

MATRIX COMPOSITION AFFECTS THE SPATIAL ECOLOGY OF A PRAIRIE PLANTHOPPER

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Abstract. To date, there is a lack of well-controlled field experiments that disentangle the effects of the intervening matrix from other landscape variables (e.g., patch geography or quality) that might influence animal dispersal among patches. We performed a field experiment to investigate how the movement of a delphacid planthopper (*Prokelisia crocea*) among discrete patches of prairie cordgrass (*Spartina pectinata*) is affected by the composition of the matrix (mudflat, native nonhost grasses, and the introduced grass smooth brome [*Bromus inermis*]). Within each matrix type, marked planthoppers were released onto experimental cordgrass patches that were made identical in size, isolation, and host plant quality. We found that the emigration rate (planthoppers lost per patch per day) was 1.3 times higher for patches embedded in the two nonhost grass matrix types than for patches in mudflat. The rate of immigration (immigrants per patch per day) 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. In addition, a survey of planthopper distributions in nature 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 nonhost 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. We suggest that the low permeability of the mudflat relative to a nonhost grass edge may explain these planthopper distributional patterns. Also, because natural cordgrass patches in mudflat were richer in nutrients than those in nonhost grasses, planthoppers may have been more likely to remain and build up densities on the former patches. We predict that the displacement of native matrix types by invasive brome will result in increased connectivity and greater spatial synchrony in densities of planthoppers among cordgrass patches.

Key words: connectivity; edge effects; edge permeability; emigration; immigration; matrix; patch quality; planthoppers; *Prokelisia crocea*; *Spartina pectinata*; spatial distribution; tallgrass prairie.

INTRODUCTION

For patchily distributed populations, the rate of interpatch 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 interpatch 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 that 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).

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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 (K. J. Haynes and J. T. Cronin, *unpublished manuscript*), we found that 60% of the studies (6 out of 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 matrix within which the patches were embedded (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 2003b), 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 tallgrass 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. 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 *Andropogon scoparius* 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 and Fig. 1). At our study areas, the matrix is composed of ~30% mudflat, 40% native nonhost 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 (K. J. Haynes, *unpublished data*). Within each matrix type, we created networks of small, experimental host plant patches each consisting of a central patch surrounded by eight satellite patches positioned 3 m away and equal distances 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 12×12 -cm pots using ProMix BX (Premier Horticulture Limited, 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 2×2 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 h), 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, USA). 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 cord grass stems. Fewer than 1% of the marked planthoppers left the patch immediately after their release (K. J. Haynes, unpublished data).

For each replicate, we released 500 adult female planthoppers (~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 planthoppers per stem [Cronin 2003b]), but was not outside the range of densities observed in more productive sites nearby (annually, densities exceed 40 planthoppers 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, 48, and 72 h postrelease. Planthoppers found on satellite patches were aspirated from the plants to avoid recounting 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 cord-

grass patches (J. T. Cronin, *unpublished manuscript*), 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 day), 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 (five during May and June 2001 and three 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 nonhost grass-bordered patches (composed of brome and/or native grasses) in 2000. All patches were >40 m² 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: 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 ultracold 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 mass) of leaves. For planthoppers, nitrogen content of leaves is considered to be a strong index of plant quality (reviewed in 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 was evaluated with a one-way ANOVA (see previous paragraph). 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, North Dakota (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 (in square meters), 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 (*Melitaea cinxia*). 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 ig-

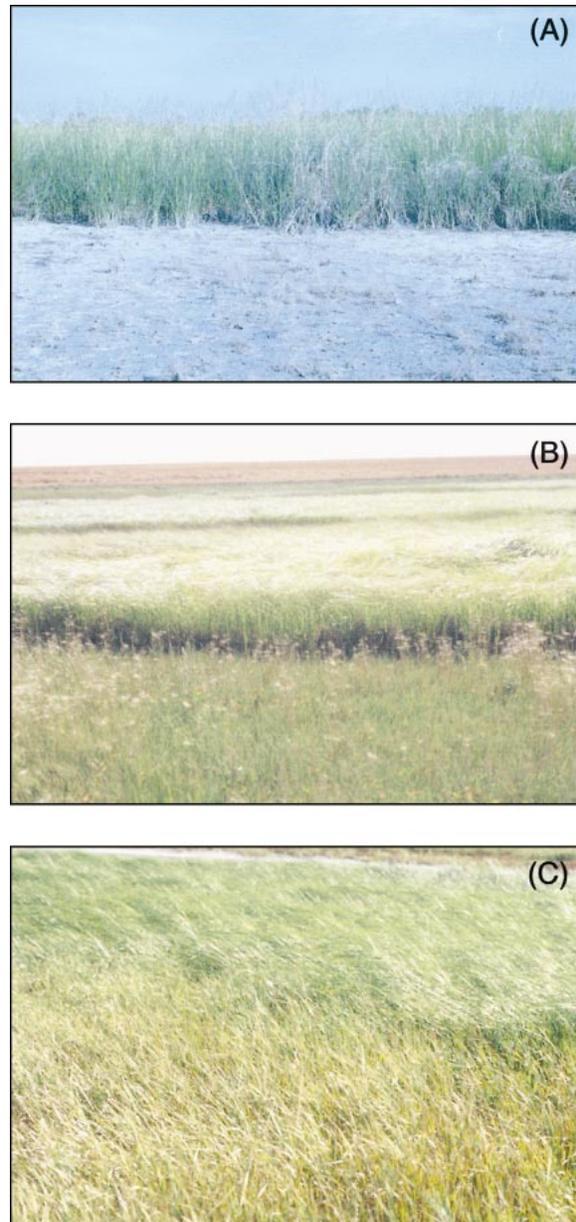


FIG. 1. Prairie cordgrass (*Spartina pectinata*; background) and the three main matrix types (foreground) within the drainage system associated with the Kelly's Slough National Wildlife Refuge, North Dakota, USA. (A) Open mudflat dominated by the low-lying herb *Salicornia rubra*. (B) A mixture of native nonhost 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.)

nored matrix effects, explained 19.5% of the variation in egg densities and 10.0% of the variation in patch occupancy rates. Here, we reanalyzed these census data, but included matrix composition in the models. For each generation, the influence of patch size, isolation, planthopper abundance (density or patch oc-

cupancy) 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., $R_{\text{total}}^2 - R_{\text{total}-1}^2$).

RESULTS

Matrix type 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. 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. 2B). Mudflat- and brome-embedded patches had the largest difference in immigration: the rate was 5.4 times higher in the latter than in 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 high rate of emigration from brome- as compared to the mudflat-embedded patches, we found that proportionately more emigrants successfully dispersed into the satellite patches in the former than in the latter matrix (Tukey's HSD, $P = 0.002$, Fig. 2C).

Within-patch distributions

In 2000, the within-patch distribution of planthoppers varied significantly with the type of matrix bor-

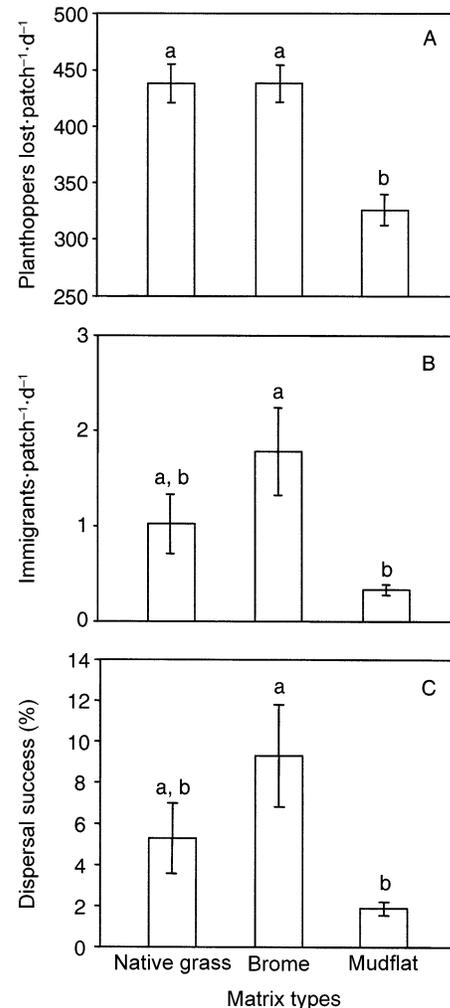


FIG. 2. Effects of the three matrix types on interpatch movement: (A) rate of planthopper loss from a release patch; (B) rate of immigration onto satellite patches; (C) percentage of planthoppers lost from the central release patch that successfully immigrated onto any of the eight surrounding satellite 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 were based on the cumulative number of immigrants captured in 72 h, because immigrants accrued at a more constant rate over the three days of the experiment. Different letters denote significant differences at the 0.05 level.

dering the patch ($F_{1,24} = 14.63$, $P = 0.001$). Planthopper densities were significantly higher at the edge than the interior of mudflat-bordered patches, but no edge effect was detected for patches bordered by nonhost grasses (Fig. 3). On average, densities (interior and edge combined) in patches bordering mudflat were comparable to those in patches bordering nonhost grass (2.9 ± 0.7 planthoppers vs. 1.9 ± 0.2 planthoppers 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 \sim 10% of the samples. We lacked

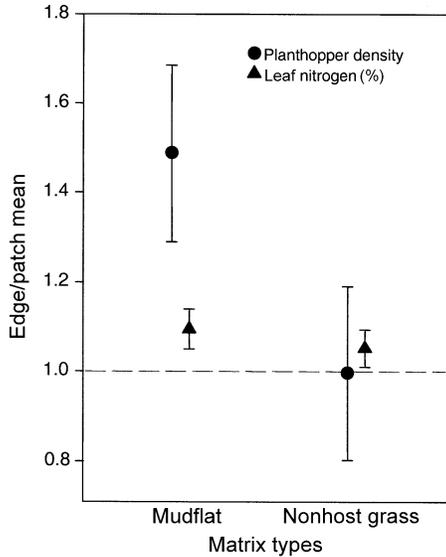


FIG. 3. Ratios (and 95% confidence intervals) of female density at the patch edge to mean patch density, or leaf nitrogen content at the patch edge to mean patch leaf nitrogen content, for patches embedded in a mudflat or a mixture of nonhost grasses (native grasses and brome). An edge-interior difference was deemed significant if the 95% confidence intervals did not overlap 1.0.

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. 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 nonhost grass-bordered patches ($1.59 \pm 0.05\%$ vs. $1.44 \pm 0.04\%$,

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 1); however, in only two of five generations 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 $19.5 \pm 4.9\%$ to $25.8 \pm 6.1\%$, an increase of 6.3% (based on R^2 values; Table 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 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 $7.6 \pm 3.3\%$ over a model without the matrix effect. All independent variables, excluding patch isolation, explained roughly equal percentages of the variation in patch occupancy (~4%).

The effect of the matrix was more compelling when evaluated over the 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.

TABLE 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	ΔR 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 in boldface (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 factor ΔR^2 is the absolute change in model R^2 after removing the matrix variable from the model with all variables included.

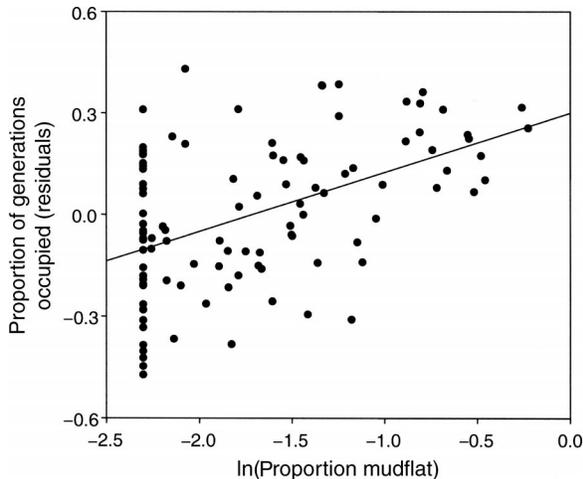


FIG. 4. The relationship between the proportion of plant-hopper generations in which a patch was occupied and the proportion of nearby matrix that consisted of mudflat. To indicate the effect of the matrix alone, the residuals from a regression model including only patch size and isolation were regressed against the matrix variable (proportion occupied (residuals) = $0.18 \times \ln(\text{proportion mudflat}) + 0.3$, $n = 105$, $R^2 = 0.24$).

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 $\sim 17\%$, and isolation explained 10%, of the variation in patch occupancy rates.

DISCUSSION

Matrix effects on dispersal

After controlling for most variables thought to influence interpatch movement, i.e., insect density and patch characteristics (size, isolation, stem density and quality), we found 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). Similarly strong effects of the matrix on dispersal have been reported for a diversity of insect species including beetles (e.g., Kareiva 1985, Bach 1988, 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 (K. J. Haynes and J. T. Cronin, *unpublished manuscript*). In our study system, matrix type and patch quality (in terms of leaf nitrogen content) were interrelated in natural (but not experimental) patches: mudflat-embedded patches were 10% richer in nitrogen levels than patches embedded in matrix com-

posed of nonhost 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 vs. 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 out of 3) found that these two landscape factors covaried (K. J. Haynes and J. T. Cronin, *unpublished manuscript*). 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 (K. J. Haynes and J. T. Cronin, *unpublished manuscript*).

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 (K. J. Haynes, *unpublished data*). Second, in a large-scale field experiment (distances between patches ranging from 5 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. 1). Relatively few planthoppers moved into and out of patches embedded in the sparsely vegetated mudflats. Patches embedded in both nonhost grass matrix types had similarly high emigration losses, but immigration tended to be higher for patches in brome than in native nonhost grasses. The introduced grass, brome, is taller than the native matrix vegetation and comparable in stature to cordgrass (Fig. 1). Inter-

estingly, most other studies have found the opposite relationship between matrix complexity and interpatch movement (Kareiva 1985, Kuussaari et al. 1996, Moilanen and Hanski 1998, Pither and Taylor 1998, Roland et al. 2000, Jonsen et al. 2001, Ricketts 2001). To gain an understanding of 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. 1). Within a cordgrass patch, planthoppers redistribute themselves at random (Cronin 2003b), but when near the mudflat edge, individuals tend to turn away (K. J. Haynes, *unpublished data*); i.e., the patch edge is hard (Stamps et al. 1987). In patches bordering nonhost grass, the edge is much softer; planthopper individuals readily cross over into the matrix and are unlikely ever to 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 nonhost grasses to prairie cordgrass (especially brome) is an important factor promoting high patch permeability. Perhaps it should be 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 vs. open fields for the meadow-inhabiting *Glanville fritillaria*; 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 interspecific 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 is ~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-embedded, as compared to nonhost 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 nonhost grasses (Fig. 3). However, because the nitrogen edge effect was similarly strong between the two matrix types, it was probably not the cause for the accumulation of planthoppers on the mudflat as compared to the nonhost grass edge. The matrix-dependent edge effect in planthopper density is likely due to other factors, including the avoidance of parasitoids (see previous paragraph [Cronin 2003a]), or the edge permeability differences between matrix types (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 (K. J. Haynes and J. T. Cronin, *unpublished data*), we found that movement paths were meandering through nonhost 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 nonhost grasses, even up to 50 m (the maximum distance found between nearest neighbor patches; J. T. Cronin, *unpublished data*). 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 nonhost 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 nonexistent 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, *unpublished data*). 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 Molain 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 ~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 interpatch 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 tallgrass 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 patches relative to nonhost grass-embedded patches have a 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 (K. J. Haynes and J. T. Cronin, *unpublished manuscript*).

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*, which 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 (J. T. Cronin, *unpublished manuscript*). The high extinction rate found for small cordgrass patches (Cronin 2003b) may be attributable to both lethal and nonlethal (predator-induced dispersal) effects of spiders (J. T. Cronin, *unpublished manuscript*). 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 nonhost 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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APPENDIX A

A description of the sampling methods used to quantify the planthopper’s within-patch distribution is available in ESA’s Electronic Data Archive: *Ecological Archives* E084-075-A1.

APPENDIX B

Patch census procedure and the analyses of planthopper distributions in nature are available in ESA’s Electronic Data Archive: *Ecological Archives*: E084-075-A2.