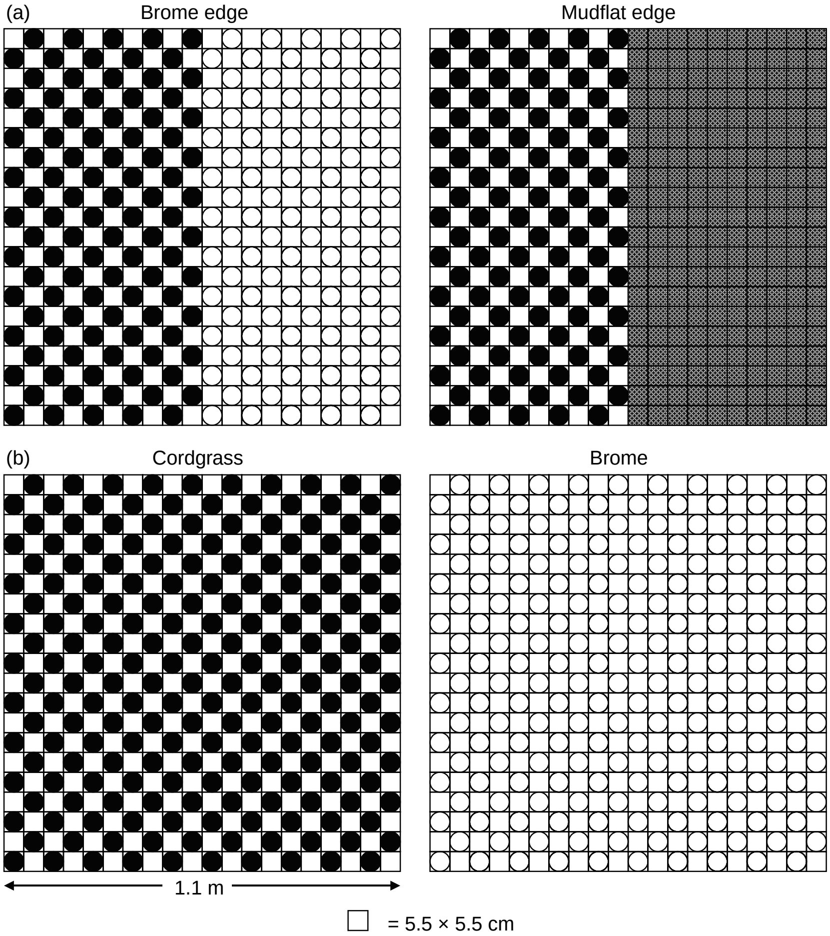

Fig. 1. Diagrams of microlandscape configurations: (a) brome- and mudflat-bordered cordgrass habitats; (b) pure cordgrass and brome habitats. Each microlandscape was arranged in a 20 × 20 grid (400 cells). Cordgrass and brome habitats were created by placing a potted plant in every other grid cell (cordgrass = closed circle, brome = open circle). Bare soil was used to represent mudflat (shaded cells).

Movement within host plant and matrix habitats

The movement behavior of individual planthoppers within pure cordgrass and brome habitats was examined within experimental microlandscapes identical (in size, and stem density) to those described above, but containing only one habitat type (Fig. 1b). Cordgrass patches of equal or lesser size (≤ 1.21 m^2) constitute 16.3% of natural cordgrass patches, and are capable of maintaining planthopper populations for many generations (Cronin and Haynes 2004).

In trial experiments, planthoppers quickly dispersed from mudflat microlandscapes that were identical in size to the microlandscapes used for cordgrass and brome. Similar results were found in nature; planthoppers that were released onto potted cordgrass plants within natural habitats of each type (cordgrass, brome, or mudflat; Haynes and Cronin 2003) exhibited a significantly higher rate of displacement through mudflat than cordgrass or brome. To accommodate the greater spatial scale of planthopper movement in the mudflat matrix, we used a large natural mudflat ($\sim$250 m^2, 30 m from nearest cordgrass patch) located within the Kelly's Slough National Wildlife Refuge (16 km west of Grand Forks, North Dakota). Although dominated by open mud, the experimental site was sparsely vegetated by *S. rubra* $<$5 cm in height.

We released and tracked a total of 139 individuals (53 in cordgrass, 54 in brome, and 32 in mudflat). Marked individuals were released into the center of the microlandscape (cordgrass and brome) or mudflat, and their positions were recorded at 10 min intervals. For the mudflat trials, in which individuals moved farther per unit time (Results), the observer marked an individual's location during each time interval with a wire flag (10 cm to the north of the individual). No insect was observed to jump or fly in response to the placement of a flag. Unlike the experiments in cordgrass and brome, movement trials in mudflat were terminated if an insect remained inactive for 1 h.

Analysis of movement paths within habitats

An individual's overall rate of movement across a landscape is contingent upon the individual's tendency to move (or remain sedentary), movement velocity, and path tortuosity (Russell et al. 2003). The tortuosity of movement was assessed by calculating the fractal dimension of each movement path. Fractal dimension-estimates (D) near 1 indicate highly linear movement, whereas estimates near 2 suggest approximately Brownian (plane-filling) movement (Hastings and Sugihara 1993). Although the idea that organisms are scale invariant with respect to their movement patterns has been criticized (Turchin 1996), using fractals as a tool for characterizing movement pathways of a species in different habitats remains a valid approach. Fractal dimensions were estimated with Fractal 4.0 software (http://www.nsac.ns.ca/envsci/staff/vnams/Fractal.htm). We used the fractal mean method, which is based on the traditional dividers method (Mandelbrot 1967, Sugihara and May 1990), but corrects for estimation errors created when the last divider step does not fall exactly on the end of the path (Nams and Bourgeois 2004). We estimated fractal dimensions based on the entire recorded movement path of each individual. Paths of four moves or less were not used in the analyses because estimates of their fractal dimension sometimes fell below the theoretical limit of 1. Paths were too short to be included for two primary reasons: the individual was lost (usually temporarily) or was sedentary (44% and 43% of the excluded paths, respectively). The lost individuals consisted exclusively of those released in brome or cordgrass with the exception of 1 individual in mudflat. Individuals that emigrated or died each accounted for an additional 7% of the excluded paths.

We measured an individual's velocity using mean step length (cm) per 10 min interval (Crist et al. 1992). The degree to which individuals remained stationary was measured as the time elapsed between movements, or residency time (Andow and Kiritani 1984). Finally, we quantified an individual's overall rate of movement using net linear displacement rate (cm h^{-1}; Goodwin and Fahrig 2002b).

To reduce bias due to differences in the duration of movement trials in mudflat versus cordgrass and brome, mean step lengths, residency times and net displacement rates were calculated based on planthopper movements recorded within the first hour after release. Displacement rate was calculated using a planthopper's distance from the release point 1 h post release. In the event that an individual was lost (15 individuals) or emigrated (1 individual) from the microlandscape in <1 h, we used the individual's last known position within the microlandscape to calculate displacement rate. The loss or failure to recapture individuals in mark–recapture studies can lead to underestimation of displacement (Turchin 1998), but this is unlikely in our study because most missing individuals were eventually re-sighted within the microlandscapes after briefly remaining hidden within the vegetation.

To test whether the above movement behaviors differed among habitats, we used ANOVA if the data distributions could be normalized with transformations and the variances were homogenous (mean step length, fractal D). Mean step length was ln-transformed, and fractal D was transformed by computing ln(D-1). In both cases, multiple comparisons between habitat types were performed with the GT2-method because of unequal sample sizes (Day and Quinn 1989).

Differences in net linear displacement rate and residency time among the three habitats were evaluated with Kruskal–Wallis tests because the data distributions were strongly right-skewed and could not be normalized by transformation (Sokal and Rohlf 1995). Multiple comparisons between habitats were performed with Fligner-Policello tests due to unequal variances (Day and Quinn 1989).

In the tests presented above, the likelihood of type I errors may have been inflated due to lack of independence among tests. For example, velocity and path tortuosity are expected to influence the net displacement rate (Crist et al. 1992). To minimize the chance of finding spurious effects of habitat type on movement, we applied a sequential Dunn-Šidák correction to the critical level of α for the omnibus test for each movement behavior ($\alpha = 0.05$).

One possible explanation for differences in movement behavior among habitats is that exposure to wind differs among habitats, particularly between open mudflats and the experimental patches of cordgrass and brome. We evaluated this possibility by testing for the presence of planthopper drift, i.e. a directional bias in movement. For each day of movement trials, we calculated the mean x- and y-coordinates of planthoppers 1 h post release within each habitat type (with the point of release at $x, y = 0$).

Drift was found to be significant if the 95% confidence intervals around the mean of these coordinates did not overlap the release point (Turchin and Thoeny 1993, Cronin et al. 2000). If we found significant drift, the data from that day of movement trials were omitted from the analyses.

Finally, we tested for associations between planthopper movement behaviors (e.g. step lengths and fractal dimensions) using Spearman's rank correlations (Sokal and Rohlf 1995). We controlled for comparison-wise error by performing sequential Dunn-Šidák corrections.

All statistical analyses were conducted using SPSS (SPSS Inc., Chicago, IL, USA) or SAS (SAS Institute, Cary, NC, USA).

Results

Movement at the patch-matrix edge

For planthoppers on the patch-matrix edge, the permeability of the edge was strongly dependent on the bordering matrix (Fisher's exact test, $P=0.018$). In patches bordering mudflat, 14.7% (5/34) of planthoppers crossed the cordgrass-mudflat edge on their first move. In contrast, the emigration rate was 3 times higher for patches bordering brome (44%, 11/25). In fact, planthoppers were as likely to cross the cordgrass-brome edge as they were to remain within the patch ($\chi^2=0.360$, df = 1, $P=0.549$).

Although the cordgrass-mudflat edge represented a relatively impermeable border, we found no tendency for planthoppers to move away from the edge. The direction of movement within patches was not significantly biased with respect to the edge (based on a comparison of angles of movement; $\chi^2=0.276$, df = 2, $P=0.871$). Planthoppers moved along and away from the edge with equal frequency (31.0%, 9/29). Similarly, 37.9% (11/29) moved inward from the edge at a 30–60° angle. Because individuals readily crossed the cordgrass–brome edge, we lacked the statistical power to test for edge-avoidance behavior in patches bordering brome. However, the results were similar (6 along the edge, 5 neutral, 3 away from the edge), suggesting that planthoppers move randomly in patches with respect to the edge.

Movement within host plant and matrix habitats

We found no evidence of directional bias in planthopper movement with the exception of the first day of movement trials in mudflat (Fig. 2). During these mudflat trials, a moderate wind (12.6 km h^{-1}) blew in from the northwest. To remove bias, the data from these trials were excluded from the following comparisons of movement behavior among habitats.

Based on the fractal dimension of planthopper movement pathways, we found significant differences in path tortuosity between all three habitats (Table 1). Planthopper movement tended to be highly linear in mudflats, circuitous in cordgrass, and of intermediate tortuosity in brome (Fig. 3a, 4).

Mean step length was more than two times greater in mudflat (40.3 ± 6.1 cm per move, mean ± SE, $n=26$) than in either cordgrass or brome (15.7 ± 2.2 and 17.2 ± 1.9 cm, $n=31$ and 25, respectively; Fig. 3b). In addition, planthoppers exhibited significantly lower median residency times in mudflat (0 min, $n=26$) and brome (0 min, $n=23$) than in cordgrass (5 min, $n=25$; Fig. 3c).

After 1 h, the median net displacement rate in both cordgrass and brome was 0 cm h^{-1} ($n=53$ and 49, respectively) and only 1 individual emigrated from a microlandscape (brome). In contrast, planthoppers moved through mudflats much faster, at a median rate of 97.0 cm h^{-1} ($n=26$; Fig. 3d).

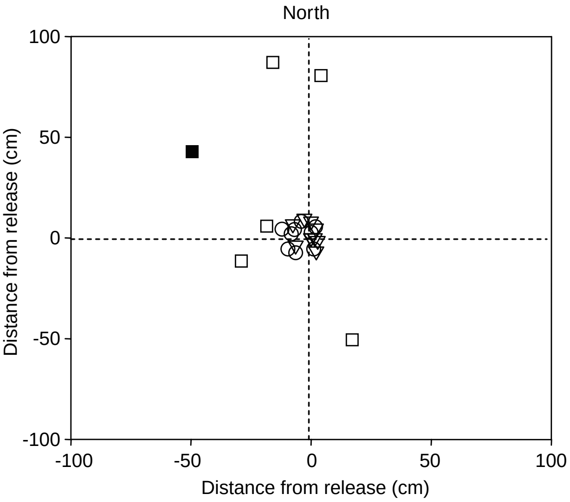

Fig. 2. Mean displacement of planthoppers on each day of movement trials in cordgrass (circles), brome (triangles), and mudflat (squares). Data are based on displacement 1 hr after planthoppers were released. The filled symbol indicates the one day of movement trials for which the 95% confidence intervals about the mean x- and y- coordinates do not overlap with the release point (intersection of the dashed lines). Confidence intervals are not shown for clarity.

The planthopper movement behaviors above were significantly correlated with one another in 2 of 6 possible pair-wise comparisons (after using sequential Dunn-Šidák to adjust for inflated type-I errors associated with conducting multiple tests). Net displacement rate was positively correlated with step length and negatively correlated with residency time (Table 2). Linear movement paths (indicated by low fractal dimensions) were associated with long step lengths and high net displacement rates, but these correlations were not significant.

Discussion

Movement at the patch-matrix edge

The landscape matrix in North American tallgrass prairie appeared to strongly affect planthopper movement at two major stages of interpatch dispersal: emigration across the patch-matrix boundary, and movement through the matrix. Although planthoppers redistribute themselves at random within cordgrass patches (Cronin 2003b), and were not repelled by the patch edge, the cordgrass-mudflat edge represented a relatively impermeable barrier to their movement. In contrast, the cordgrass–brome edge was effectively invisible (sensu Jeanson et al. 2003); individuals moved across the edge as frequently as they moved within the

Table 1. Effect of habitat type on planthopper movement behavior. Results from the multiple comparisons tests among habitats (C = cordgrass, B = brome, M = mudflat) are summarized in the "effect" column.

Dependent variable	Test	Test statistic	df	P	Effect
All habitats compared					
Fractal dimension	ANOVA	F = 20.472	2,25	<0.001*	M < B < C
Step length (cm)	ANOVA	F = 14.457	2,79	<0.001*	M < C,B
Residency time (min)	Kruskal–Wallis	H = 6.344	2	<0.042*	M < C
Net displacement rate (cm h^{-1})	Kruskal–Wallis	H = 54.158	2	<0.001*	M > C,B

*Significant results after using a sequential Dunn–Šidák correction to protect against inflated type-I error.

patch (e.g. away or along the edge). These findings confirm our previous prediction, derived from field mark-recapture experiments (Haynes and Cronin 2003), that brome edges are more permeable to the planthopper. Sparsely vegetated mudflats form very clear borders with cordgrass patches. In contrast, the boundary between cordgrass and brome appears less distinct because brome is similar in height and appearance to cordgrass (photographs in Haynes and Cronin 2003). We suspect that the resemblance of brome to cordgrass is an important factor underlying high patch permeability. Higher permeability of edges between similar, as compared to contrasting, habitats may be a common pattern among herbivorous insects (Kareiva 1985, Lawrence and Bach 1989, Kuussaari et al. 1996, Ries and Debinski 2001; but see Collinge and Palmer 2002).

The effect of the matrix on patch permeability may explain field census data (Haynes and Cronin 2003) showing that planthoppers aggregate near the perimeter of mudflat-bordered patches, but not against patch edges bordering non-host grasses (brome or native grasses). The density edge effects in the former patches may be explained by the tendency for individuals to avoid crossing the patch edge, but not to be repelled into the patch interior. Using a model based on diffusive movements, Cantrell and Cosner (1998) found that individuals may pool against an edge of low permeability such as the cordgrass-mudflat edge. This prediction is also supported by recent field studies. Animal movements

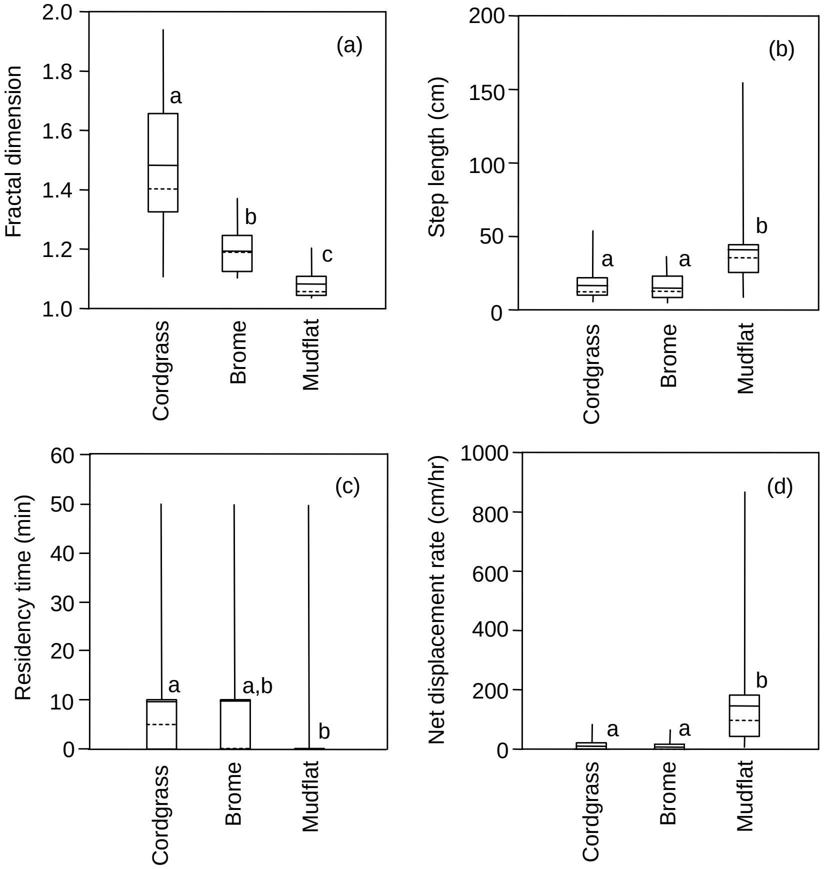

Fig. 3. Box and whisker plots showing the effects of the three habitat types on planthopper movement behaviors: (a) fractal dimension of movement paths; (b) step length; (c) residency time; (d) net linear displacement rate. The boxes show the interquartile range and the whiskers show the range. The solid and dashed horizontal lines within a box indicate the mean and median values, respectively. Different letters denote significant differences at the α = 0.05 level after multiple comparisons tests.

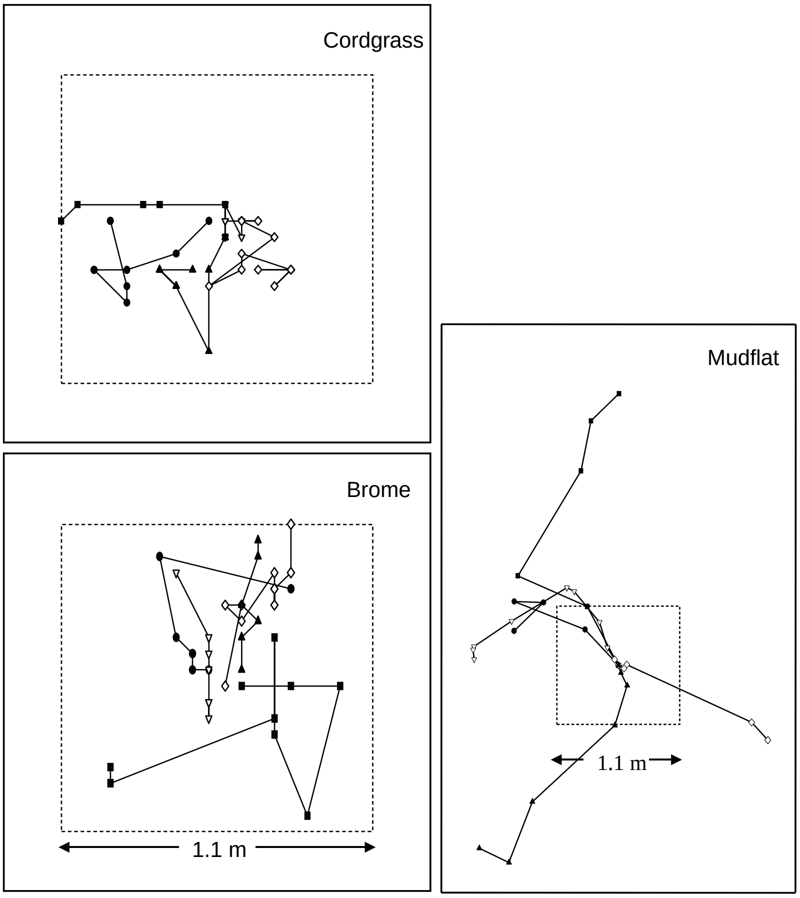

Fig. 4. Representative movement paths in each habitat. Five paths were randomly selected from those ≥4 steps. Movement observations in cordgrass and brome habitats were conducted in 1.1 × 1.1 m experimental patches (box indicated with dashed line). Although observations in mudflat were conducted in a large naturally occurring mudflat (~250 m^2), a box equal in area to the cordgrass and brome microlandscapes is shown for comparison. For each path, the starting point near the center of the microlandscape and locations at 10 min intervals are shown (different symbols for each path).

can be conveyed along hard habitat edges (Haddad 1999, Desrochers et al. 2003) leading to aggregations near the perimeter of suitable habitat patches (Bider 1968, Desrochers and Fortin 2000, Desrochers et al. 2003). Desrochers et al.'s (2003) study of the Siberian flying squirrel (*Pteromys volans*) is one the few to investigate how the permeability of different patch-matrix edges affect the generation of density edge effects. In this study, squirrel densities were higher near forest edges due in part to their unwillingness to enter surrounding open habitats.

To date, most studies have attributed edge effects in animal density to differences in some aspect of habitat quality between the edge and interior of patches, such as differences in host-plant quality, microclimate, or predator abundance (Cappuccino and Martin 1997, Rothman and Roland 1998, McGeoch and Gaston 2000). In natural cordgrass patches, plant quality differs between the edge and interior of patches irrespective of matrix composition. Foliar nitrogen concentration (a strong indicator of plant quality to various planthopper species; Cook and Denno 1994) is ~14% higher at the patch edge (relative to the interior) in patches bordering both mudflat and non-host grasses (Haynes and Cronin 2003). Therefore, plant quality can not explain why planthoppers amass along the edge of mudflatbordered cordgrass patches and not brome-bordered cordgrass patches. Instead, the matrix-dependent edge effect in planthopper density is probably the result of other factors, such as differences in edge permeability or the foraging behavior of the planthopper's main parasitoid, *Anagrus columbi* (Hymenoptera: Mymaridae). This egg parasitoid avoids foraging near the edge of cordgrass patches that are embedded in mudflat (preferring the patch interior), but forages evenly throughout patches bordering nonhost grasses (brome or native grasses; Cronin 2003a). Thus, it is

Table 2. Spearman's rank correlation matrix for planthopper movement behaviors.

Behavior	Fractal dimension	Step length	Residency time
Step length (cm)	−0.455		
Residency time (min)	−0.024	−0.246	
Net displacement rate ($cm\ h^{-1}$)	−0.423	0.841*	−0.345*

*Significant correlation after sequential Dunn–Šidák correction to adjust for inflated type-I error.

possible that planthopper oviposition near the patch edge in mudflat-bordered patches is favored evolutionarily by the reduced risk of parasitism (Werner and Hall 1988, Orrock and Danielson 2005).

Movement behavior and connectivity

The effect of matrix composition on the rate of interpatch movement (i.e. connectivity) in this system is likely attributable to matrix-specific differences in cordgrass-edge permeability and movement behavior within the matrix. The extremely high permeability of cordgrass-brome edges may contribute substantially to the higher rate of interpatch movement in the brome matrix (Haynes and Cronin 2003, Cronin and Haynes 2004). Schtickzelle and Baguette (2003) have reported similar findings in their work on the bog fritillary butterfly (*Proclossiana eunomia*). High edge permeability is considered to be critical for promoting connectivity (Schtickzelle and Baguette 2003); however, the primary factor affecting edge permeability for the butterfly appears to be the extent of habitat fragmentation rather than composition of the matrix. For the planthopper, connectivity is further enhanced by higher dispersal success (i.e. proportion of dispersing individuals that successfully immigrate into a patch) in the brome than mudflat matrix (Haynes and Cronin 2003). This latter effect of the matrix may be the result of differences in movement behavior while in transit between patches.

Movement-behavior results from our experimental microlandscapes were consistent with findings from previous field-based studies (Cronin 2003b). Based on a mass release of marked planthoppers in natural stands of cordgrass and a matrix of native non-host grasses, planthoppers exhibited median displacement rates (3.75 and 10 cm h^{-1}, respectively; based on recaptures after 24 h; Cronin 2003b) that correspond very closely to rates for individuals in microlandscapes (3.6 and 5.9 cm h^{-1}, based on non-truncated movement paths). In addition, planthoppers that emigrated from experimental cordgrass patches placed within natural habitats of each type (cordgrass, brome, or mudflat; see Haynes and Cronin 2003), exhibited significantly lower median displacement rates in cordgrass and brome than in mudflat (K. J. Haynes, unpubl.). In the same experiment, the planthoppers also appeared to move in a more circuitous fashion through cordgrass and brome than mudflat (K. J. Haynes, pers. obs.). Thus, our present findings appear to reflect differences in planthopper movement behavior among these habitats in nature.

The relatively slow and tortuous movement of planthoppers in cordgrass and brome, as opposed to mudflat, is likely attributable to the structural complexity of these prairie landscape habitats. Insect movement is consistently reported to be slow and tortuous in structurally complex habitats, and more rapid and linear in simple or open habitats (Zalucki and Kitching 1982, Crist et al. 1992, Jonsen and Taylor 2000). Whereas movement differed strongly between planthoppers in cordgrass and the mudflat matrix, we detected no differences in step length, residency time, or net displacement rate between cordrgrass and brome (Table 1). These results are somewhat surprising given that cordgrass is the planthopper's sole host plant. One possible explanation for the correspondence between planthopper movement in cordgrass and brome matrix is the structural similarity of these two grasses (Haynes and Cronin 2003).

Tortuous movements, as detected for planthoppers in the brome matrix (Fig. 3a, 4), may increase the likelihood that dispersers will encounter and colonize cordgrass patches. When patches are spatially aggregated, as in our study system (J. T. Cronin, unpubl.), empirical and theoretical studies suggest that linear movement may be less efficient for locating resource patches than other forms of tortuous movement (e.g. random walk, foray search, Archimedean spirals, Evans 1976, Baars 1979, Kareiva and Odell 1987, McIntyre and Wiens 1999, Zollner and Lima 1999, Conradt et al. 2003). Under these circumstances, the concept of matrix resistance (Ricketts 2001) does not fit our system well. Matrix resistance, measured in terms of the rate of individual movement, is generally thought to reduce connectivity (Schooley and Wiens 2004, Stevens et al. 2004). Although the mudflat is a low-resistance matrix (e.g. one that promotes linear movement, high net displacement), dispersal success is much higher for planthoppers moving through a brome than mudflat matrix (Haynes and Cronin 2003). The planthoppers' linear movements in mudflat may be poorly suited to colonizing spatially aggregated cordgrass patches because they may increase the chance of passing by nearby cordgrass patches (Zollner and Lima 1999). The effects of matrix composition on within-matrix movement behavior have been reported in previous studies (Crist et al. 1992, Goodwin and Fahrig 2002a, 2002b). Very few studies, however, have evaluated the underlying role of movement tortuosity in determining the effect of the matrix on connectivity (but see Jonsen and Taylor 2000).

The tortuosity of movement through the matrix is one of many potential mechanisms underlying matrix effects on dispersal success. Differences in abiotic conditions between matrix types could potentially influence dispersal success; however, this does not appear to be the case for the planthopper. Microclimate conditions (wind, temperature, humidity) vary only slightly between the mudflat and brome matrix types (Cronin and Haynes 2004). Another potentially important factor is the risk of being eaten by predators while moving through the matrix (Aars et al. 1999, Rothermel and Semlitsch 2002). For example, Aars et al. (1999) attributed low rates of dispersal success in root voles (*Microtus oeconomus*) to high mortality by avian predators when voles ventured into an open matrix. For the planthopper, we have found that spiders, the main source of predation for planthoppers (Cronin et al. 2004), differ in abundance among matrix types. Spider densities are highest in native nonhost grasses, intermediate in brome and virtually zero in mudflats (Cronin et al. 2004). Although it appears counterintuitive that dispersal success is highest in matrix habitats with high spider densities (i.e. brome), we do not yet know the relationship between spider density and risk of predation or how vegetation structure might influence perceptual ranges of spiders.

Conclusions

This represents one of very few studies to examine the behavioral underpinnings of matrix effects on the distribution and dispersal of a spatially structured population (but see Jonsen and Taylor 2000, Collinge and Palmer 2002, Goodwin and Fahrig 2002a, Schooley and Wiens 2003, Revilla et al. 2004). Patch-matrix permeability may play an important role in the generation of edge effects in planthopper density. The accumulation of planthoppers near the edge of mudflat-bordered patches may result because individuals avoid crossing the patch edge, but are not repelled into the patch interior. In contrast, the lack of an edge effect in patches bordering brome may be due to an inability of planthoppers to distinguish between cordgrass and brome at the patch edge; individuals were as likely to cross the patch edge as they were to remain within the patch. As humans continue to fragment natural landscapes, edge effects in animal distribution might be especially common where human activities in the matrix create a stark contrast between matrix and patch (e.g. forest remnants embedded within agricultural matrix; Desrochers and Fortin 2000, Desrochers et al. 2003).

Finally, we reveal an intriguing and potentially important process by which matrix composition can influence connectivity. By increasing the tortuosity of animal movement paths, high-resistance matrix types may promote connectivity by increasing encounters with nearby patches (Zollner and Lima 1999). In our system, planthopper movement was slower and more tortuous in the brome than mudflat matrix, yet colonization success is much greater in the brome matrix. This effect is antithetical to widely held views about the role of matrix resistance in the connectivity of landscapes. We would add that because patches are spatially aggregated in most systems (Conradt et al. 2003), including our own, the importance of this novel effect for dispersal and the spatial ecology of species might be underappreciated.

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