

**HERBIVORE MOVEMENT AND SPATIAL POPULATION DYNAMICS IN A
HETEROGENEOUS LANDSCAPE**

A Dissertation

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ABSTRACT

To date, few metapopulation studies have isolated the effects of the intervening matrix from other attributes of landscape structure (e.g., patch geography or quality) that might influence dispersal among patches. Furthermore, there has been little exploration of the mechanisms underlying effects of the matrix on the spatial ecology of species. In this dissertation, I examine how the movement and distribution of the planthopper *Prokelisia crocea* within and among host-plant patches (prairie cordgrass, *Spartina pectinata*) is affected by the composition of the matrix [the invasive grass smooth brome (*Bromus inermis*), native non-host grasses, or mudflat]. First, using a mark-recapture study in networks of experimental cordgrass patches that were made identical in size, isolation, and plant quality, I found that the interpatch movement rate of the planthopper was highest in the brome matrix, intermediate in the native grass matrix, and lowest in mudflat. Second, field surveys revealed that individuals accumulated against patch edges in mudflat-bordered patches, but not in patches bordered by non-host grasses. Among patches, incidence and density increased with the proportion of the matrix composed of open mud. Third, I investigated the behavioral bases of these matrix effects using individual movement trials. Whereas movement through mudflat was highly linear, movement was much more tortuous through brome. Within patches, brome edges were three times more permeable to emigration than mudflat edges. I suggest that the effect of matrix composition on the rate of planthopper movement among patches is driven largely by differences in movement tortuosity within the matrix. Tortuous movement through brome likely increases the planthopper's rate of encounter with spatially aggregated host-plant patches. Furthermore, the effect of the matrix on the planthopper's within-patch distribution can be attributed to the differences in edge permeability between

matrix types. Finally, a literature review revealed that matrix composition and patch quality often covary in plant-herbivore systems, and that most matrix studies have failed to experimentally or statistically isolate the effects of the matrix from potential patch-quality effects on dispersal. These findings highlight the value of a mechanistic understanding of the links between landscape structure and dispersal in spatial ecological population studies.

CHAPTER 1

INTRODUCTION

Natural populations typically exist in fragmented landscapes rather than continuous homogenous habitat (reviewed in Hanski 1999). Anthropogenic activities of the last century have greatly increased the spatial subdivision of populations (Wilcox and Murphy 1985, Saunders et al. 1991). For patchily distributed populations, the rate of movement among patches (i.e., connectivity) is critical to patterns of patch occupancy, regional population dynamics, and the spatial spread of populations (Hanski 1994, 1999, Stacey et al. 1997). Although populations occupying small habitat patches are at high risk of extinction (MacArthur and Wilson 1967), species can persist regionally among patches connected by dispersal, i.e., as a metapopulation (Levins 1970). Inter-patch dispersal promotes the re-establishment of populations on vacant patches (Levins 1970) and the prevention of local extinctions within patches (Brown and Kodric-Brown 1977). Attributes of landscape spatial structure, such as heterogeneity in patch characteristics (size, isolation, quality) often strongly influence dispersal and connectivity (reviewed in Hanski 1999).

Most studies of subdivided populations that have examined factors influencing patch connectivity have stressed the importance of the size and isolation of patches (e.g., Thomas and Harrison 1992, Hanski 1994, Hill et al. 1996, Doak 2000). Relatively few studies have emphasized that variation in patch quality can be important to inter-patch dispersal (e.g., Hanski and Thomas 1994, Matter and Roland 2002), despite the fact that patch quality can have stronger effects than patch geography on patch occupancy, population turnover rates, and metapopulation persistence (Hanski and Thomas 1994, Briers and Warren 2000, Fleishman et al. 2002). For an herbivore, the availability of preferred host-plant food resources (e.g., nectar producing flowers for butterflies) can be a major factor influencing patch quality and inter-patch dispersal rates (e.g., Brommer and Fred 1999, Matter and

Roland 2002). In addition, most empirical and theoretical studies have largely ignored the effect of the intervening habitat (i.e., the matrix) on the movement of animals among patches (Taylor et al. 1993, Wiens 1997, Tischendorf and Fahrig 2000). Omission of this component of the landscape is arguably a major flaw in the development of metapopulation theory (Wiens et al. 1993, Wiens 1997; but see Molainen and Hanski 1998). While the emphasis placed on matrix heterogeneity represents a major distinction between landscape ecology and metapopulation theory (Wiens 1997, Hanski 1999), studies in both disciplines have a potential flaw in common. Most metapopulation and landscape ecology studies have implicitly assumed that the variables which define the structure of landscapes (e.g., patch size, matrix, patch quality) vary independently of one another (e.g., Kuussaari et al. 1996, Moilanen and Hanski 1998, Ricketts 2001, Ries and Debinski 2001; but see Wiens et al. 1985, Summerville and Crist 2001).

Patch quality in particular is likely to covary with other landscape attributes. For a diversity of organisms and for herbivores in particular, landscape structure is often defined by the patchiness of their host plants (Wiens 1976, Kareiva 1983, Wiens et al. 1985). The characteristics of host-plant patches (e.g., species composition, soil nutrient levels, plant survival, vegetational structure) are often strongly influenced by the nature of the surrounding environment or matrix (Wiens et al. 1985, Pickett and Cadenasso 1995). Thus, the quality of vegetation patches to herbivores may often depend on the type of matrix within which the patches are embedded. For example, a vegetation patch surrounded by a bare matrix may be richer or poorer in nutrients than a patch surrounded by a forest matrix (as a result of differences in competition for nutrients and light, soil conditions, flow of water, etc.; Wiens et al. 1985, Weathers et al. 2001, Pickett and Cadenasso 1995). Patch-quality interactions with

the surrounding landscape may be common in many plant-herbivore systems, particularly those with distinctly different matrix types (e.g., a pasture versus forest matrix; Kuussaari et al. 1996).

Despite recent emphasis on the effects of landscape heterogeneity on dispersal and population dynamics, much work will be required to fully resolve the role of the matrix in herbivore spatial ecology. First, there is a lack of well-controlled field experiments capable of isolating the effects of matrix composition from other attributes of the landscape with the potential to influence dispersal such as patch quality. Second, there is a need to assess the relative importance of the matrix and patch geographical variables (e.g., size, isolation) to the spatial distribution of organisms. Third, the mechanistic bases of matrix effects on the interpatch movement and spatial distributions of species remain largely unexplored (but see Jonsen and Taylor 2000; Goodwin and Fahrig 2002).

The planthopper *Prokelisia crocea* (Hemiptera, Delphacidae) represents a model organism for testing landscape ecology theory and for elucidating the mechanisms whereby the matrix affects herbivore spatial dynamics. The planthopper population is naturally subdivided among spatially discrete host-plant patches (prairie cordgrass, *Spartina pectinata*) which are embedded in distinct matrix types (mudflats, mixtures of native grass species, and stands of the exotic grass smooth brome [*Bromus inermis*]). Moreover, because the characteristics of the host-plant patches (i.e., size, spatial patterning, and nutritional quality) are easily controlled or altered, and dispersal occurs over short distances of < 100 m (Cronin 2003), the planthopper population is very well-suited to small-scale manipulative experiments.

In the following chapter (chapter 2), I evaluated the hypothesis that planthopper dispersal among patches is directly influenced by the composition of the matrix using a mark-

release-recapture experiment conducted in networks of experimental cordgrass patches. In addition, field census data were used as a basis for examining whether planthopper spatial distributions within and among patches vary with matrix composition in accordance with predictions of the above field experiment. Furthermore, these data allowed me to assess the relative contributions of matrix composition and patch geography (size, isolation) to the distribution of planthoppers. In chapter 3, I reviewed the literature on the effects of matrix composition on the interpatch movement of herbivores in order to evaluate whether the hypothesis that matrix composition directly influences dispersal and landscape connectivity has been adequately tested. I also outlined hypotheses for why patch quality and matrix composition may frequently covary in plant-herbivore systems. My findings are used to make specific recommendations for how studies can definitively determine whether matrix composition influences herbivore movement. The main impetus of the chapter 4 study of individual movement behavior was to determine the underlying mechanisms whereby matrix composition affects the interpatch movement and within-patch spatial distribution of the planthopper (see Chapter 2).

In chapter 5, I suggest that this dissertation project makes several unique contributions to the field of landscape ecology: 1) the project represents one of very few to definitively ascertain whether the composition of the matrix affects herbivore dispersal independently of patch quality; 2) a behavioral approach is used to understand the mechanisms whereby landscape structure influences herbivore dispersal and spatial distribution; 3) few other studies have attempted to understand the effects of landscape change caused by the spread of exotic plants on the spatial dynamics of native fauna; and 4) the project includes a long-term plan of using experimental data to develop a mechanistic spatially explicit model to predict

effects of alterations to the tallgrass prairie ecosystem (fragmentation, invasion of exotic plants into the matrix) on planthopper population dynamics.

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CHAPTER 2

MATRIX COMPOSITION AFFECTS THE SPATIAL ECOLOGY OF A PRAIRIE PLANTHOPPER¹

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INTRODUCTION

For patchily distributed populations, the rate of inter-patch dispersal (i.e., patch connectivity) is a critical factor influencing patterns of patch occupancy and regional population dynamics (Hanski 1994, 1999, Stacey et al. 1997). The majority of metapopulation studies have emphasized the importance of patch size and isolation on the movement of animals among patches, while ignoring the effect of the intervening habitat; i.e., the matrix (Taylor et al. 1993, Wiens 1997, Tischendorf and Fahrig 2000). In contrast, recent field studies on insects have revealed dramatic effects of the matrix on inter-patch movement or connectivity (e.g., Jonsen et al. 2001, Ricketts 2001). Jonsen et al. (2001), for example, found that colonization of leafy spurge patches (*Euphorbia esula*) by an *Apthona* flea beetle was much greater within a grass than a shrub matrix. Heterogeneous dispersal rates, owing to differences in matrix composition, theoretically can have complex effects on the regional dynamics of a subdivided population (Gustafson and Gardner 1996, Vandermeer and Carvajal 2001).

By affecting movement patterns, the composition of the matrix may influence not only the among- but also the within-patch distribution of animals. High patch occupancy rates and/or densities may be promoted by a matrix favoring high patch connectivity (via the recolonization of vacant patches and the rescue effect; Levins 1970, Brown and Kodric-Brown 1977), or by a matrix which inhibits emigration (Kuussaari et al. 1996, Cronin 2003a). Within-patches, the matrix may affect the distribution of a species by influencing the flow of individuals across the patch edge. Some matrix types may make the patch edge hard (i.e., inhibit emigration; Stamps et al. 1987) and cause organisms to aggregate near the patch perimeter (Cantrell and Cosner 1999), whereas other matrix types may favor softer patch

edges and no density edge effect. Although edge effects can significantly influence species interactions and community structure (Fagan et al. 1999), few studies have examined whether they are matrix dependent (but see Tschardt et al. 2002, Cronin 2003a).

Despite the recent emphasis on the effects of matrix composition on dispersal and spatial population dynamics, there is a lack of well-controlled field experiments that disentangle the effects of the matrix from other landscape variables that might influence dispersal. To date, the majority of matrix studies have focused on the dispersal of organisms among patches in natural landscapes (e.g., Moilanen and Hanski 1998, Roland et al. 2000, Jonsen et al. 2001; but see Karieva 1985). Under these circumstances, there is a risk that matrix composition may be confounded with other landscape features such as patch geography or quality. For example, patches embedded in a bare matrix may be richer in nutrients than patches embedded in a forest matrix (as a result of reduced competition for nutrients and light, different soil conditions, etc.). In a recent literature review (chapter 3), we found that 60% of the studies (6/10) failed to experimentally or statistically isolate the effects of the matrix from potential patch-quality effects on herbivore dispersal. To isolate the effects of matrix types on patch connectivity, studies are needed that account for variability among patches; e.g., by using experimentally created patches.

In this study, we experimentally tested the hypothesis that the movement of the planthopper *Prokelisia crocea* Van Duzee (Hemiptera: Delphacidae) among patches of its host plant [*Spartina pectinata* Link (Poaceae)] is directly influenced by the type of matrix within which the host-plant patches are embedded. We created experimental networks of cordgrass patches that differed only in the type of intervening matrix (mudflat, a mixture of native grasses, or the introduced grass *Bromus inermis* Leyss). Among matrix types, we

tested for differences in emigration and immigration rates of marked planthoppers. In addition to the field experiment, we used census data as the basis for testing whether the within- and among-patch distributions of planthoppers were correlated with matrix type in accordance with the predictions from the above field experiment. We also assessed whether the matrix was of more, less, or equal importance to patch geography (size and isolation) in affecting the spatial distribution of these planthoppers. Finally, we addressed how changes in the structure of the matrix, particularly through the invasion and spread of exotic plant species, may influence the planthopper's regional population dynamics. *Prokelisia crocea* represents a model organism for testing metapopulation or landscape theory because: (1) the planthopper population is naturally subdivided among very discrete host-plant patches that are embedded in very distinct matrix types, (2) dispersal is two-dimensional and occurs over small distances of < 100 m (Cronin 2003a), and (3) the characteristics (e.g., size, nutritional quality) and spatial arrangement of patches are easily manipulated.

METHODS

Prairie Landscape and Life History

Prairie cordgrass is a native species associated with hydric grasslands and marshes of North America (Hitchcock 1963). In the tall-grass prairies of North Dakota, cordgrass grows in discrete patches ranging in size from single stems to 4-ha monospecific stands (Cronin 2003a, c). The matrix within which these patches are embedded can be classified into three main vegetation types (Fig. 2.1): 1) periodically flooded mudflats sometimes dominated by saltwort (*Salicornia rubra* Nels.), 2) mixtures of predominantly native grass species of similar height (primarily foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb., and little bluestem *Schizachyrium scoparium* Michx.), and 3) nearly monospecific

stands of smooth brome (*B. inermis*). Brome has become established in the Great Plains of the United States and Canada by invading disturbed prairie (D'Antonio and Vitousek 1992), and through repeated introductions to prevent soil erosion and provide animal graze (Wilson 1989, Larson et al. 2001). Brome is similar in stature and appearance to cordgrass, and both species are markedly taller than most native grasses (Wilson and Belcher 1989; Fig. 2.1). At our study areas, the matrix is composed of approximately 30% mudflat, 40% native non-host grasses, and 30% brome.

The planthopper's biology is described by Holder and Wilson (1992) and Cronin (2003a,b,c). The planthopper is a phloem-feeding specialist of cordgrass and is the plant's most common herbivore. In North Dakota, the planthopper exhibits two distinct generations per year, with peaks in adult abundance in mid June and early August. Adults are wing-dimorphic but populations are > 90% macropterous. The adult stage lasts approximately three weeks, during which time females lay eggs along the midrib of the adaxial surface of cordgrass leaves.

Matrix Types and Dispersal

The effects of the matrix on planthopper movement among cordgrass patches was experimentally tested within the drainage system associated with the Kelly's Slough National Wildlife Refuge (located 16 km west of Grand Forks, North Dakota, USA). In Kelly's Slough, the three matrix types occupy different regions of the prairie. Mudflats tend to be a few decimeters lower than other matrix habitats, but otherwise there are no observable differences in slope, aspect, or wind exposure among matrix types that might influence planthopper movement (unpublished data). Within each matrix type, we created networks of small experimental host-plant patches each consisting of a central patch surrounded by eight

FIG. 2.1. Prairie cordgrass (*Spartina pectinata*; background) and the three main matrix types (foreground) within the drainage system associated with the Kelly's Slough National Wildlife Refuge, North Dakota, USA. (A) Open mudflat dominated by the low-lying herb *Salicornia rubra*. (B) A mixture of native non-host grasses, of intermediate height and complexity. (C) The invasive grass smooth brome (*Bromus inermis*), similar in structure and appearance to prairie cordgrass. (Photographs by K. J. Haynes).



satellite patches positioned 3 m away and equal distance apart. Cordgrass used in the experimental patches was obtained as small rhizomatous shoots excavated at the beginning of the spring from the same source patch. Shoots were potted in 16 cm x 16 cm pots using ProMix BX[®] (Premier Horticulture Ltd, Rivière-du-Loup, Québec, Canada) potting soil and propagated under identical conditions in an outdoor garden. Each experimental patch consisted of four pots in a 2 H 2 arrangement that was sunk flush to the ground. Six cordgrass stems, 0.5 - 0.75 m in height, were present in each pot. Although patches of this size are small relative to the range found in nature (1 stem to 4 hectares), the frequency of occurrence of these small patches (#0.10 m²) is 10% (Cronin 2003b). Patch networks were positioned at least 25 m away from natural cordgrass patches.

The planthoppers were collected with a sweep net from nearby cordgrass habitat, chilled during transport and then marked with Dayglo fluorescent powder (Dayglo Corporation, Cleveland, Ohio). The marker was visible on planthoppers after a week in the field, even after heavy rains, and did not reduce planthopper survivorship or dispersal in laboratory experiments (Cronin 2003b). In order to minimize mortality, planthoppers were marked and released within an hour after collection. Planthopper movement was slow at first, and generally involved walking or hopping onto the cordgrass stems. Less than 1% of the marked planthoppers left the patch immediately after their release (unpublished data).

For each replicate, we released 500 adult female planthoppers (ca. 20 per stem). Males were not included in the study because they were scarce relative to females and are potentially less important to the spatial spread of the species. The lack of males in experimental patches likely did not bias female movement patterns because 1) mate searching is primarily a male trait in planthopper species (Denno et al. 1991) and 2) most females are

mated prior to dispersal (Cronin 2003b). This release density was high relative to the levels normally observed at Kelly's Slough (typically - 0.1 per stem; Cronin 2003b), but was not outside the range of densities observed in more productive sites nearby (annually, densities exceed 40 per stem in some patches; J.T. Cronin, personal observation). Because the planthopper's emigration rate is density dependent and high for small patches (Cronin 2003b), we anticipated high emigration rates in this study.

To assess rates of emigration and immigration, counts of planthoppers on each patch were made at 24 h, 48 h, and 72 h post release. Planthoppers found on satellite patches were aspirated from the plants to avoid re-counting them during subsequent inspections.

Planthopper loss from the central release patch can be attributed to both emigration and within-patch mortality. Because predators were scarce on experimental patches in all matrix types, and the type of surrounding matrix was found to be unrelated to the density of a major group of generalist predators (spiders) in natural cordgrass patches (Cronin et al. 2004), we assumed that within-patch mortality was matrix independent; thus, differences in the number of planthoppers lost from release patches were attributed to differences in emigration rates.

Colonization of satellite patches was measured in two ways: the immigration rate (number of immigrants per patch per d) and dispersal success. Dispersal success ($=$ [summed number of immigrants on all eight satellite patches] / [number released - number remaining on central patch]) was based only on those individuals that disappeared from the central patch, and thus accounts for potential differences among matrix types in the number of emigrants departing from the central release patch. We carried out eight replicate releases in each matrix type over two planthopper generations (5 during May and June 2001 and 3 during August, 2001). One replicate release per matrix type was completed before initiating a new set of replicates;

the order of releases among matrix types was determined by random draw. Differences in mean emigration, immigration, or dispersal success among matrix types were evaluated with separate randomized block ANOVAs, in which matrix type was a fixed main effect and generation was a blocking effect (Kirk 1995). Multiple-comparison tests among the three matrix types were performed using Tukey's HSD test (Day and Quinn 1989).

For the analyses of emigration loss, we used the 24-h recapture data because the majority of the emigration events occurred within this period. On the other hand, immigrants accrued at a more constant rate over the three day length of the experiment. Therefore, the immigration rate and dispersal success were based on the cumulative number of immigrants captured in 72 h. Both the immigration rate and dispersal success were *ln*-transformed to normalize their distributions and homogenize variances among matrix treatments.

Within-patch Distribution

To determine if the planthopper's within-patch distribution was related to the matrix type, we censused planthopper densities at the edges and interiors of 14 mudflat-bordered and 12 non-host grass bordered patches (composed of brome and/or native grasses) in 2000. All patches were $> 40 \text{ m}^2$ in area. The census was conducted within the Kelly's Slough National Wildlife Refuge drainage. A second census was conducted in 2001 and included 10 patches from each of the three matrix types. For each census, we estimated adult female density per stem at two paired locations within each patch, at the edge and at 2 m into the interior (details provided in Appendix A).

We tested whether the within-patch distribution of planthoppers varied among matrix types by performing an ANOVA on the ratio of female density at the patch edge to the average density for the whole patch ($\text{edge} / [(\text{edge} + \text{interior}) / 2]$). We used the edge to

patch mean ratio instead of edge to interior ratio because some patch interiors had zero densities. In addition, this ratio was approximately normally distributed and homogeneous in variance. Within a matrix, an edge effect was deemed present if the 95% confidence intervals around the density ratio did not overlap 1.0.

One possible explanation for within-patch differences in planthopper distributions among matrix types may be that plant quality at the edge and interior of patches differs among matrix types. Immediately following the density census in 2000, we randomly selected three cordgrass stems from the edge and 2 m into the interior of each patch, and collected the topmost unfurled leaf. The leaves were immediately placed on dry ice, and later stored in an ultra cold freezer at -70°C. Samples were subsequently lyophilized (72 hours) and ground in a Wiley Mill. Elemental analysis using gas chromatography was performed by the Agricultural Services Laboratory at Pennsylvania State University to determine percent nitrogen (percent dry weight) of leaves. For planthoppers, nitrogen content of leaves is considered to be a strong index of plant quality (Cook and Denno 1994). Differences among matrix types in the ratio of percent nitrogen at the patch edge to the mean for the whole patch were evaluated with a one-way ANOVA. For patches within each matrix, an edge effect was deemed present if the 95% confidence intervals about this ratio did not overlap 1.0.

Among-patch Distribution

The relationship between patch geography (size, isolation) and the among-patch distribution of planthoppers was determined from a five generation census (1999-2001) of 25 - 142 discrete cordgrass patches in Site 104, 20 km west of Grand Forks, ND (Cronin 2003c). In this study, we estimated the mean number of planthopper eggs per cordgrass stem as well as the presence or absence of eggs for each patch and generation (Appendix B). For each

focal patch, we measured its size (m^2), isolation from the nearest neighbor patch in each of four quadrants (a function of the linear distance to, and size of, each neighbor; Cronin 2003b), and the composition of the surrounding matrix. The quantification of each of these measures is described in detail in Appendix B. Because mudflat was deemed to be the most different landscape feature in terms of its effect on planthopper movement (see Results), our index of the matrix was the proportion of a 3-m buffer surrounding a patch that was composed of mudflat. Moilanen and Hanski (1998) used a similar approach to quantifying the matrix for the Glanville fritillary. In a previous analysis of these census data, Cronin (2003b) found that planthopper egg densities and patch-occupancy rates generally increased with increasing patch size and egg abundance in the previous generation, but were unaffected by isolation. Averaged across generations, the regression models used by Cronin (2003b), which ignored matrix effects, explained 19.5% of the variation in egg densities and 10.0% of the variation in patch occupancy rates. Here, we re-analyzed these census data, but included matrix composition into the models. For each generation, the influence of patch size, isolation, planthopper abundance (density or patch occupancy) in generation $t - 1$, and matrix composition was determined for two dependent variables: planthopper egg densities (using multiple least-squares regression) and whether or not a patch was occupied by planthoppers in generation t (using logistic regression) (see Appendix B). In addition to determining whether patch density or occupancy was influenced by the matrix, these tests also allowed us to evaluate the relative contributions of the matrix and patch geography variables (size, isolation) to explaining the among-patch variation in planthopper abundance. The relative contribution of each variable was determined as the absolute change in R^2 after the removal of one variable from the model (i.e., $R^2_{\text{Total}} - R^2_{\text{Total} - 1}$).

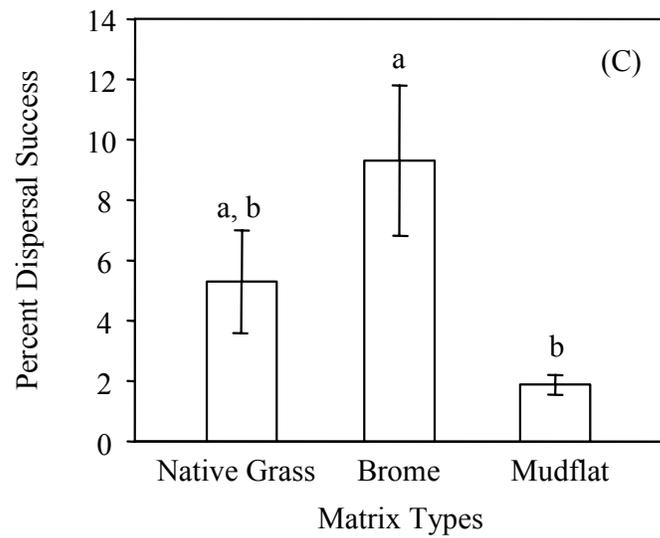
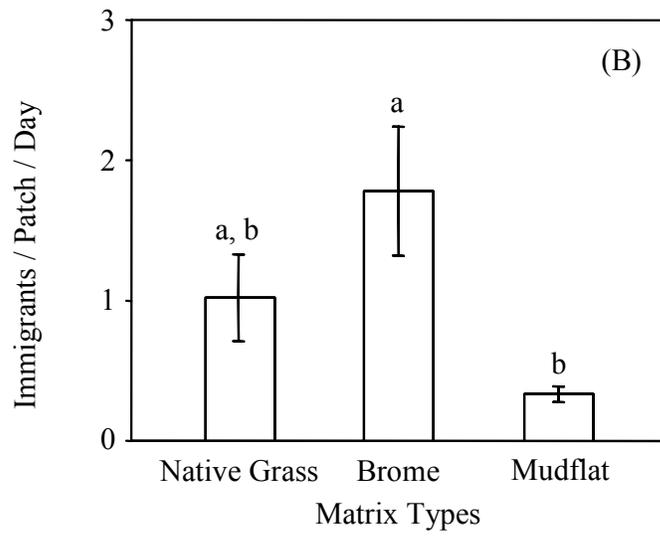
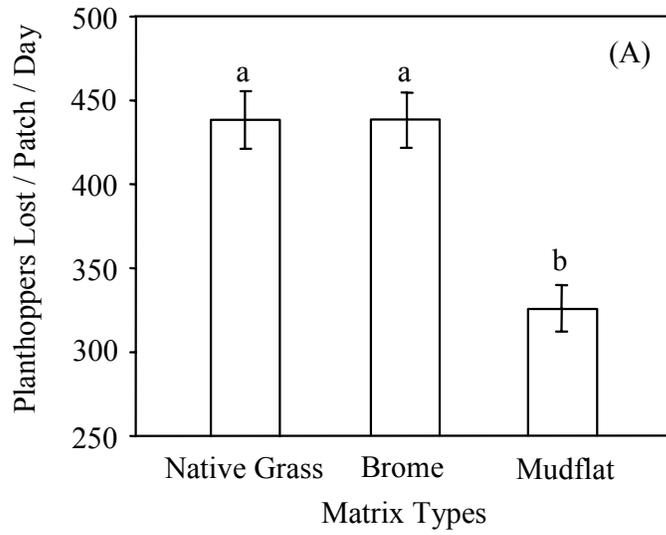
RESULTS

Matrix Types and Dispersal

The loss rate of planthoppers from the release patch differed significantly among the matrix types within which the cordgrass patches were embedded ($F_{2,20} = 18.42$, $P < 0.001$, Fig. 2.2A). Patches embedded in mudflat lost 25.8% fewer planthoppers in a 24-h period than patches embedded in either native grass or brome (Tukey's HSD, $P < 0.001$). Loss rates from patches in both grass matrix types were high but equivalent ($P > 0.99$). From the first planthopper generation to the second (blocking factor) the loss rate of planthoppers was indistinguishable ($F_{1,20} = 1.41$, $P = 0.25$).

Immigration rates for satellite patches located 3 m from a source patch were low overall (mean \pm 1 SE, 1.04 ± 0.22 immigrants per patch per day), but varied significantly with matrix type ($F_{2,20} = 7.94$, $P = 0.003$, Fig. 2.2B). Mudflat- and brome-embedded patches had the largest difference in immigration: the rate was 5.4 times higher in the latter than the former matrix (Tukey's HSD, $P = 0.002$). Intermediate rates of immigration occurred within the native grass matrix; however, the rate in the native grass matrix was not significantly different from the rates for the mudflat ($P = 0.13$) or brome ($P = 0.15$) matrix. Although loss rates were similar between planthopper generations, the immigration rate decreased significantly from the first to the second generation (a mean decline of 1.0 planthopper; $F_{1,20} = 15.21$, $P = 0.001$). Dispersal success, the percentage of planthoppers lost from the central patch that dispersed onto any of the eight satellite patches, differed significantly among matrix types ($F_{2,20} = 7.60$, $P = 0.004$) in qualitatively the same manner as the number of immigrants. After accounting for the higher emigration from brome- than mudflat-embedded

FIG. 2.2. Effects of the three matrix types on inter-patch movement: (A) rate of planthopper loss from a release patch (number lost per patch per d); (B) rate of immigration onto satellite patches (number of immigrants per patch per d); and (C) percentage of planthoppers lost from the central release patch that successfully immigrated onto any of the eight surrounding satellite patches. Data are means \pm 1 SE. Loss was calculated using the 24-h recapture data because the majority of the emigration events occurred within this period. In contrast, the immigration rate and dispersal success was based on the cumulative number of immigrants captured in 72 h because immigrants accrued at a more constant rate over the three day length of the experiment. Different letters denote significant differences at the 0.05 level.



patches, we found that proportionately more emigrants successfully dispersed into the satellite patches in the former than latter matrix (Tukey's HSD, $P = 0.002$, Fig. 2.2C).

Within-patch Distribution

In 2000, the within-patch distribution of planthoppers varied significantly with the type of matrix bordering the patch ($F_{1,24} = 14.63$, $P = 0.001$). Planthopper densities were significantly higher at the edge than interior of mudflat-bordered patches, but no edge effect was detected for patches bordered by non-host grasses (Fig. 2.3). On average, densities (interior and edge combined) in patches bordering mudflat were comparable to those in patches bordering non-host grass (2.9 ± 0.7 versus 1.9 ± 0.2 per 100 stems, respectively; $t_{24} = 0.40$, $P = 0.69$). In 2001, planthopper densities were low (53.6% lower than in 2000), with zero densities in ~10% of the samples. We lacked the statistical power to adequately test for the presence of edge effects in this second year; however, no trends were evident.

Leaf nitrogen levels, measured during 2000, were significantly higher at the edge than the interior for patches bordered by both types of matrix (Fig. 2.3). The magnitude of the nitrogen edge effect did not vary significantly between matrix types ($F_{1,22} = 2.30$, $P = 0.143$). Overall, leaf-nitrogen levels in mudflat-bordered patches were 10% higher than in non-host grass-bordered patches ($1.59 \pm 0.05\%$ versus $1.44 \pm 0.04\%$, respectively; $t_{22} = 2.58$, $P = 0.017$). Finally, the correlation between mean planthopper density and mean percent nitrogen was positive but not significant (Spearman's rank correlation, $R_s = 0.16$, $P = 0.268$).

Among-patch Distribution

Based on our analysis of the distribution of planthopper egg densities among cordgrass patches, we found in all five generations that density increased with an increase in the proportion of mudflat in the matrix (Table 2.1); however, in only two of five generations

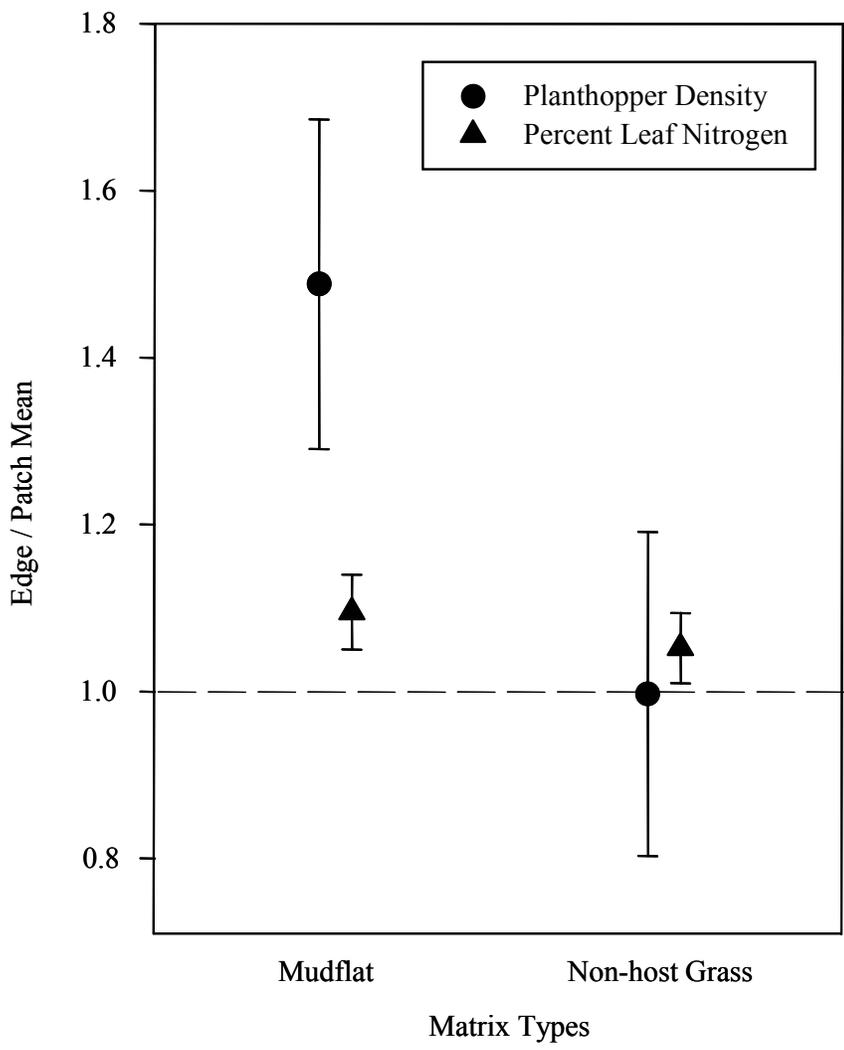


FIG. 2.3. Ratios (\pm 95 % confidence intervals) of female density at the patch edge to mean patch density, or leaf nitrogen content at the patch edge to mean patch leaf nitrogen content, for patches embedded in a mudflat or a mixture of non-host grasses (native grasses and brome). An edge-interior difference was deemed significant if the 95% confidence intervals did not overlap 1.0.

TABLE 2.1. The effect of matrix composition, patch size, isolation, and planthopper density in generation $t - 1$ on planthopper egg densities or patch occupancy in generation t .

Dependent Variable†	Generation	n	Full Model		Size P	Isolation P	Generation ($t - 1$) P	Matrix	
			$R^2‡$	P				P	$\Delta R^2§$
Density	1999 – II	25	0.305	0.50	0.012	0.954	---	0.114	0.076
	2000 – I	95	0.068	0.093	0.276	0.345	---	0.031	0.049
	2000 – II	95	0.403	<0.001	0.003	0.055	<0.001	<0.001	0.152
	2001 – I	101	0.342	<0.001	0.001	0.564	0.04	0.002	0.069
	2001 – II	138	0.171	<0.001	0.006	0.064	0.004	0.617	0.002
Occupancy	1999 – II	25	---	---	---	---	---	---	---
	2000 – I	98	0.190	0.004	0.413	0.204	---	<0.001	0.165
	2000 – II	98	0.267	<0.001	<0.001	0.351	0.004	0.353	0.012
	2001 – I	101	0.153	<0.001	0.004	0.409	0.591	<0.001	0.088
	2001 – II	138	0.082	0.013	0.460	0.017	0.965	0.011	0.04

Note: Significant P -values after using a sequential Dunn-Šidák correction to adjust for inflated type I error are indicated with bold type (see Appendix B).

† Least-squares regression was used for egg density, and logistic regression was used for patch occupancy.

‡ We report McFadden's ρ^2 instead of R^2 for logistic regressions.

§ The absolute change in model R^2 after removing the matrix variable from the model with all variables included is indicated by ΔR^2 .

was this effect significant. Overall, adding matrix composition to a regression model that already included patch size, isolation and density in the previous generation (Cronin 2003b), improved the model fit from $R^2 = 19.5\%$ to $R^2 = 25.8\%$; an increase of 6.3% (based on R^2 values; Table 2.1). On average, the matrix, patch size and density at $t - 1$ contributed equally to explaining the variation in egg densities among patches (means of 7.4% , 6.3% and 7.2% , respectively; based on tests with all variables included). Similarly, patch occupancy rates increased significantly with the proportion of mudflat in the patch matrix in 3 of 4 generations (Table 2.1). The inclusion of matrix heterogeneity in the model also resulted in a small but significant improvement in the explanatory power of the model: McFadden's ρ^2 (the logistic regression equivalent of the coefficient of determination; see Appendix B) increased by 7.6% over a model without the matrix effect. All independent variables, excluding patch isolation, explained roughly equal percentages of the variation in patch occupancy ($\approx 4\%$).

The effect of the matrix was more compelling when evaluated over the entire course of the five-generation study. The proportion of generations in which a patch was occupied was strongly influenced by the matrix, increasing significantly with the proportion of the nearby matrix composed of mudflat ($n = 105$, $P < 0.001$, Fig. 2.4). The addition of the matrix variable to a model that included patch size and isolation (Cronin 2003b) increased the model R^2 from 26.1% to 44.1% . The matrix and patch size each explained $\approx 17\%$, and isolation explained 10% , of the variation in patch occupancy rates.

DISCUSSION

Matrix Effects on Dispersal

After controlling for most variables thought to influence inter-patch movement, i.e., insect density and patch characteristics (size, isolation, stem density and quality), we found

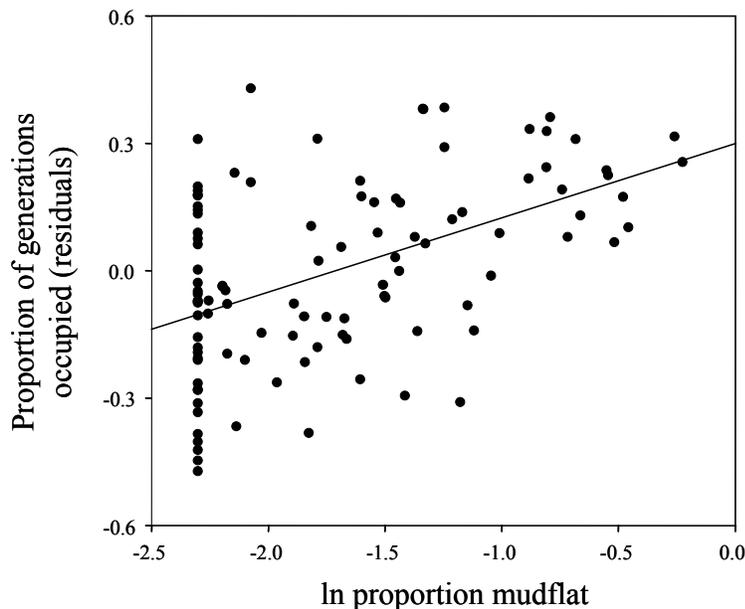


FIG. 2.4. The relationship between the proportion of planthopper generations in which a patch was occupied and the proportion of nearby matrix that consisted of mudflat. To indicate the effect of the matrix alone, the residuals from a regression model including only patch size and isolation were regressed against the matrix variable (proportion occupied [residuals] = $0.18 \times [\ln \text{proportion mudflat}] + 0.3$, $n = 105$, $R^2 = 0.24$).

that planthopper movement differed substantially among matrix types. Emigration was 1.3 times higher, and immigration into patches 3 m away was 5.4 times higher, for brome-embedded patches than for mudflat-embedded patches (the two most disparate matrix types; Fig. 2.2). Similarly strong effects of the matrix on dispersal have been reported for a diversity of insect species including beetles (e.g., Bach 1988, Kareiva 1985, Jonsen et al. 2001), butterflies (e.g., Kuussaari et al. 1996, Ricketts 2001), and a bush cricket (Kindvall 1999). However, it is unclear from the majority of these studies whether the observed effects were due purely to differences among matrix habitats or to some other factor that may have been confounded with the matrix (chapter 3). In our study system, matrix type and patch quality (measured as the nitrogen content of leaves) were interrelated in natural (but not

experimental) patches: mudflat-embedded patches were 10% richer in nitrogen levels than patches embedded in matrix composed of non-host grasses. Reduced interspecific competition, or nutrient-rich soils may have been responsible for the higher nitrogen levels of patches in mudflats. We might expect to find similar patch-quality differences in other study systems, particularly those with distinctly different matrix types (e.g., a grass versus shrub matrix; Jonsen et al. 2001). Of the few studies that have evaluated the relationship between matrix composition and patch quality, all of them (3/3) found that these two landscape factors covaried (chapter 3). Because patch quality is known to influence emigration (Cook and Denno 1994, Kuussaari et al. 1996, Fownes and Roland 2002) and immigration (Matter and Roland 2002), differences in patch connectivity among matrix types may be due, partially or wholly, to plant-quality effects. Therefore, studies that control for patch quality (this study; Kareiva 1985, Bach 1988) are necessary to disentangle the role of the matrix from other confounding factors (chapter 3).

Although we have controlled for heterogeneity in patch characteristics while varying matrix type, it is conceivable that differences in planthopper movement among the matrix types could be attributed to site differences (e.g., soil conditions, elevation differences) rather than the matrix itself. This possibility arises because each matrix type occupied different regions of Kelly's Slough (owing to the natural distribution of matrix types), and therefore experimental replicates for each matrix type were also spatially divided. However, two independent lines of experimental evidence argue against the possibility that site differences were responsible for the observed matrix effect. First, at an experimentally created cordgrass-matrix boundary (derived from potted cordgrass, brome or mud), individual planthoppers were significantly more reluctant to emigrate into the mudflat than the brome matrix (chapter

4). Second, in a large scale field experiment (distances between patches ranging from 3 to 50 m), in which cordgrass patches and the matrix (mudflat or brome) were experimentally derived, we also found higher connectivity among patches in brome than in mudflat (J.T. Cronin, unpublished data). In total, our three independent experiments provide compelling evidence that the composition of the matrix is the causal agent affecting planthopper movement.

For the planthopper, both emigration and immigration tended to increase with the structural complexity of the matrix (see Fig. 2.1). Relatively few planthoppers moved into and out of patches embedded in the sparsely vegetated mudflats. Patches embedded in both non-host grass matrix types had similarly high emigration losses, but immigration tended to be higher for patches in brome than in native non-host grasses. The introduced grass, brome, is taller than the native matrix vegetation and comparable in stature to cordgrass (Fig. 2.1). Interestingly, most other studies have found the opposite relationship between matrix complexity and inter-patch movement (Kareiva 1985, Kuussaari et al. 1996, Pither and Taylor 1998, Moilanen and Hanski 1998, Roland et al. 2000, Jonsen et al. 2001, Ricketts 2001). To gain an understanding for this difference in dispersal behavior, we examine below the processes of emigration and immigration in the planthopper.

The mudflat-cordgrass boundary is much more distinct than the boundary formed between cordgrass and the other two matrix types (Fig. 2.1). Within a cordgrass patch, planthoppers redistribute themselves at random (Cronin 2003*b*), but when near the mudflat edge, individuals tend to turn away (chapter 4); i.e., the patch edge is hard (Stamps et al. 1987). In patches bordering non-host grass, the edge is much softer; planthopper individuals readily cross over into the matrix and are unlikely to ever return (K. J. Haynes, unpublished

data). This pattern of low permeability in patches with well defined edges is supported by other recent studies (e.g., Kuussaari et al. 1996, Haddad 1999). We surmise that the resemblance of non-host grasses to prairie cordgrass (especially brome) is an important factor promoting high patch permeability. Perhaps it should be of no surprise that previous studies have found higher emigration rates into less complex matrix types because in those studies the most structurally complex matrix is often the most different from the host patch (e.g., closed forest versus open fields for the meadow-inhabiting Glanville fritillary; Kuussaari et al. 1996).

The difference in patch-edge permeability among matrix types may explain the matrix dependent within-patch distribution of planthoppers. Based on a diffusion-model framework, densities are predicted to accumulate against a low-permeability edge such as a mudflat (Cantrell and Cosner 1999). These edge aggregations can potentially affect population dynamics through increased intra- and inter-specific competition and altered interactions with natural enemies (Fagan et al. 1999). One example involves the planthopper's primary parasitoid, *Anagrus columbi* (Hymenoptera: Mymaridae). In mudflat embedded patches, *A. columbi* avoids the patch edge (density of foraging females are - 60% lower at the patch edge than the patch interior, Cronin 2003a). The refuge that exists for the planthoppers at the mudflat edge may explain the higher densities generally found in mudflat-, as compared to non-host grass-embedded patches (Cronin 2003a), and promote outbreaks in these patches (see Kareiva and Odell 1987).

To date, most mechanistic explanations for edge effects have focused on patch quality, such as the microclimate, predator abundance or host-plant quality at the patch edge relative to the interior (e.g., Young and Mitchell 1994, Cappuccino and Martin 1997, Rothman and

Roland 1998, McGeoch and Gaston 2000). In this study, we did find that nitrogen content of leaves, a strong index of plant quality to many planthopper species (reviewed in Cook and Denno 1994), was significantly higher on the edge than the interior of patches bordering both mudflats and non-host grasses (Fig. 2.3). However, because the nitrogen edge effect was similarly strong between the two matrix types, it was not likely the cause for the accumulation of planthoppers on the mudflat, as compared to the non-host grass edge. The matrix-dependent edge effect in planthopper density is likely due to other factors, including the avoidance of parasitoids (see above, Cronin 2003a), or the edge permeability differences between matrix types noted above (see Fagan et al. 1999).

The relatively high immigration success of planthoppers (both in terms of immigration rate and dispersal success) moving through structurally complex, as opposed to simple, matrix types is likely attributable to their movement behavior in the matrix. In a study in which individual planthoppers were tracked moving through different habitat types (chapter 4), we found that movement paths were meandering through non-host grasses (complex matrix) and more linear through mudflats (simple matrix) (see also Zalucki and Kitching 1982, Jonsen and Taylor 2000, Goodwin and Fahrig 2002). Therefore, after emigrating from an experimental source patch embedded in mudflat, planthoppers may have been likely to pass by the satellite patches 3 m away without encountering them. The fate of these individuals is unknown, but their success in locating a new cordgrass patch does not improve relative to individuals moving through non-host grasses, even up to 50 m (the maximum distance found between nearest neighbor patches; J.T. Cronin and K.J. Haynes, unpublished manuscript). In contrast, planthoppers moving through either grass matrix may have encountered satellite patches more often, due to higher turning rates and (or) longer residence times in the vicinity of the patches.

Because planthoppers have similar survival rates when caged (without predators) on non-host matrix plants and mudflat (K.J. Haynes, unpublished data), differences in immigration success among matrix types are not due to differences in habitat harshness. Finally, predation was also unlikely to explain differential immigration rates because predators were almost non-existent in the mudflats where immigration rates were the lowest.

Based on the patterns of emigration and immigration, we infer that the connectivity among cordgrass patches would be highest within a brome matrix, and lowest within a mudflat matrix. Patches in a native grass matrix would have intermediate connectivity. Although, this assessment of connectivity applies to patches that are only 3 m apart, a mark-recapture study in an ongoing field experiment has revealed that this pattern is upheld for patches separated by up to 50 m (J.T. Cronin and K.J. Haynes, unpublished manuscript). The implications of these differences in connectivity are addressed below.

Among-patch Distribution of Planthoppers

Traditionally, studies involving patchily distributed populations have emphasized the importance of patch size and isolation in determining their distributions (see Hanski 1999). The roles of other landscape-level factors such as the matrix rarely have been considered (but see e.g., Kuussaari et al. 1996, Moilanen and Hanski 1998), but their inclusion in spatial population studies may be crucial to understanding species distributions among patches (Wiens et al. 1993, Wiens 1997; but see Molainen and Hanski 1998). In our study system, patch geography (primarily patch size) and matrix composition contributed approximately equally toward explaining the variation in planthopper density distributions and incidence among patches. In general, large patches that were embedded in a predominantly mudflat matrix had the highest probability of being occupied and the greatest planthopper density.

The explanatory power of these two variables was generally low within a generation, but improved greatly when extended over five generations (from about 14% to 34% of the variation explained). We conclude that the matrix does matter (see Ricketts 2001), not only to the planthopper's patterns of inter-patch movement, but also to their spatial distributions. Bach (1984) reported a similar finding in her study of factors influencing the distribution of the chrysomelid beetle *Acalymma innubum* - the matrix was more important than the effect of patch size. In contrast, both Kareiva (1985) and Moilanen and Hanski (1998) found the matrix to be unimportant relative to patch structure (size, isolation) in determining the distribution of their respective study organisms (*Phyllotreta* flea beetles and the Glanville fritillary). We are aware of no other studies that assessed the relative importance of patch size, patch isolation and the matrix to the distributions of species among patches. If future studies add credence to our conclusions that the matrix matters relative to patch geography, then conservation programs may need to focus not only on protecting patches and providing corridors or stepping stones between them, but also on the quality of the matrix (e.g., Janzen 1983, Saunders et al. 1991, Wiens 1997).

In North Dakota tall-grass prairies, matrix type and patch quality are interrelated. The increase in planthopper density or patch occupancy with an increase in the proportion of mud in the matrix could have been due to the direct effects of the matrix on planthopper movement. In particular, the low permeability of a mudflat-cordgrass edge could have resulted in the retention and buildup of planthoppers within those patches (see also Moilanen and Hanski 1998). Alternatively, plant quality may have been partially, or wholly, responsible for the increased density and occupancy of planthoppers on cordgrass patches in mudflat; mudflat- relative to non-host grass-embedded patches have 10% higher leaf-nitrogen

content. In general, planthopper species are known to build up densities on nitrogen-rich patches, either via increased survivorship/reproduction or reduced emigration (reviewed in Cook and Denno 1994). Although we have not assessed the impact of a 10% difference in plant nitrogen on *P. crocea* movement or performance, a field census with the congener *P. marginata* (Denno et al. 1980) indicated that small changes in nitrogen levels can have appreciable effects on planthopper distributions. Moilanen and Hanski's (1998) work with the Glanville fritillary is one of the few studies to evaluate the effect of patch quality (based on several environmental variables) and matrix composition on herbivore distributions among patches. In this study, patch quality was deemed more important than the matrix; however, the two factors were evaluated separately and no tests were performed to determine if they were correlated. An important avenue of future research in landscape ecology would be to address the likely interactions that exist between the matrix and plant quality, and quantify their direct and interactive effects on metapopulation structure and dynamics (Haynes and Cronin, unpublished data).

Besides matrix composition and patch geography, what other factors might contribute to the considerable amount of unexplained variation in planthopper abundances among patches? In light of the previous paragraph, spatial variation in host-plant nutritional quality (e.g., leaf-nitrogen content) may play a major role in affecting planthopper distributions. The nitrogen concentration of host-plants is believed to play a strong role in the population dynamics of phloem feeding insects such as planthoppers (reviewed in Cook and Denno 1994). For example, studies with the conspecific planthoppers *P. dolus* and *P. marginata*, that feed on *S. alterniflora*, suggest that plant nutritional quality has stronger effects on planthopper distributions and population dynamics than top-down factors such as spider

predators (Denno et al. 2002) or the egg parasitoid *A. sophiae* (Moon and Stiling 2002). However, top-down effects from spiders can have strong effects on planthopper density, particularly if the vegetation is sufficiently complex (i.e., if thatch is present) and if host-plant nutritional quality is low (Denno et al. 2002). For bottom-up and top-down effects to improve our predictions about the distribution of planthoppers among patches, they must also vary across the landscape. In our system, the effect of plant quality on planthopper distributions is currently under investigation. However, we do know that the abundance of spiders in cordgrass patches is negatively correlated with patch size and independent of patch isolation and matrix composition (Cronin et al. 2004). The high extinction rate found for small cordgrass patches (Cronin 2003b) may be attributable to both lethal and non-lethal (predator-induced dispersal) effects of spiders (Cronin et al. 2004). In contrast to these predators, *A. columbi*, the dominant parasitoid of the planthopper, has little impact on the among-patch distribution of its host. In general, the distribution of *A. columbi* simply mirrors that of the planthopper (Cronin 2003a).

Invasion of Smooth Brome into the Prairie

Anthropogenic activities in natural landscapes not only have direct effects on patch connectivity (by altering patch geography), but also can affect connectivity through their influence on matrix composition and quality. Exotic plants, which are becoming increasingly dominant in human-disturbed landscapes (Drake et al. 1989, D'Antonio and Vitousek 1992), may have a substantial impact on the landscape matrix. In our study system, mudflat and native non-host grasses do not differ considerably in their effects on planthopper connectivity among cordgrass patches. As traditional metapopulation models have implicitly assumed

(Hanski 1999), these native habitat types combine to form a relatively homogeneous matrix through which the planthopper disperses. The invasion of smooth brome into the prairie landscape likely results in a significant increase in matrix heterogeneity; a brome-dominated landscape has significantly greater connectivity than a mudflat-dominated landscape. The long-term consequences of the introduction and spread of smooth brome to the regional dynamics of the planthopper are potentially significant. High connectivity of local populations embedded in a brome matrix may help to prevent local extinctions (via the rescue effect) and increase global metapopulation stability (Brown and Kodric-Brown 1977). Alternatively, high connectivity may increase the risk of metapopulation extinction by increasing the synchronization of local populations (Harrison and Quinn 1989, Grenfell et al. 1995). We are currently investigating the spatial and temporal population dynamics of the planthopper in large-scale experimentally created brome and mudflat landscapes.

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CHAPTER 3

CONFOUNDING OF PATCH QUALITY AND MATRIX EFFECTS IN HERBIVORE MOVEMENT STUDIES¹

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INTRODUCTION

Traditionally, metapopulation studies have emphasized the roles of patch size and isolation on the connectivity among patches (e.g., Thomas and Harrison 1992, Hanski 1994, Hill et al. 1996). In recent years, empirical and theoretical studies have considered the effects of the intervening habitat (i.e., the landscape matrix) on the movement of animals among patches (Taylor et al. 1993, Wiens 1997, Tischendorf and Fahrig 2000). For herbivores distributed among discrete host-plant patches, the general consensus is that the matrix matters (reviewed in Ricketts 2001, Cronin 2003). This conclusion may be premature because matrix studies have tended to ignore the confounding effects of other factors, most notably, host-plant patch quality.

Here, we describe how matrix composition frequently may covary with patch quality in plant-herbivore systems. In addition, we review the literature on the effects of matrix composition on the interpatch movement of herbivores. Our purpose was to evaluate whether the hypothesis that matrix composition directly influences dispersal and landscape connectivity has been adequately tested. Although we have placed the focus of this paper on movement and connectivity, we recognize that matrix structure may also influence a variety of other processes such as habitat selection (Best et al. 2001, Lawler and Edwards 2002), response to patch edges (Cronin 2003, chapter 2), and risk of predation (Wilcove 1985, Roos 2002). We chose to focus on connectivity because it represents a key parameter involved in determining the structure, dynamics and persistence time of subdivided populations (Hanski 1999). Finally, we suggest how future studies can provide more definitive tests of matrix effects on movement, and discuss the value of integrating patch quality into dispersal studies conducted at the landscape scale.

Confounding of Matrix Effects and Patch Quality

The characteristics of vegetation patches (e.g., species composition, tissue-nitrogen levels, vegetation structure) may often vary with the composition of the surrounding matrix (Wiens et al. 1985, Pickett and Cadenasso 1995). Thus, the quality of host-plant patches to herbivores may often depend on the type of matrix within which the patches are embedded. For example, leaf-nitrogen levels in patches of prairie cordgrass were significantly higher in mudflat- as compared to grass-embedded patches (chapter 2). The higher densities of specialized delphacid planthoppers in the former patches may be due to reduced emigration from patches bearing more nutritious host plants (see also Cook and Denno 1994). Similarly, laboratory feeding trials with the chrysomelid beetle *Acalymma innubum*, showed that this specialist herbivore preferentially fed upon leaves from patches of the cucurbit *Cayoponia americana* growing outside of a forest relative to leaves from patches growing at the forest edge (Bach 1984). Effects of forest canopy shading on leaf chemistry and toughness were suggested as explanations for the greater preference for leaves from patches growing in the open (Bach 1984).

Patch quality might vary with the type of surrounding matrix for the following three reasons. First, background abiotic conditions (e.g., edaphic characteristics, topography) may determine host-plant quality, as well as the distributions of both host-plant patches and matrix types (Wiens et al. 1985). Despite a lack of concrete examples in matrix studies, this would appear to be a likely scenario given that soil characteristics such as nutrient availability are known to influence both plant species distributions (Parker 1991, Swaine 1996, Sultan et al. 1998) and the nutritional quality of plants to specialist herbivores (Feller 1995, Moon et al. 2000, Gratton and Denno 2003). Second, the quality of the patch may be influenced by the

type of bordering matrix. Matrix plants may interact with patch plants at the patch-matrix edge via competition for light, space, or nutrients and thus reduce the overall quality of patch plants. The strength of this effect will likely vary depending on the composition of the matrix. For example, by planting three types of matrix vegetation (tomatoes planted in the ground, tomatoes in pots, no tomatoes) around small host plant patches (squash), Bach (1988) demonstrated that below-ground competition with matrix vegetation caused a reduction in the growth of the host plants. In addition, the matrix effect on patch quality need not be restricted to the patch perimeter. The matrix can influence large-scale flows of water, wind, and fire well into the interior of patches (Wiens et al. 1985, Pickett and Cadenasso 1995, Gascon et al. 2000, Weathers et al. 2001). For example, fires originating in agricultural matrix can penetrate deeply into Amazonian forest remnants, leading to the degradation and eventual demise of the forest (Gascon et al. 2000, Cochrane and Laurance 2002). Third, patch quality could potentially influence the composition of the surrounding matrix through the same mechanisms outlined above. Irrespective of the underlying causes, close associations between patch quality and the nearby landscape matrix may be common in many plant-herbivore systems, particularly those with distinctly different matrix types (e.g., a pasture versus forest matrix; Kuussaari et al. 1996).

For an herbivore, the quality of host plant patches can be a major factor influencing interpatch dispersal rates. Most of the existing information on this subject involves the study of spatially structured butterfly populations. Butterflies may respond to a low density of nectar producing flowers (an indicator of patch quality) either by increasing emigration (Gilbert and Singer 1973, Kuussaari et al. 1996) or decreasing immigration (Kuussaari et al. 1996, Matter and Roland 2002). In addition, Hanski et al. (2002) found that female *Melitaea*

cinxia exhibit higher emigration from patches containing only the less preferred of two potential host plants used for oviposition. Consequently, if patch quality and the type of surrounding matrix frequently covary, previous reports of a matrix effect on dispersal (Table 3.1) may actually be flawed because the matrix effect is confounded with patch quality.

LITERATURE REVIEW

Methodology

We searched the following journals from 1970 to the present for studies that examined the effects of matrix composition on some aspect of herbivore movement among suitable host-plant patches (e.g., emigration, immigration, patch transfer): *American Naturalist*, *Biological Control*, *Canadian Entomologist*, *Ecology*, *Ecological Entomology*, *Environmental Entomology*, *Journal of Animal Ecology*, *Journal of Applied Entomology*, *Journal of Economic Entomology*, *Journal of Insect Behaviour*, *Landscape Ecology*, *Oecologia*, and *Oikos*. We only included papers whose studies described clearly defined patches and more than one matrix type. Corridor studies were therefore excluded from the search (e.g., Fahrig and Merriam 1985, Aars and Ims 1999). Similarly, we excluded studies in which species readily utilize at least one type of matrix habitat as a source of nutrition (e.g., Pither and Taylor 1998, Roland et al. 2000). The search was conducted using Web of Science (<http://isi1.isiknowledge.com>) with the following key words: connectivity, dispersal, emigration, fragmentation, immigration, landscape, matrix, and movement. In addition, we included our own study (chapter 2).

For each study meeting our criteria, we evaluated whether the matrix effect could be distinguished from a patch-quality effect on herbivore movement. An effect of matrix composition on interpatch dispersal cannot be proven without experimentally manipulating

the matrix and having patch quality be made constant (by growing plants in a common garden) or randomly distributed among matrix treatments, *or* by directly quantifying movement (e.g., net displacement, path tortuosity) within different matrix types in the absence of nearby patches. The incorporation of one or more patch-quality measures (among the many that are possible) into the analysis of a matrix effect, e.g., as covariates, was not considered sufficient to rule out patch quality as a confounding factor. To further elucidate the possible relationship between patch quality and the matrix, we asked three subsidiary questions from each study system: 1) was there an assessment of whether patch quality varied with the composition of the matrix; 2) was there a test to determine whether patch quality influenced movement; and 3) were the patches in the study landscape natural or experimentally created? In addressing these questions, we drew from all published work associated with each particular study system, and combined publications on the same study system as a single study (chrysomelid beetles: Bach 1988, Lawrence and Bach 1989; *Trirhabda borealis*: Goodwin and Fahrig 2002a, 2002b).

Results and Conclusions

We found eleven studies suitable for inclusion in this review, all of which focused on phytophagous insects. Admittedly, our search did not yield a large number of studies, no doubt a result of the recent popularity of the subject of matrix effects on dispersal and landscape-level dynamics and the difficulty in performing these studies. However, we felt it important to call attention to the issue of reporting significant matrix effects on herbivore movement when the effects may in fact be due to variation in patch quality. More than one-half of the studies (6/11) did not meet our criteria for establishing that matrix composition influenced interpatch movement rates, independent of patch quality (Table 3.1). All of the

TABLE 3.1. Study systems in which matrix effect on herbivore dispersal among host-plant patches was examined. We report whether a matrix effect was adequately demonstrated based one of two criteria, whether the authors (1) experimentally controlled patch quality or randomly distributed patches of unknown quality among matrix treatments, or (2) directly quantified movement within each matrix type in the absence of suitable patches. An affirmative response to either criteria fulfilled our requirement for demonstrating a direct matrix effect. We also report whether the authors tested for patch quality effects on interpatch movement, and whether patch quality varied with matrix type. Finally, we list whether the study was performed in a landscape consisting of natural or experimentally created patches.

Species	Criteria			Tests performed			References
	Matrix effect adequately demonstrated?	Quality constant or randomly distributed?	Within-matrix movement?	Quality effects on movement?	Matrix-quality association?	Patches natural or experimental?	
<i>Battus philenor</i>	Yes	Yes	No	No	No	Natural	Rausher 1981
<i>Acalymma innubum</i>	No	No	No	No	Yes	Natural	Bach 1984
<i>Phyllotreta</i> beetles	Yes	Yes	No	No	No	Experimental	Kareiva 1985
Chrysomelid beetles	Yes	Yes	No	Yes	Yes	Experimental	Bach 1988
							Lawrence and Bach 1989
<i>Melitaea cinxia</i>	No	No	No	Yes	No	Natural	Kuussaari et al. 1996
<i>Metriopectera bicolor</i>	No	No	No	No	No	Natural	Kindvall 1999
<i>Apthona</i> beetles	No	No	No	No	No	Natural	Jonsen et al. 2001
butterflies	No	No	No	Yes	No	Natural	Ries and Debinski 2001
butterflies	No	No	No	Yes	No	Natural	Ricketts 2001
<i>Trirhabda borealis</i>	Yes	Yes	Yes	No	No	Experimental	Goodwin and Fahrig 2002a
							Goodwin and Fahrig 2002b
<i>Prokelisia crocea</i>	Yes	Yes	No	No	Yes	Experimental	chapter 3

studies that did not establish a direct matrix effect on movement were conducted in naturally occurring patches (i.e., those not created experimentally). Under these circumstances, patch quality and the type of surrounding matrix may covary (Wiens et al. 1985, Pickett and Cadenasso 1995). In fact, for all three studies that examined the covariation between the matrix and patch quality (*Acalymma innubum*: Bach 1984, chrysomelid beetles: Bach 1988; Lawrence and Bach 1989, *Prokelisia crocea*: chapter 2), a significant relationship was detected. Given the strong effects of patch quality on emigration and immigration in many systems (e.g., Kuussaari et al. 1996, Matter and Roland 2002), differences in interpatch movement rates that were attributed to matrix types actually may have been due, in whole or in part, to patch quality differences among matrix types (chapter 2). The jury on whether the matrix matters (sensu Ricketts 2001) is still out in six of eleven cases.

Of the five studies that provided convincing evidence that the observed matrix effects on interpatch dispersal were not due to the confounding effects of patch quality, three were performed in experimental landscapes in which patches were formed from potted plants grown under common garden conditions (Kareiva 1985, Bach 1988, chapter 2). In the remaining two studies (Rausher 1981, Goodwin and Fahrig 2002a), the matrix treatments were randomly distributed among patches. Thus, systematic bias in patch quality among matrix types was unlikely. In one of the latter studies, matrix effects on movement were also determined directly by tracking individuals through different matrix types (Goodwin and Fahrig 2002b).

It was not our intention with this paper to make a blanket criticism of large-scale, non-manipulative studies. For several studies in naturally occurring patches, the species were either endangered (the Glanville fritillary, Kuussaari et al. 1996), the ecosystem imperiled

(tall-grass prairie, Ries and Debinski 2001), or the scale of movement too large (Kuussaari et al. 1996, Ries and Debinski 2001, Ricketts 2001), rendering landscape manipulations impractical. For such species, studies conducted in small experimental patch networks would be biologically meaningless.

RECOMMENDATIONS

We feel that there are certain steps that can be taken to more clearly differentiate the roles of matrix structure and patch quality on interpatch movement when landscape manipulations are not possible. First, measurements of movement rates among natural patches embedded in different matrix types can be coupled with dispersal experiments that directly examine movement patterns *within* each matrix type (e.g. Goodwin and Fahrig 2001b, chapter 4). Second, we recommend that ecologists examine whether patch quality varies with matrix composition (Table 3.1). Finally, ecologists should examine patch-quality effects on dispersal, ideally through the direct manipulation of patch quality attributes. For many large-scale systems, this may be surprisingly easy. A good example is the work by Matter and Roland (2002) in which the removal of nectar-producing flowers from meadows reduced immigration rates of male alpine butterflies (*Parnassius smintheus*). Four of the studies listed in Table 3.1 did test patch quality effects on movement, however, these tests were generally correlative (Kuussaari et al. 1996, Ricketts 2001, Ries and Debinski 2001). The pitfall to this approach is that patch-quality variables not considered may also influence movement.

To definitively ascertain a matrix effect on dispersal and population dynamics, variation in patch quality must be experimentally controlled or manipulated. Ideally, dispersal studies are needed in which patch quality, patch size, and matrix composition are

manipulated independently; e.g., by using experimentally created patches. Besides elucidating the direct effects of landscape attributes on dispersal, a controlled experiment can reveal potential interactive effects of different landscape variables. Patch quality and matrix composition may affect dispersal synergistically or antagonistically rather than additively. For example, emigration rates from host-plant patches may be greatly reduced when patches of high nutritional quality are coupled with a resistant matrix (i.e., one inhibiting emigration). In contrast, other matrix types may favor such high emigration rates that patch-quality effects are overridden. To date, both empirical studies and metapopulation/landscape models have ignored possible interactive effects of landscape variables on dispersal and population dynamics. We conclude that a more comprehensive approach to addressing landscape-matrix questions should integrate patch quality into the study of animal movement.

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CHAPTER 4

INTERPATCH MOVEMENT AND EDGE EFFECTS IN HETEROGENEOUS LANDSCAPES: THE ROLE OF BEHAVIORAL RESPONSES TO MATRIX COMPOSITION

INTRODUCTION

Over the past decade, interest in the role of the landscape matrix in the distribution and dynamics of fragmented populations has increased considerably (e.g., Wiens 1997, Roland et al. 2000, Vandermeer and Carjaval 2001, Cronin 2003a). Mounting empirical evidence has revealed that the matrix can have substantial effects on the rate of interpatch movement or connectivity (reviewed in Ricketts 2001, chapter 3). For example, Ricketts (2001) found that connectivity for a number of butterfly species was much greater within a willow thicket matrix than a conifer forest matrix. Furthermore, recent studies have shown that certain matrix types can promote density edge effects, such that herbivores or their natural enemies amass near the perimeter or interior of host-plant patches (Tschardt et al. 2002, Cronin 2003a, chapter 2). To date, however, there has been little empirical exploration of the mechanistic basis of matrix effects on either interpatch movement or the generation of edge effects in animal density (but see Jonsen and Taylor 2000, Goodwin and Fahrig 2002a).

By modifying the behavioral response to the patch edge, the composition of the surrounding matrix may influence the distribution of a species within a patch. Matrix types that favor 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 1999, Fagan et al. 1999). In contrast, such edge effects might not occur if the matrix favors a softer edge and individuals readily move across the patch-matrix edge and out of the patch. Edge effects have been found in many insect populations (e.g., Cappuccino and Martin 1997, Davies and Margules 1998, Rothman and Roland 1998); however, the underlying mechanisms are often unclear (McGeoch and Gaston 2000). Because matrix heterogeneity is

a characteristic feature of many ecological landscapes, our understanding of mechanisms generating edge effects is likely to benefit from detailed study of how matrix composition influences individual movement behaviors near patch edges.

Interpatch movement rates are likely to be influenced by the permeability of the patch-matrix edge (e.g., see Jonsen and Taylor 2000, Schtickzelle and Baguette 2003), but also by movement behaviors within the matrix itself. 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 because it influences the probability that a searching individual will encounter patches embedded in the matrix (Lima and Zollner 1996, Zollner and Lima 1999). If this is a significant factor influencing dispersal success, effects of matrix composition on tortuosity (e.g., Crist et al. 1992, Goodwin and Fahrig 2002b, Jonsen and Taylor 2000) may be important mechanisms underlying effects of the matrix on connectivity. To evaluate this possibility, there is a need for empirical studies of movement behavior that focus on species in which the matrix is known to affect dispersal success. For example, higher colonization rates of riparian habitat by calopterygid damselflies in partially forested than forested landscapes (Pither and Taylor 1998) may be attributed to directed movement through pastures 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; chapter 2, J.T. Cronin and K.J. Haynes, unpublished manuscript), but we do not yet

understand the underlying behavioral basis for these matrix effects. Previous mark-recapture experiments conducted in networks of host-plant patches (Prairie cordgrass, *Spartina pectinata* Link; Poaceae) revealed that connectivity is 3-10 times higher in a matrix composed of the exotic grass smooth brome (*Bromus inermis* Leyss) than in a mudflat matrix. In addition, field census data show that planthoppers tend to accumulate against the edges of mudflat-bordered cordgrass patches but not in patches bordering non-host grasses (native grasses or brome). Herein, we examine movement behaviors of individual planthoppers within the interiors of cordgrass patches and two different matrix habitats (brome and mudflat), and at the edge of cordgrass patches differing in the type of bordering matrix. Our findings are used to elucidate the mechanisms underlying effects of the matrix on the planthopper's interpatch movement rate and within-patch distribution.

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 m² to 4-ha monospecific stands and nearest neighbor patches are separated from one another by < 50 m (Cronin 2003a b,c, J. T. Cronin and K.J. Haynes, unpublished manuscript). 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 has become established in the North American Great Plains by invading disturbed prairie (D'Antonio and

Vitousek 1992), and through repeated introductions to prevent soil erosion and provide animal graze (Wilson 1989, Larson et al. 2001). Brome is similar in stature and appearance to cordgrass, and both species are markedly taller than most native grasses (chapter 2). Within our study areas, the matrix is divided among the three matrix types in approximately equal proportions (chapter 2).

The planthopper feeds solely on the sap of cordgrass and is the plant's most common herbivore (Holder and Wilson 1992, Cronin 2003a,b,c). In North Dakota, the planthopper exhibits two distinct generations per year, with peaks in adult abundance in mid June and early August. Adults are wing-dimorphic, but populations are primarily composed of macropterous individuals (> 90%). A recent study by Cronin (2003b) characterized planthopper populations occurring within prairie remnants as having mainland-island metapopulation structure with frequent extinction-recolonization events and moderately high connectivity among cordgrass patches.

Experimental Design

The movement behavior of individual planthoppers was examined in experimental patches of cordgrass or brome in a common garden (located at The University of North Dakota, Grand Forks, North Dakota, USA), or in natural mudflats within the Kelly's Slough National Wildlife Refuge (located 16 km west of Grand Forks, North Dakota). Patches of cordgrass and brome (1.1 H 1.1 m) 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 patch consisted of 200 potted plants arranged in a 20

H 20 grid (400 cells), where every other cell contained a potted plant (- 30 cm tall). The density of stems established within the experimental patches ($165.3/\text{m}^2$) was within the range of densities found in natural cordgrass patches. This low density, relative to natural patches, was necessary to allow accurate tracking of very small planthoppers (- 2 mm). Patches of this size ($\# 1.21 \text{ m}^2$) constitute 16.3% of natural cordgrass patches, and are capable of maintaining planthopper populations for several generations (J.T. Cronin and K.J. Haynes, unpublished manuscript). Our studies of movement in the mudflat matrix were conducted in the center of a larger natural mudflat (- 250 m^2) because pilot studies showed that 1) planthoppers quickly left experimental mudflat patches identical in size to those used for cordgrass and brome, and 2) although planthoppers in nature often perch for several hours on a single stem of cordgrass or brome, they almost never settle in mudflats (K.J. Haynes, unpublished data).

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 appears to have 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; chapter 2).

We released and tracked a total of 139 individuals (53 in cordgrass, 54 in brome, and 32 in mudflat). Individuals were released on relatively calm (wind $< 12.6 \text{ km/hr}$) and sunny days between 0900 and 1300 and then tracked for 5 to 13 hours each (1800 - 2200). In the cordgrass and brome habitats, planthoppers were released onto a plant in the center of the experimental patch, and then planthopper locations were recorded at 10-min intervals as the grid cell above which an individual was located (Turchin et al. 1991). Up to 4 individuals,

each marked with a different color, were released at one time within a single experimental patch.

In the mudflat trials, in which individuals moved farther per unit time (see Results), the observer marked an individual's location during each 10-min 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 (above), a trial was terminated if an insect remained inactive for 1 hr.

Analysis of Movement Paths in Different 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 overall tortuosity of movement was assessed by calculating the fractal dimension (D) of each movement path. Fractal D estimates near 1 indicate highly linear movement, while estimates near 2 suggest approximately Brownian (plane-filling) movement (Hastings and Sugihara 1993). Fractal D's were estimated with 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 directly on the end of the path (V. Nams, unpublished manuscript). Paths of 4 moves or less were not used in the analyses below because estimates of their fractal D frequently fell outside the theoretical limits of 1 to 2. Paths were too short to be included for two primary reasons: the individual was sedentary (51%), or the individual was lost before several moves could be recorded (32%).

We measured an individual's velocity using mean step length (cm) per 10-min interval (Crist et al. 1992). The degree to which individuals engaged in sedentary behaviors (e.g.,

resting, feeding) was measured as the time elapsed between movements, or residency time (Andow and Kritani 1984). Finally, we quantified an individual's overall rate of movement using net linear displacement rate (cm/hr; Goodwin and Fahrig 2002b). To eliminate potential bias in the estimation of this parameter created by abandoning individuals within mudflat earlier than those in cordgrass or brome, the displacement rate was calculated using a planthopper's distance from the release point 1-hr post release (i.e., before any individuals were abandoned).

To test whether the movement behaviors presented in the paragraphs above differed among habitats we used ANOVA for cases in which the variance was homogeneous and the data could be normalized with transformations (mean step length, fractal D). Mean step length was ln-transformed, and fractal D was transformed by computing $\ln(D-1)$. For both mean step length and fractal dimension, multiple comparisons between habitat types were done using the GT2-method because it performs well with unequal sample sizes with equal variances (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 skewed to the right (Sokal and Rohlf 1995). Multiple comparisons between habitats were performed with Fligner-Policello tests due to unequal variance among habitats (Day and Quinn 1989). Finally, we compared the frequency with which individuals left the brome and cordgrass patches with a Fisher's exact test because it is robust with small sample sizes (Sokal and Rohlf 1995).

In the analyses presented above, the potential for Type I errors may have been inflated due to lack of independence among tests. For example, step lengths and path tortuosity

(measured using fractal dimension) are expected to influence the net displacement rate (Crist et al. 1992). To protect against finding spurious effects of habitat composition on these movement behaviors, 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 may be that exposure to wind differs among habitat types, 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. Drift in the movement trials conducted each day was tested by calculating the mean x- and y-coordinates of planthoppers 1 hr post release (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 (Cronin et al. 2000, 2001).

Movement at the Patch-matrix Boundary

To examine the planthopper's behavioral responses to patch-matrix edges, we created 1.1 H 1.1 m experimental patches identical to those described above but with a linear edge through the center of the patch between cordgrass on one side of the patch and the matrix on the other. In all replicates, one side of the patch contained pure cordgrass. The other side of the patch contained either brome or mudflat (a flat surface of bare potting soil). Marked individuals were released into the center of the arena on one of the edge-most cordgrass plants, and their positions were recorded at 10-min intervals.

We tested whether edge permeability, as measured by the frequency with which individuals emigrated into the matrix in their first movement from their release location, differed between the brome and mudflat edges with a chi-square test (Sokal and Rohlf 1995).

Among individuals that did not emigrate, we tested whether the planthoppers exhibited avoidance of the patch edge by examining the direction of their first movement. Movements from the edge were divided into one of three directional categories (of absolute angles with respect to the edge) which would be equally likely to occur if movement was random: those moving near the edge (0-30E), those moving away from the edge (60-90E), and those moving between these two extremes (30-60E). We examined whether movement was biased towards any of these directions by performing separate chi-square tests for each type of bordering matrix.

RESULTS

Effect of Landscape Composition on Movement

Based on the fractal dimension of planthopper movement pathways, we found significant differences in path tortuosity between all three habitats (Table 4.1). On average, planthopper movement was highly linear in mudflats (D near 1), circuitous in cordgrass, and of intermediate tortuosity in brome (Fig. 4.1A). Mean step lengths were ~2 times greater in mudflat (37.6 ± 5.4 cm per move, mean \pm 1 SE, $n = 30$) than in cordgrass and brome (~18.5 cm; Figs. 4.1B). Example movement pathways in Figure 4.2 illustrate these differences in behavior among habitats.

In addition to influencing the characteristics of the movement pathway, the habitat influenced the length of time that a planthopper paused between movements (i.e., residency time). Planthoppers exhibited significantly lower median residency times in mudflat (0 min, $n = 32$) than in cordgrass (10 min, $n = 41$) or brome (10 min, $n = 43$; Fig. 4.1C).

After 1-hr, the median net displacement rate in both cordgrass and brome was 0 cm/hr ($n = 53$ and 49, respectively). In contrast, planthoppers moved through mudflats much faster,

TABLE 4.1. Effect of habitat type on planthopper movement behaviors. 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	<i>df</i>	<i>P</i>	Effect
<u>All habitats compared</u>					
Fractal dimension	ANOVA	F = 13.608	2, 28	< 0.001*	M<B<C
Step length (cm)	ANOVA	F = 14.986	2, 110	< 0.001*	M<C,B
Residency time (min)	Kruskal-Wallis	H = 46.270	2	< 0.001*	M<C,B
Net displacement rate (cm/hr)	Kruskal-Wallis	H = 64.413	2	< 0.001*	M>C,B
<u>Cordgrass and brome compared</u>					
Number exiting arena	Fisher's exact test	none	1	0.002*	B>C

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

at a median pace of 83.6 cm/hr ($n = 32$; Fig. 4.1D). Although the displacement rate was indistinguishable between individuals within cordgrass and brome, the frequency with which individuals left the patches was much higher for brome (25.9%) than cordgrass (3.8%).

We found no evidence of directional bias in planthopper movement with the exception of the first day of movement trials in mudflat (Fig. 4.3). On this day, a moderate wind blew in from the northwest. Because none of the movement parameters that we examined (e.g., mean step length, fractal dimension, see above) were significantly correlated with daily values of mean absolute drift (i.e., net displacement of planthoppers; $P \geq 0.1$), the differences in movement behavior among habitats are probably not the result of differences in wind speeds among days.

Behavior at the Patch Edge

For planthoppers on the patch-matrix edge, the permeability of the edge was strongly dependent on the bordering matrix ($\chi^2 = 6.255$, $df = 1$, $P = 0.012$). In patches bordering

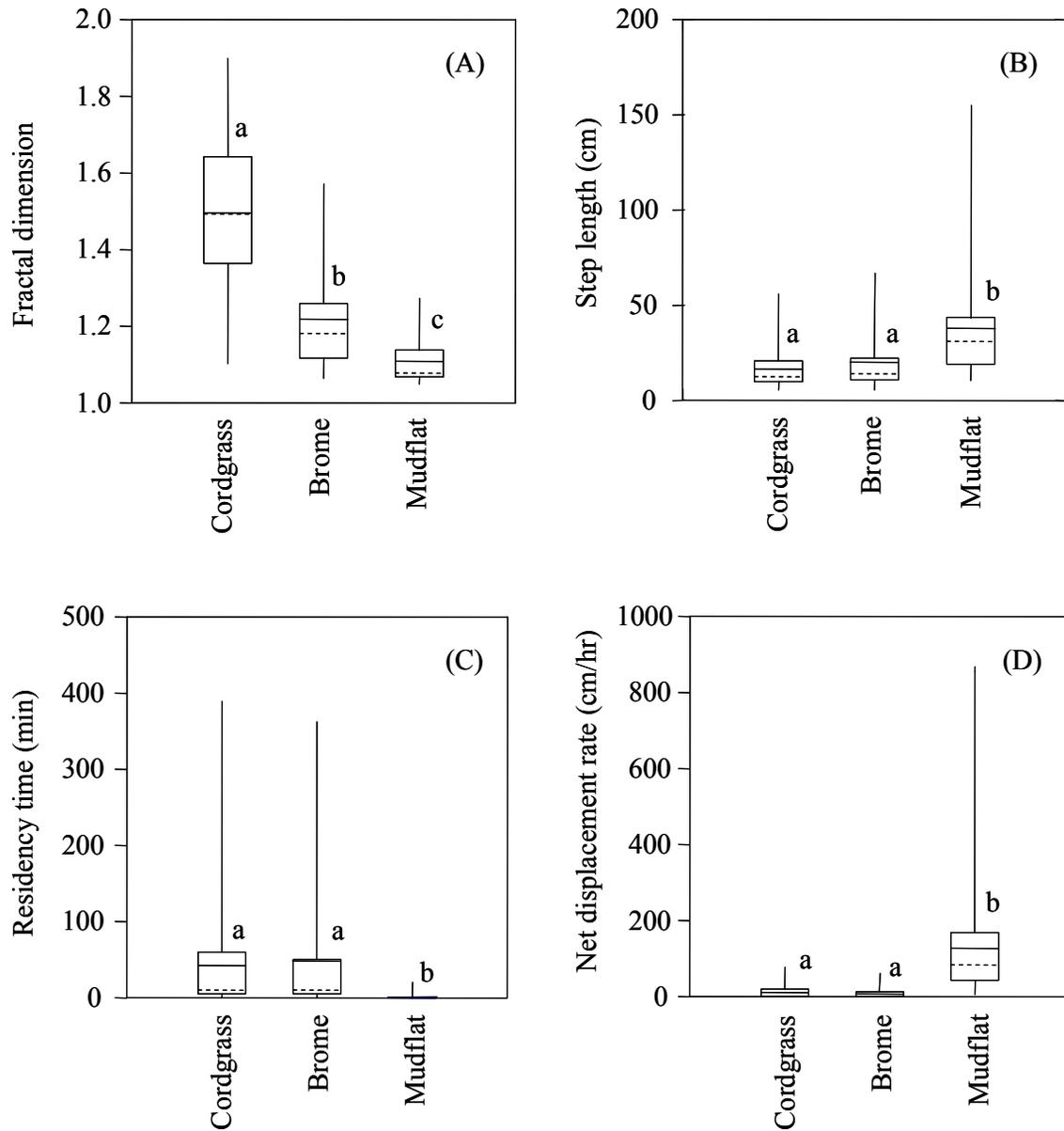


FIG 4.1. Box and whisker plots showing the effects of the three habitat types on planthopper movement behaviors: (A) fractal dimension of movement paths; (B) step length; (C) residency time; (D) net linear displacement rate. The solid and dashed horizontal lines indicate the mean and median values, respectively. The boxes show the interquartile range and the whiskers show the range. Different letters denote significant differences at the $\alpha = 0.05$ level.

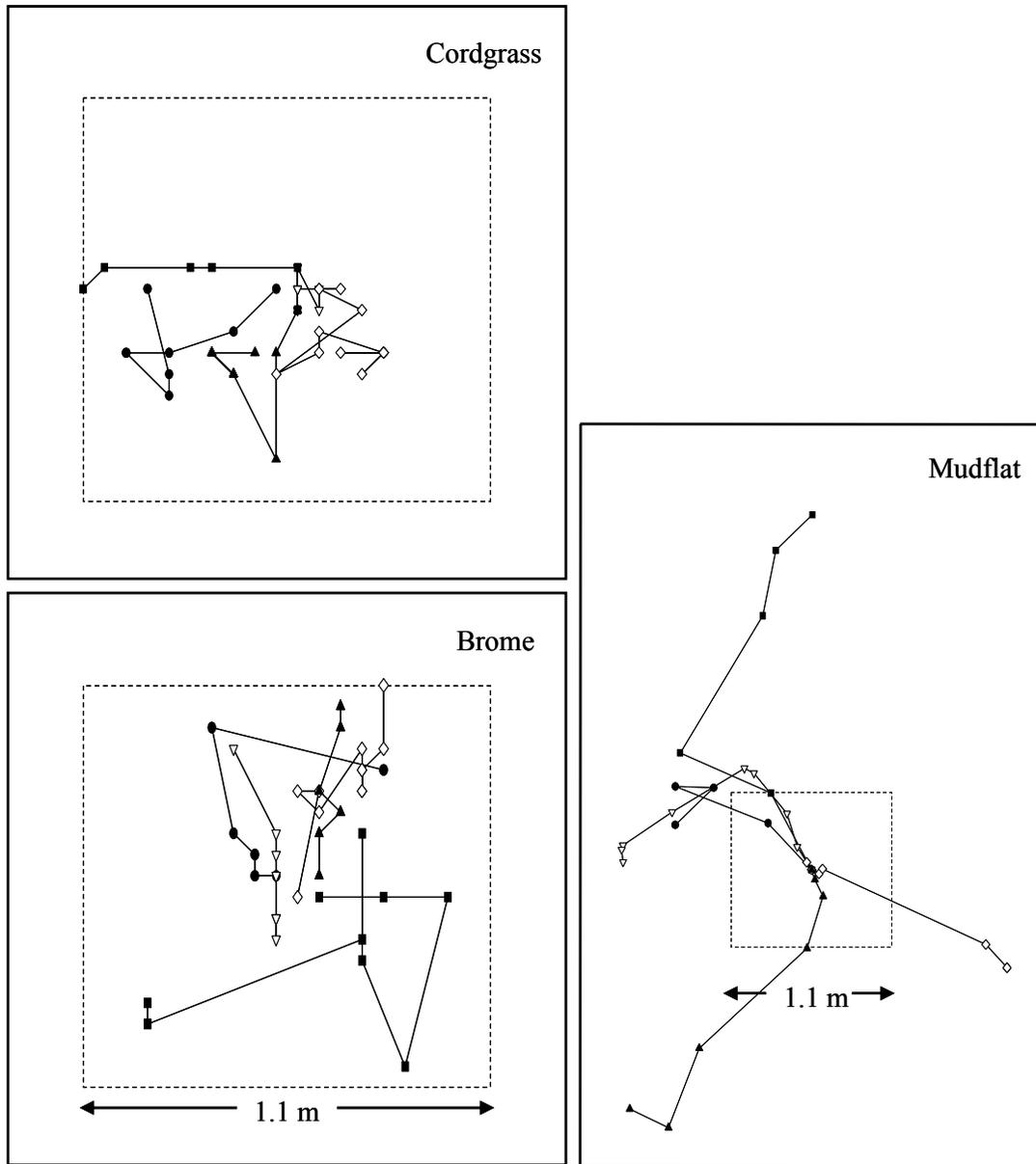


FIG 4.2. Representative movement paths in each habitat. Five paths were randomly selected from those \$4 steps. Movement observations in cordgrass and brome habitats were conducted in 1.1 m H 1.1 m experimental patches (box indicated with dashed line). Although observations in mudflat were conducted in a large naturally occurring mudflat (~ 250 m²), a box equal in area to the cordgrass and brome patches is shown for comparison. For each path, the starting point near the center of the patch and locations at 10-min intervals are shown (different symbols for each path).

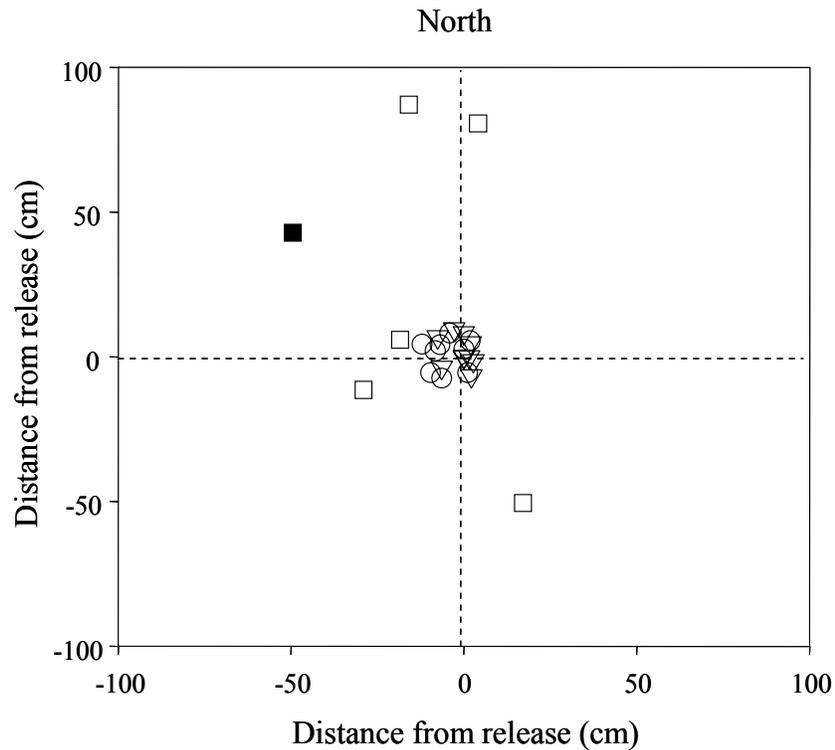


FIG 4.3. Mean displacement of planthoppers on each day of movement trials in cordgrass (circles), brome (triangles), and mudflat (squares). Data are based on displacement 1 hr after planthoppers were released. The filled symbol indicates the one day of movement trials for which the 95% confidence intervals about the mean x- and y- coordinates do not overlap with the release point (intersection of the dashed lines).

mudflat, 14.7% (5/34) of planthoppers crossed the cordgrass-mudflat edge on their first move. In contrast, the emigration rate was much 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 ($\chi^2 = 3.586$, $df = 2$, $P = 0.116$). Whereas 17.2% (5/29) of individuals moved away from the edge, 37.9% (11/29)

moved along the edge. In addition, 44.8% (13/29) moved neither away from the edge nor along the edge, and instead moved from the edge at a 30E - 60E 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 (5 along the edge, 4 neutral, 5 away from the edge), suggesting that planthoppers move randomly in patches with respect to the edge.

DISCUSSION

Movement Behavior at the Patch-matrix Edge

The landscape matrix of North American tallgrass prairie appears to strongly affect the movement behaviors of the planthopper within patches of cordgrass. Although planthoppers redistribute themselves at random within cordgrass patches (Cronin 2003b), and do not appear to be repelled by the patch edge, the cordgrass-mudflat edge represents 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 patch (e.g., away or along the edge). These findings confirm our previous prediction, based on measurements of emigration rates from patches within natural matrix types (chapter 2), that brome edges are more permeable to the planthopper. Sparsely vegetated mudflats form very distinct borders with cordgrass patches. In contrast, the boundary between cordgrass and brome appears to be much softer because brome is similar in height and appearance to cordgrass (for photographs see chapter 2). High permeability of edges between similar habitats may be a common pattern among herbivorous insects (e.g., Kareiva 1985, Kuussaari et al. 1996, Haddad 1999). Thus, the resemblance of brome to cordgrass may be an important factor underlying high patch permeability.

The effect of the matrix on patch permeability may explain field census data (chapter 2) showing that planthoppers aggregate near the perimeter of mudflat-bordered patches, but not against patch edges bordering non-host grasses (brome or native grasses). Using a model based on diffusive movements, Cantrell and Cosner (1999) found that individuals may pool against a barrier to movement such as the cordgrass-mudflat edge. This prediction is well supported by field studies. Animal movements are often channeled along hard habitat edges (e.g., 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. (2003), for example, found that Siberian flying squirrel (*Pteromys volans*) densities were higher near forest edges due in part to their unwillingness to enter the surrounding open habitat.

Density edge effects may often be created by differences in some aspect of habitat quality between the patch edge and the interior, such as differences in host-plant quality, microclimate, or predator abundance (e.g., Young and Mitchell 1994, Cappuccino and Martin 1997, Rothman and Roland 1998, McGeoch and Gaston 2000). In our study system, the higher densities of planthoppers near the edge of patches could conceivably be due to the higher nitrogen concentration of cordgrass leaves at the patch edge (foliar nitrogen is ~14% higher at the edge than interior; chapter 2). However, two lines of evidence suggest that host plant quality is not responsible for the observed edge effect. First, the edge effect in plant quality occurs regardless of the type of surrounding matrix (chapter 2). Second, in this study, we attempted to experimentally eliminate the differences in host plant quality that occur between the edge and interior of patches. Another possible explanation for the edge effect stems from the foraging behavior of the specialist egg parasitoid *Anagrus columbi*

(Hymenoptera: Mymaridae). The parasitoid avoids foraging on the edge of cordgrass patches embedded in mudflat but non-host grasses (brome or native grasses; Cronin 2003a). Thus, it is possible that planthopper oviposition near the patch edge in mudflat-bordered patches is favored evolutionarily by the reduced risk of parasitism. We suggest that the effect of matrix composition on planthopper edge effects is most likely a result of a fixed behavioral avoidance of parasitoids through oviposition near the cordgrass-mudflat edge, and (or) differences in edge permeability among matrix types.

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 both patch 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 that occurs in the brome matrix (chapter 2, J.T. Cronin and K.J. Haynes, unpublished manuscript). The importance of this mechanism as a factor underlying connectivity is supported by other recent studies (e.g., see Moilanen and Hanski 1998, Schtickzelle and Baguette 2003). For the planthopper, connectivity is then further enhanced by higher dispersal success (i.e., increased immigration success among dispersing individuals) in the brome than mudflat matrix (chapter 2). This latter effect of the matrix is likely attributable to the complexity of the movement path through brome (Fig. 4.2). In brome, planthoppers will often perch upon stems for extended periods of time much as they do on cordgrass, and it is likely that this behavior contributes to their meandering movement. In contrast, planthoppers tended to move in a highly linear fashion through mudflat (Fig. 4.2). This pattern of movement in mudflats is consistent with studies reporting linear movement of foraging insects through open or resource-lacking

habitats (e.g., Zalucki and Kitching 1982; Crist et al. 1992; Jonsen and Taylor 2000). When patches are spatially aggregated, as in our study system (J.T. Cronin, unpublished data), a simulation study suggests that linear movement away from a source patch may increase the chance of missing the nearby patches (Zollner and Lima 1999). Tortuous movements, as detected for planthoppers in the brome matrix, should increase the likelihood of dispersers encountering new host-plant patches. To date, very few studies have evaluated the role of movement tortuosity in determining the effect of matrix composition on the rate of interpatch movement (but see Jonsen and Taylor 2000). Differences in movement behavior among matrix types have been reported in other previous studies (e.g., Crist et al. 1992, Goodwin and Fahrig 2002a,b), but none were conducted within study systems in which the matrix was known to affect connectivity. In light of empirical and theoretical studies suggesting that area-restricted searching is an efficient strategy for locating resource patches that are aggregated spatially (e.g., Evans 1976, Baars 1979, Kareiva and Odell 1987, McIntyre and Wiens 1999), our supposition that tortuous movement in brome promotes connectivity seems plausible.

The differences in planthopper movement behavior in mudflat relative to cordgrass and brome were not likely due to the use of natural landscapes (mudflat) versus experimental patches (cordgrass and brome). First, planthoppers that emigrated from experimental cordgrass patches (potted plants) placed within natural habitats of each type (cordgrass, brome, or mudflat; see chapter 2), had significantly greater median displacement rates in mudflat than cordgrass or brome (K.J. Haynes, unpublished data). Second, pilot observations in experimental mudflat patches (identical in size to those used for cordgrass and brome) indicated that planthoppers quickly left the patch (K.J. Haynes, unpublished data). Finally, in

a mark-recapture experiment conducted in natural stands of cordgrass and a matrix of native non-host grasses, planthoppers exhibited median displacement rates (3.75 and 10 cm/hr, respectively; based on recaptures after 24 hrs; Cronin 2003b) that correspond very closely to our findings in experimental patches (3.6 and 5.9 cm/hr, based on non-truncated movement paths). Thus, our experimental results correspond closely with field data and appear to accurately reflect how planthopper movement behavior differs among these habitats.

Connectivity in a fragmented landscape can depend critically upon dispersal success (Jonsen et al. 2001, Jonsen and Taylor 2000, Wiens et al. 1997), and the tortuosity of movement through the matrix is one of many potential mechanisms underlying matrix effects on dispersal success. The risk of being eaten by predators while moving through the matrix may be an important factor influencing dispersal success (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*) after they ventured into an open matrix to high mortality caused by avian predators. 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 lower in a brome matrix than in cordgrass or a native non-host grass matrix; Cronin et al. 2004), and are virtually absent from mudflats (unpublished data). Therefore, predation is probably not responsible for the higher dispersal success of planthoppers in brome relative to mudflat matrix. Habitat harshness also does not appear to influence matrix resistance - planthoppers have similar rates of survival when caged (without predators) on mudflat and nonhost matrix vegetation (K.J. Haynes, unpublished data); and microclimate conditions (wind, temperature, humidity) vary only slightly between the mudflat and brome matrix types (J.T. Cronin and K.J. Haynes, unpublished manuscript, K. Baum,

unpublished data). Finally, the distance from which individuals detect habitat patches (perceptual range) can be a crucial factor influencing dispersal success (Lima and Zollner 1996), and recent studies have shown that perceptual range can be affected by the intervening matrix (Zollner and Lima 1997, Schooley and Wiens 2003). Greater perceptual range in open rather than closed matrix types (e.g., field vs. forest) may be a common pattern in foraging animals using either visual or olfactory cues (Murlis et al. 1992, Zollner and Lima 1997, Schooley and Wiens 2003). Because the planthopper has greater dispersal success in brome than in sparsely vegetated mudflats, perceptual range is unlikely to be an important component of matrix resistance.

Conclusions

This study represents one of the first to integrate detailed study of individual movement behavior into an examination of the consequences of the matrix for the dispersal and distribution of a spatially structured population (see also Jonsen and Taylor 2000, Goodwin and Fahrig 2002a). The effect of matrix composition on the planthopper's interpatch movement rate may be driven largely by differences among matrix types in the permeability of patch edges to emigration and the tortuosity of movement within the matrix. Also, the permeability of the patch-matrix edge may play an important role in the generation of edge effects in planthopper density. Clearly, further study is needed before we can assess how commonly such a mechanism underlies edge effects in other species inhabiting heterogeneous landscapes. Finally, this study provides useful information for the development of spatially explicit reaction-diffusion models to explore the effects of habitat edges and the matrix on the planthopper's spatial and temporal population dynamics (J. Reeve, J. T. Cronin and K. J. Haynes, unpublished data).

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CHAPTER 5

CONCLUSIONS

SUMMARY

In this dissertation, I investigated the role of landscape heterogeneity in the movement and spatial distribution of the planthopper *Prokelisia crocea*. The field experiment presented in chapter 2 revealed that the composition of the intervening matrix directly influenced the movement rates of the planthopper among discrete patches of prairie cordgrass (*Spartina pectinata*). Within each matrix type (mudflat, native non-host grasses, and the introduced grass smooth brome [*Bromus inermis*]), marked planthoppers were released onto experimental cordgrass patches that were made identical in size, isolation, and host-plant quality. I found that the emigration rate was 1.3 times higher for patches embedded in the two non-host grass matrix types than for patches in mudflat. The rate of immigration into patches isolated by 3 m was 5.4 times higher in the brome than in the mudflat matrix. Patches in the native grass matrix had intermediate immigration rates. Based on these patterns of emigration and immigration, I concluded that the planthopper's interpatch movement rate (or connectivity) would be highest within a brome matrix, intermediate in a native grass matrix, and lowest in a mudflat matrix.

In addition, field surveys revealed that both the within- and among-patch distributions of the planthopper were related to the composition of the matrix. Within-patches, individuals accumulated against mudflat edges (relative to patch interiors) but not against non-host grass edges. Among patches, incidence and density increased with the proportion of the matrix composed of open mud. The matrix was equal to that of patch geography (size and isolation) in its ability to explain the distribution of the planthopper.

Given that brome-dominated landscape has significantly greater connectivity than landscape dominated by native matrix types, the consequences of the spread of smooth brome

into North American grasslands for the regional dynamics of the planthopper are potentially significant. One possible consequence is that high connectivity of local populations embedded in a brome matrix may help to prevent local extinctions (via the rescue effect) and increase global metapopulation stability (Brown and Kodric-Brown 1977). However, based on a recent multi-generation monitoring study of experimental cordgrass patches, Cronin and Haynes (unpublished manuscript) found higher rates of extinction among local populations embedded within the brome matrix than the mudflat matrix. It appears that potential benefits to the planthopper populations from increased immigration into patches in the brome matrix were overridden by extremely high rates of emigration (Cronin and Haynes, unpublished manuscript).

The effects of matrix composition on the movement and spatial distribution of the planthopper are likely attributable to planthopper movement behavior within the matrix and at the patch-matrix edge. In chapter 4, movement behaviors of individual planthoppers were examined within the interiors of cordgrass patches and two different matrix habitats (brome and mudflat), and at cordgrass patch edges differing in the type of bordering matrix. Movement was highly linear in mudflats, but circuitous in cordgrass and brome (especially cordgrass). In addition, the movement of individuals within mudflats differed from those in cordgrass and brome by higher velocity, shorter pauses between movements, and higher net displacement rate. Edge permeability also differed strongly between mudflat- and brome-bordered patches. In patches bordering mudflat, 14.7% of planthoppers released near the patch edge crossed the cordgrass-mudflat edge on their first move. In contrast, planthoppers in patches bordering brome crossed the cordgrass-brome edge as frequently as they moved within the patch. Despite the low permeability of the mudflat edge, planthoppers exhibited no

behavioral avoidance of patch edges, i.e. no preference for moving away from the edge.

These data are used to elucidate the behavioral mechanisms underlying effects of the matrix on planthopper populations that we reported in chapter 2. Connectivity appears to be higher in the brome matrix due to (1) the extremely high permeability of patches in the brome matrix, and (2) circuitous movement through this matrix promoting high encounter rates with patches. In addition, our finding that the planthopper exhibits edge effects in patches bordering mudflat (but not non-host grasses) may be due to the combined effects of diffusive movement within patches (Cronin 2003), low permeability of cordgrass-mudflat edges, and the absence of edge-avoidance behavior.

Although the landscape matrix is increasingly incorporated into spatial-ecological population studies, little consideration has been given to the likely possibility that patch quality is confounded with the composition of the matrix surrounding each patch. For example, the nutritional quality of host-plant patches to an herbivore may be highly correlated with matrix composition (e.g., chapter 2), consequently obfuscating the importance of the matrix itself to interpatch dispersal. From a literature survey of the effects of the matrix on herbivore movement among host-plant patches (chapter 3), I found that 55% of the studies (6/11) failed to experimentally or statistically isolate the effects of the matrix from potential patch-quality effects on dispersal. Most studies consisted of mark-recapture experiments in natural landscapes where the matrix was not controlled or manipulated (but see, e.g., Kareiva 1985, chapter 2). Of the few studies that evaluated the relationship between matrix composition and patch quality, all of them (3/3) found that these two landscape factors covaried. These data suggest that in most matrix studies, apparent effects of the matrix on dispersal may wholly, or in part, be due to underlying differences in patch quality. For the

planthopper, both emigration and immigration are directly influenced by the composition of the surrounding matrix (chapter 2). These effects of the matrix on planthopper movement could underlie the relationships between matrix composition and the distribution of planthoppers in nature. The retention and buildup of planthoppers within cordgrass patches bordered by mudflat, particularly near the patch edge (chapter 2), is likely attributed to the low permeability of patches bordered by mudflat. Exploration of the effects of patch quality on the movement and spatial distribution of the planthopper is the focus of a forthcoming study (K.J. Haynes and J.T. Cronin, unpublished data).

FUTURE DIRECTIONS IN LANDSCAPE ECOLOGY

This dissertation points to important avenues for future research in landscape ecology. A particularly fertile area for research would be to explore the mechanistic linkages between movement behavior in heterogeneous landscapes and the distribution and dynamics of animal populations (Wiens et al. 1993, 1997, Lima and Zollner 1996). With this in mind, data from the chapter 4 study are being used to build spatially explicit reaction-diffusion models to examine how several aspects of landscape structure (matrix composition, habitat edges, size and configuration of patches) influence the spatial patterning and stability of interactions between the planthopper and its specialist egg parasitoid *A. columbi* (J. Reeve, J.T. Cronin, K.J. Haynes, unpublished data). We also hope to use this model framework to evaluate the hypothesis that planthopper movement behaviors may generate the edge effects we see in patches bordered by mudflat (chapter 2).

In addition, theory and empirical studies to date have ignored the likely possibility that landscape variables (e.g., patch quality, matrix composition) covary in nature and have interactive (non-additive) effects on dispersal (e.g., Kuussaari et. al 1996, Moilanen and

Hanski 1998, Ricketts 2001, Ries and Debinski 2001; but see Wiens et al. 1985, Summerville and Crist 2001, chapter 2). Therefore, many current population models may inaccurately predict how landscape structure influences metapopulation dynamics. Studies conducted in systems amenable to experimental manipulation of landscape structure are necessary to address this problem. In chapter 2, I show that matrix composition and patch quality are interrelated in prairie cordgrass patches in North Dakota; leaf nitrogen content was higher for patches embedded in mudflat than for patches in brome. However, both the independent and interactive effects of patch quality on dispersal are unknown. During the summer of 2003, I manipulated patch quality, matrix composition, and patch size to examine the independent and interactive effects of these variables on the emigration rate of the planthopper from host-plant patches. The results of these experiments are expected to significantly increase our current understanding of how landscape structure influences the movement, spatial distribution, and regional dynamics of the planthopper. In combination with these experiments, we will examine whether the spatial distributions of the planthopper in nature are consistent with our mechanistic understanding of the links between landscape structure and dispersal.

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APPENDIX A

WITHIN-PATCH DISTRIBUTION SAMPLING DESIGN

Adult female density was measured at two paired locations within each patch, at the edge and at 2 m from the edge. In 2000, each sample consisted of 8 unidirectional sweeps with a sweep net (parallel to the edge and approximately 0.75 m in length). In 2001, planthopper densities were measured with a D-vac insect vacuum (Rincon-Vitova, Ventura, California) with a 0.08-m² sampling head. For each sample, the head was placed at 10 points for 3 s each, and approximately 0.5 m apart along the edge or interior. Planthopper numbers per sample (in both 2000 and 2001) were converted to numbers per cordgrass stem by estimating mean stem densities (per m²) in each replicate patch (separate estimates for the edge and interior). This was accomplished by measuring the average number of stems within a 25 × 25 cm sampling frame placed at three random locations at the edge and interior of the patch.

We offer several lines of evidence to suggest that samples taken at 2 m inward from the patch edge are representative of the patch interior in general, and that potential edge effects likely do not extend this far into the patch interior. First, a pilot study indicated that planthopper densities between 1 m and 3 m into the patch interior were lower than the densities at the patch edge (K.J. Haynes, unpublished data). Second, significant differences in plant quality were found to also exist between the patch edge and only 2 m into the interior (see Results). Finally, planthoppers are relatively immobile when moving within a patch (Cronin 2003), suggesting that the intermixing of individuals between the edge and 2 m into the interior is likely to be low.

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APPENDIX B

PATCH CENSUS PROCEDURE AND ANALYSES OF PLANTHOPPER DISTRIBUTIONS IN NATURE

Census Procedure

In our censuses of the distribution of planthoppers among patches, we recorded egg density per stem and the presence or absence of eggs for each patch. We chose to focus on egg instead of adult densities because single point-in-time estimates of the latter might not reflect the density of residents within a patch over the course of an entire generation (ca. 3 wk). Also, we note that adult female density is positively correlated with egg density within patches (Cronin 2003a,b). Each census was conducted near the end of a planthopper generation (mid July, late August) when egg-laying was near completion and oviposition scars were apparent. At these times, planthopper-infested leaves possessed a nearly complete record of the sum total of planthopper eggs laid during a generation (including dead eggs and chorions cast by emerging nymphs). A 25 cm × 25 cm sampling frame was haphazardly placed at three locations within each patch. Within the sampling frame we counted the number of cordgrass stems, and collected a maximum of 10 infested leaves from each patch (for patches < 1.0 m², the maximum was set at 3 leaves). When no infested leaves were found in the sampling frames we intensively searched the entire patch to determine the presence or absence of planthopper eggs. The intent of this sampling scheme was to minimally alter planthopper densities over time. The number of planthopper eggs laid in collected leaves was determined by dissection using a stereo-scopic microscope. Planthopper egg density (eggs/stem) per patch was estimated as $([\text{mean eggs/stem}][\text{mean infested stems/frame}]) / (\text{mean total stems/frame})$.

The number of patches in the census increased over time from 25 in the first generation, to 142 in the fifth generation. The size of each patch was measured every census year between planthopper generations using a combination of digital photographs and

differential GPS measurements. Patches ranged in size from 0.1 - 126.7 m², and averaged (\pm SE) 7.4 ± 1.2 m² (Cronin 2003a,b). Patch isolation, which is dependent upon the linear distance to, and size of, surrounding patches (Hanski 1994, Hanski and Kuussaari 1995), was determined from the nearest neighbor in each of 4 quadrats (NE, NW, SE, and SW). Here, our index of isolation, I , was computed as:

$$I = \frac{1}{\sum_i^4 A_i e^{-D_i}}$$

where A_i and D_i are the area of (m²) and distance to the nearest patch in the i^{th} quadrat, respectively. Larger values of I indicate greater patch isolation. Although Moilanen and Nieminen (2002) have argued that nearest neighbor measures poorly predict colonization events, we have found that I is highly correlated with an isolation measure that is based on all cordgrass patches within 40 m of a focal patch ($R = 0.80$, $n = 25$, $P < 0.001$; Cronin 2003a,b).

The matrix surrounding focal patches was quantified by estimating the proportion of ground cover within 3 m of the patch that consisted of each of the three matrix types (mudflat, native non-host grass, smooth brome). We estimated the proportion coverage of each matrix type occurring within quadrats (25 cm \times 25 cm) placed at 0, 1, 2, and 3 m from the patch edge. To standardize sampling effort throughout the entire 3 m buffer, the number of quadrat samples at each distance increased with patch size and distance from edge (4 to 16 compass directions). Our index of the matrix was computed as the proportion of the 3 m buffer composed of mudflat.

Analysis of Distributional Patterns

We tested the effect of the matrix and additional variables (patch size, isolation, and planthopper density in the previous generation [t-1]) on planthopper density and patch

occupancy with multiple least-squares regression and logistic regression, respectively. All continuous variables were ln-transformed prior to analysis to normalize their distributions (because of zeros in density and proportion mudflat, 0.1 was added to each estimate prior to transformation). The distribution of planthopper densities became less normal over the course of 5 generations because the number of vacant patches increased with time. Analyses with and without zeros produced the same qualitative results. Therefore, we considered the tests to be robust to this violation of model assumptions and report tests including zero densities.

For the logistic-regression analysis of patch occupancy, the binomial variable (planthopper presence/absence) was logit-transformed (Hosmer and Lemeshow 2000). We used patch occupancy at $t - 1$ as a categorical independent variable. G-tests were used to evaluate the statistical significance of each independent variable, patch size, isolation, matrix composition and occupancy at $t - 1$ (Hosmer and Lemeshow 2000). To describe the fit of the model we report McFadden's Rho squared (ρ^2), which is comparable to the R^2 of a least-squares regression (Hosmer and Lemeshow 2000).

There were two potential sources of inflated type-I error in the tests described above: the lack of independence among planthopper generations, and conducting two non-independent tests on each generation (least squares and logistic regression). Non-independence among generations was most likely to be due to autocorrelations in planthopper density or patch occupancy. Because the effects of density/occupancy at $t - 1$ are partitioned in the regression models, the effects of patch size, isolation and the matrix on density/occupancy at t are expected to be independent among generations. To minimize the chance of finding spurious density/occupancy effects of generation $t - 1$ on generation t , we applied a sequential Dunn-Šidák correction to our critical level of α ($= 0.05$) for all tests

involving planthopper abundance (Sokal and Rohlf 1995). For the two within-generation regression analyses, the error rate for tests of the effects of patch size, isolation and the matrix on the dependent variable was set at $\alpha' = 0.025$.

Finally, a multiple regression analysis was performed to determine whether the proportion of generations in which the patch was occupied was influenced by the composition of the matrix, patch size and isolation. Patches not added until 2001 (generations 4 and 5) were excluded from the analysis. All of the independent variables were ln-transformed prior to analysis.

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APPENDIX C

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17/03/2004

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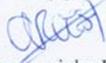
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VITA

Kyle Haynes was born December 30, 1971, in Canoga Park, California, to Katherine and Kent Haynes. He grew up in the nearby town of Chatsworth, attending Chatsworth Elementary, Lawrence Jr. High, and Chatsworth High School. His interest in the natural world was inspired by many hours of exploring the foothills of the Santa Susana Mountains, as well as the many family vacations spent touring the natural areas and parks within the Western half of the United States. In 1990, Kyle enrolled in the University of California at Santa Barbara and majored in ecology and evolution. From 1995 to 1998, he attended Utah State University under the supervision of Dr. Gary E. Belovsky, spending summers at the National Bison Range near Moiese, Montana, studying the foraging ecology of grasshoppers. During Kyle's final summer and fall in Utah, he was employed by The Utah Department of Wildlife Resources to monitor the survivorship and distribution of migratory bird species at several remote locations throughout the state. Kyle began his doctoral studies in spatial ecology at The University of North Dakota in January of 2000, under the supervision of Dr. James T. Cronin. The Cronin lab migrated south to Louisiana State University in August of 2001.