

MOVEMENT AND SPATIAL POPULATION STRUCTURE OF A PRAIRIE PLANTHOPPER

JAMES T. CRONIN¹

Department of Biological Sciences, 206 Life Sciences Building, Louisiana State University,
Baton Rouge, Louisiana 70803-1715 USA

Abstract. The transfer of organisms among patches is a key process influencing the spatial structure and regional dynamics of a population; yet, detailed experimental studies of animal movement among patches are uncommon. I performed a series of mark–recapture studies to quantify the movement of a planthopper, *Prokelisia crocea* (Hemiptera: Delphacidae), among discrete patches of its host plant, prairie cordgrass (*Spartina pectinata*). Results from these dispersal studies were used to predict the natural distributions and to characterize the spatial population structure of *P. crocea*. Planthopper emigration loss per patch increased linearly with the density of female conspecifics and was nonlinearly related to patch size (small > large > intermediate sized patches). Planthopper spatial spread was diffusive and 2.7 times faster among cordgrass patches in a heterogeneous habitat (patches embedded in nonhost vegetation) than within a homogeneous habitat (pure cordgrass). Immigration by planthoppers was an increasing function of patch size but was independent of patch isolation (at the scale of this study). The natural distribution of planthoppers in a prairie fragment, obtained from a survey of 146 cordgrass patches over five generations, was well predicted from the dispersal experiments. Planthopper densities and patch occupancy rates were positively correlated with patch size (cordgrass patches ≥ 0.8 ha were continually occupied), but uncorrelated with patch isolation. Based on this survey, the rate of patch extinction was 21% per generation, highest in small and moderately isolated patches, and approximately equal to the recolonization rate per generation. Finally, the dynamics of local patch populations were asynchronous, even for patch pairs <10 m apart. I conclude that *P. crocea* exhibits a population structure most closely resembling a mainland–island metapopulation, but with high patch connectivity. Under these circumstances, processes operating within the few mainland patches are probably more important than regional processes (patch extinctions/recolonizations) in influencing population persistence.

Key words: asynchronous dynamics; diffusion; emigration; extinction; immigration; mainland–island; mark–recapture; metapopulation; patch connectivity; *Prokelisia*; recolonization; *Spartina*.

INTRODUCTION

For a population of herbivores living among discrete host-plant patches, the transfer of individuals among patches is a key process influencing both its spatial structure and regional dynamics (Tilman and Kareiva 1997, Hanski 1999). If movement among patches is rare, population dynamics will be governed by within-patch processes. Low-to-moderate rates of movement allow for the formation of a classical metapopulation (Levins 1970), and through the rescue effect (Brown and Kodric-Brown 1977), can make unstable local dynamics stable at the regional level (Hanski 1999). High rates of movement tend to cause an ensemble of patches to coalesce into one large patchy population (Harrison et al. 1995, Harrison and Taylor 1997). A high inter-patch movement rate promotes spatial synchrony and may be neutral or negative in its effect on regional

persistence (Reeve 1988, Allen et al. 1993, Hanski 1999).

Because dispersal is so intimately associated with the spatial structure and dynamics of a subdivided population, quantification of immigration, emigration, and the pattern of spatial spread, as well as assessing the factors that influence movement in natural landscapes, is critically important (Ims and Yoccoz 1997, Hanski 1999). Factors that influence animal dispersal are diverse and include both bottom-up (e.g., plant nutritional quality, intraspecific competition; Thomas and Singer 1987, Denno and Roderick 1992) and top-down (e.g., predator abundances; Lima and Dill 1989, Kratz 1996) forces. Aspects of landscape structure, including patch size, isolation, edge characteristics, and structure of the intervening matrix have also been shown to profoundly affect interpatch movement (Ims and Yoccoz 1997, Wiens 1997, Hanski 1999, Cronin 2003a, b).

To date, most studies of the movement and spatial structure of herbivorous insect populations have been with holometabolous species, e.g., butterflies, beetles, and flies (Roslin and Koivunen 2001, Shirley and Sibly

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¹ E-mail: jcronin@lsu.edu

2001; butterflies reviewed in Hanski 1999). Hemimetabolous insects, such as grasshoppers, planthoppers, and leafhoppers, scarcely have been studied (but see With and Crist 1995, Kindvall 1996, Briers and Warren 2000). These latter taxa dominate the insect herbivore faunas of grassland ecosystems (e.g., Haddad et al. 2000), which are perhaps the most imperiled and fragmented ecosystems in the world (Samson and Knopf 1996). By studying this group of important grassland species, it will be possible to better understand how the degradation and loss of grassland habitats will affect herbivore population structure and dynamics. Moreover, as called for by Holyoak and Ray (1999), additional studies that define the spatial structure of populations are needed to advance the development of spatial population-dynamic theory. Here, I report on the movement and population structure of an abundant planthopper that feeds on a native grass species of the North American Great Plains.

I performed a series of mark–release–recapture field experiments that were designed to quantify the movement of *Prokelisia crocea* (Hemiptera: Delphacidae) among discrete patches of the host plant, prairie cordgrass (*Spartina pectinata*). In particular, I examined the effects of patch size and planthopper density on emigration; patch size and isolation on immigration; and the pattern, rate, and range of planthopper spatial spread in homogeneous (within large cordgrass patches) relative to heterogeneous (many small discrete cordgrass patches) landscapes. Results from these dispersal studies were used to characterize the spatial population structure of *P. crocea* and make predictions about the natural distributions of these planthoppers. These predictions were evaluated against five generations of data on planthopper abundances among up to 146 discrete cordgrass patches in a tall-grass prairie.

METHODS

Life history

Within hydric prairie fragments of North America, prairie cordgrass, *S. pectinata*, is a common native plant species (Hitchcock 1963). In tall-grass prairie of northeastern North Dakota, cordgrass occurs in numerous discrete patches ranging in size from well less than 1 m² to several hectares (see Appendix A). The maximum isolation of a cordgrass patch from its nearest neighbor is only ~46 m.

Numerically, the most common herbivore of prairie cordgrass is the delphacid planthopper, *P. crocea* (Holder and Wilson 1992, Cronin 2003a, b). *Prokelisia crocea* is monophagous (Holder and Wilson 1992) and undergoes two distinct generations per year in the northern Great Plains (Cronin 2003a, b). First-instar nymphs overwinter beneath the sheaths of senescent cordgrass leaves. During the spring, nymphs pass through five instars while feeding on the phloem extracted from cordgrass leaves, and then mature into

adults from early to mid-June. Adults are primarily macropterous: >90% of the females and males are long-winged (*unpublished data*). Eggs are laid along the midrib of the adaxial surface of cordgrass leaves. For the second generation that follows, adults reach a peak in early August.

Because of the generally wide separation among existing prairie fragments (Samson and Knopf 1996), planthopper dispersal is expected to be restricted almost entirely to within a fragment. Hence, I focused my movement studies on this, within-fragment, spatial scale. Also, for two reasons I focused this study on the movements of female planthoppers. First, males occur at densities that are usually 5–20 times less than females (*unpublished data*). Second, captured females are almost always mated (*unpublished data*), suggesting that the spatial spread of this species is not contingent upon male dispersal ability.

Immigration

The geographic variables patch size and isolation are considered to be of overriding importance in determining the likelihood of an immigration event (Hanski 1994, 1999). In this experiment, I de-faunated natural cordgrass patches and then examined how the number of immigrants per patch varied with patch size and distance from a large source patch of planthoppers. This study was conducted in Site 104, 20 km west of Grand Forks, North Dakota (47.94184° N, 97.31036° W). A 1.4-ha cordgrass patch served as the main source of planthoppers. Adjacent to this source patch, I selected 33 smaller patches that varied in size from 0.07 to 29.2 m² (79% of the patches fall within this range) and distance from the source by 0.7–45.9 m (maximum nearest-neighbor distance ~46 m; *unpublished data*). Planthopper adults and nymphs were removed from these patches by vacuuming the entire patch with a D-vac (Rincon-Vitova, Ventura, California, USA) and discarding the planthoppers. The process was repeated at 20-min intervals until the collection produced no planthoppers (usually ≤6 repetitions). To establish the source patch as the main source of planthoppers, I vacuumed planthoppers off of all other cordgrass patches within 50 m of the target patches.

After 7 d, the target patches were vacuumed and all planthoppers collected. Cordgrass stem density (number per square meter) per patch was determined as the mean of three stem counts from within a 1/4 × 1/4 m sampling frame (randomly placed in the patch). Least-squares regression was used to determine the effect of patch size and isolation on either immigrant number or density (planthoppers/cordgrass stem) per patch. Prior to analysis, all variables were ln-transformed to achieve normality in their distributions.

Emigration

In this study, I focused on the effects of conspecific density and patch size on planthopper emigration. In

general, herbivores are predicted to have higher emigration rates at high relative to low conspecific densities (e.g., Denno and Roderick 1992, Herzig 1995) and in small relative to large patches (e.g., MacGarvin 1982, Kareiva 1985). Potential plant-quality effects on planthopper emigration (e.g., Denno et al. 1985) were ignored in favor of an emphasis on how geographic variables affect dispersal. Also, the effects of predatory arthropods and matrix heterogeneity on emigration were addressed in separate studies (K. J. Haynes and J. T. Cronin, *unpublished manuscript*).

Planthopper density effects.—To determine if conspecific density influences emigration rates, I released female planthoppers at one of three densities (1, 3, or 10 insects per stem) onto small, experimentally created cordgrass patches. These densities represent moderate, high, and outbreak density conditions, respectively (Cronin 2003a, b). The cordgrass patches were derived from potted plants (six stems per 16 × 16 cm pot) that were grown under a common outdoor environment; thus, differences in plant quality were minimized. A patch consisted of four pots in a 2 × 2 array and sunk flush to the ground. Thirty experimental patches were placed into the prairie, separated from any other cordgrass by at least 10 m.

Planthoppers were marked with fluorescent powders (see Appendix B) and released into patches. These powders last the lifetime of an adult planthopper in the field (~2 wk, *unpublished data*) and do not adversely affect their survivorship or dispersal (Appendix B). At 6, 24, and 48 h, patches were revisited and the number of planthoppers remaining recorded. A repeated-measures ANOVA was used to determine the effect of planthopper density (fixed factor) and census period (repeated measure) on the loss rate per patch ($[\text{number released} - \text{number remaining}] / \text{number released}$). Differences among density treatments (for each time period) were evaluated with Tukey's hsd pairwise comparisons test.

Patch size.—To determine the relationship between patch size and emigration, I selected from Site 104 discrete cordgrass patches that fell into one of three size categories: $\leq 0.30 \text{ m}^2$ ($0.21 \pm 0.02 \text{ m}^2$, mean ± 1 SE, range: $0.08\text{--}0.28 \text{ m}^2$, $n = 10$), $0.30\text{--}0.75 \text{ m}^2$ ($0.52 \pm 0.06 \text{ m}^2$, range: $0.32\text{--}0.64 \text{ m}^2$, $n = 5$), and $1.75\text{--}2.25 \text{ m}^2$ ($1.90 \pm 0.11 \text{ m}^2$, range: $1.75\text{--}2.23 \text{ m}^2$, $n = 5$). Patches within this size range represented 29% of the cordgrass patches in Site 104. I focused on these smaller patches for two reasons: (1) it is logistically impractical to obtain sufficient insects for release, and to recapture all insects, from larger patches; and (2) it is these smaller patches where critical patch size effects are likely to be evident.

Experimental cordgrass patches were vacuumed to remove all planthopper adults and nymphs, as well as predatory arthropods and potential competitors. I then estimated mean stem density per patch as described previously. Fluorescent-marked adult female planthop-

pers were placed in the patch at a density of two per stem. Males were also added to each patch at a density corresponding to ambient levels, one per five stems. On a given day, two small, one medium, and one large patch were stocked with planthoppers. Five days later, the patches were thoroughly vacuumed and the planthoppers collected. A total of five repetitions (blocks) of this procedure were performed, spread over one week. The effect of patch size (fixed effect) and date (block effect) on the proportional loss of females from patches ($1 - [\text{number recaptured} / \text{total released}]$) was determined with a completely randomized block ANOVA (males were too scarce to quantify their dispersal). Pairwise contrasts were determined with Tukey's hsd tests.

Within and among patch redistribution

I quantified the pattern of redistribution of planthoppers when released into two types of landscapes: (1) a large homogeneous cordgrass patch ($>1 \text{ ha}$) and (2) a collection of small cordgrass patches embedded in a nonhost grass matrix. For the homogeneous landscape, 500 fluorescent-marked female planthoppers were released into the center of an expansive cordgrass patch (between 1000 and 1100 hours). At 24-h, D-vac samples (5 s and 0.085 m^2 per sample) were collected at 1-m intervals radiating outward from the release point to 10 m. The number of replicate samples increased from 4 samples at 1 m to 60 samples at 10 m. For each distance, the mean number of recaptures per sample was converted to a density; i.e., the number per square meter of cordgrass. A total of five replicate releases was performed during June of 2000.

To quantify the redistribution of planthoppers in a patchy landscape, I established small satellite cordgrass patches (four 16 × 16 cm pots) that radiated outward to 9 m from a same-sized central release patch. Satellite patches were established at 1.5 m ($n = 4$), 3.5 m ($n = 8$), 6.0 m ($n = 12$), 9.0 m ($n = 15$), and 12 m ($n = 18$), and were spaced equal distance apart within each annulus. The matrix within which these patches were embedded consisted of nonhost native grasses and no other cordgrass occurred within 50 m of the central patch. I released 500 marked female planthoppers onto the central patch (between 1000 and 1100 hours), and then counted all marked individuals that were present on each patch 24 h later. The numbers captured at each distance were converted into a density (numbers per square meter). Five replicates of this experiment were conducted concurrently with the homogeneous landscape experiment.

The 24-h density distributions of planthoppers for releases in a homogeneous or heterogeneous cordgrass landscape were compared to the predictions of two models of diffusion: a simple model based on the Gaussian distribution that assumes a homogeneous population of dispersers (Okubo 1980) and a more complicated model that accounts for heterogeneous rates

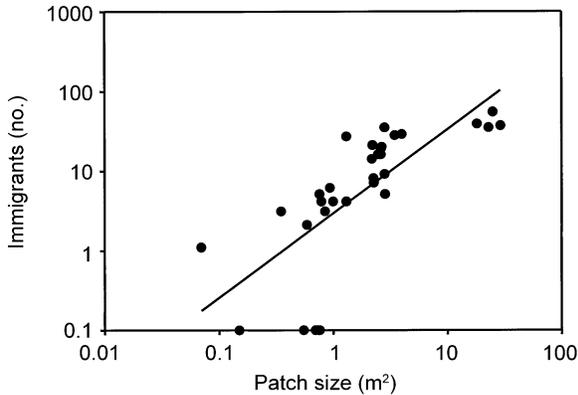


FIG. 1. The effect of patch size on the number of immigrant planthoppers (note log scale) captured in previously vacant patches (males and females combined). The line was fit by least-squares regression ($R^2 = 0.65$, $P < 0.001$).

of diffusion in the population (Cronin et al. 2000). The models, and their statistical evaluation are reported in Appendix C.

Planthopper distribution in nature

The preceding experimental studies were used to derive predictions regarding the distribution of planthoppers among cordgrass patches in a prairie landscape. These predictions were evaluated against the natural distribution of planthoppers obtained from a census spanning five generations (1999–2001) and up to 146 cordgrass patches from Site 104. For each generation, I ascertained the presence/absence and density (mean eggs/stem) of planthoppers for each patch (see Appendix D for details). I then quantified the effect of patch size, isolation, and planthopper abundance (mean eggs/stems, or presence/absence in a patch) in generation $t - 1$ on two dependent variables: planthopper egg densities and whether or not a patch was occupied by planthoppers in generation t (see Appendix D).

Asynchrony in local host dynamics is a necessary condition for long-term persistence at the metapopulation level (Levins 1970, Hanski 1991, 1999). Using the census data, I quantified the spatial synchrony in planthopper egg densities with respect to the distance between patches (Appendix D). The expectation is that spatial synchrony should be highest between patches in close proximity to one another and decrease with distance between patches. For comparison, I also examined the synchrony in population abundances from three prairie fragments that were 3.4–10.3 km apart that had been censused for adult planthoppers for eight generations (1998–2001).

RESULTS

Immigration

Seven days after the de-faunation treatment, 27 of 33 patches were recolonized by planthoppers. The ln-number of immigrants per patch increased linearly with

patch size but was unaffected by distance to the large source patch (model $R^2 = 0.623$, $P_{\text{size}} < 0.001$, $P_{\text{isolation}} = 0.64$; Fig. 1). The density of immigrants (mean number/cordgrass stem/patch) was invariant with respect to patch size (model $R^2 = 0.03$, $P = 0.68$), indicating that larger patches did not attract proportionately more planthoppers than smaller patches. Finally, males and females responded in the same way to patch geography (area: $P_{\text{male}} = 0.001$, $P_{\text{female}} < 0.001$; isolation: $P_{\text{male}} = 0.41$, $P_{\text{female}} = 0.36$).

Emigration

Planthopper density effects.—The loss of planthoppers from cordgrass patches increased significantly with increasing planthopper density ($F_{2,27} = 23.0$, $P < 0.001$; Fig. 2). At 6 h, the loss rate differed significantly among all three density treatments (based on a separate one-way ANOVA for the 6-h sampling period and Tukey's HSD pairwise comparisons tests; $P < 0.01$). For subsequent census periods, the loss rate was lowest for the low-density treatment ($P < 0.02$), but the medium- and high-density treatments were indistinguishable ($P > 0.75$). The loss rate increased with time ($F_{2,54} = 60.1$, $P < 0.001$) and there was a significant time \times density interaction ($F_{4,54} = 5.1$, $P = 0.001$). The interaction was likely due to the amelioration of the density effects over time as losses approached 100%. Finally, predators were so scarce on these patches that differences in losses among density treatments could not be attributed to predation.

Patch size.—For patches with sizes < 2.25 m², the loss rate was strongly influenced by patch size ($F_{2,11} = 25.19$, $P < 0.001$). The smallest patches had the highest loss rate, followed by the large-, and then medium-sized, patches (Tukey's hsd for all pairwise comparisons, $P \leq 0.012$; Fig. 3).

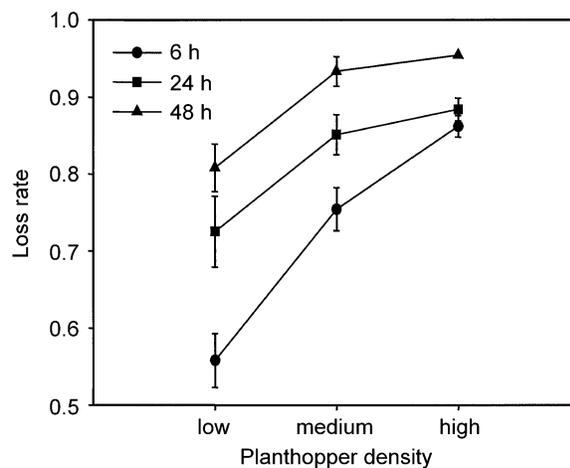


FIG. 2. The effect of female planthopper density (low = 1/stem, medium = 3/stem, and high = 10/stem) on the loss rate ($[\text{number released} - \text{number remaining at the next census}] / \text{number released}$) at 6, 24, and 48 h postrelease. Mean loss rates ± 1 SE are presented.

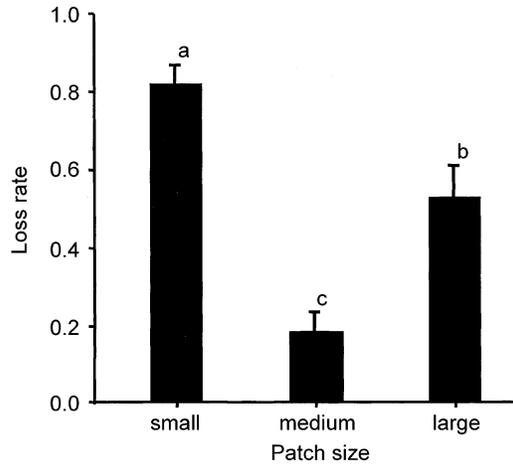


FIG. 3. The effect of patch size on female planthopper loss rates (mean ± 1 SE). Patches were divided into three categories: small, 0.21 ± 0.02 m² ($n = 10$); medium, 0.52 ± 0.06 m² ($n = 5$); and large, 1.90 ± 0.11 m² ($n = 5$). Means associated with different letters are significantly different at $P \leq 0.012$.

Within and among patch redistribution

The redistribution of female planthoppers following their release within large homogenous cordgrass patches was well described by a simple diffusion model (Appendix E, Fig. 4). Because of the very close model fit to the dispersal data ($R^2 = 0.95$), it was unnecessary to evaluate the heterogeneous diffusion model in this case. For the redistribution of planthoppers in the heterogeneous landscape (Appendix E, Fig. 4), the model fit was not quite as high ($R^2 = 0.75$). The relationship between $\ln(N_t)$ and r^2 exhibited some nonlinearity; however, in fitting the heterogeneous diffusion model to these data, I detected no significant heterogeneity in diffusion rates (95% CI for $Z_1 - Z_2$: $-84.8, 52.6$; see Appendix E). There was insufficient heterogeneity in the dispersal of planthoppers among patches to accept this model as a description of the redistribution process for these planthoppers.

Based on the simple diffusion model, I predicted that within cordgrass patches the median dispersal distance during a 24-h period was very short, <1 m on average (Appendix E). Median dispersal distances in the heterogeneous landscape were greater, averaging 2.4 m in 24 h ($t_8 = 9.85$, $P < 0.001$). Similarly, the radius encompassing 95% of the dispersing individuals was 2.5 times greater for planthoppers in the heterogeneous as compared to the homogeneous landscape (6.9 vs. 2.7 m).

Planthopper distribution in nature

For the majority of planthopper generations, planthopper densities increased significantly with increasing patch size and the density of planthoppers one generation earlier (Appendix F). Where comparisons were possible, the effect of density at $t - 1$ averaged 35%

greater than the effect of patch size on density at t (based on an evaluation of standardized coefficients). Increasing isolation caused a significant decline in planthopper densities in only the second generation of 2000. Overall, the regression model had little explanatory power: R^2 averaged 0.20 ± 0.05 among five generations.

The likelihood that a cordgrass patch was occupied by planthoppers was generally determined by the same factors that affected patch egg densities. Patch size appeared to be the most important factor: in one-half of the generations, larger patches were significantly more likely to be occupied than smaller patches (see Appendix F). Patch isolation consistently had a negative effect and the presence of planthoppers at $t - 1$ consistently had a positive effect on the frequency of patches occupied, but the trends were significant only in one generation each (Appendix F). The logistic model also had low explanatory power: ρ^2 (comparable to R^2 ; see Appendix D) averaged 0.10 ± 0.05 . Over the duration of this study, 35.2% of the island patches and all of the mainland patches continually sustained a planthopper population (based only on patches monitored for at least four generations). The proportion of generations in which the patch was occupied increased significantly with increasing patch size and decreasing isolation (Fig. 5).

Patch extinctions (planthoppers present at $t - 1$ and absent at t) occurred at a frequency of $21.1 \pm 7.3\%$ ($n = 4$), but $26.1 \pm 15.4\%$ ($n = 3$) and 51.0% ($n = 2$) of those extinct patches were recolonized one and two generations later, respectively. As patch size increased, extinction rates decreased ($\chi^2 = 9.65$, $df = 2$, $P =$

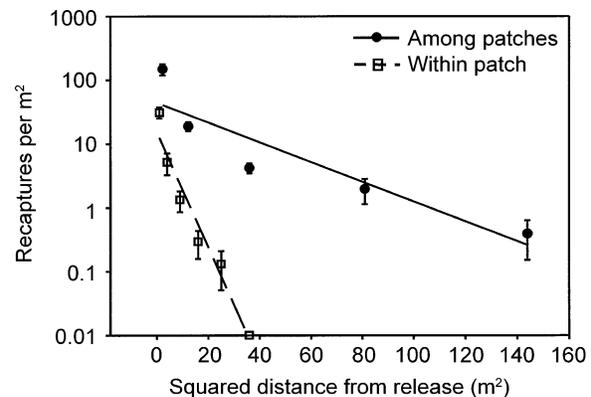


FIG. 4. Female planthopper density distributions 24 h following their release in either a homogeneous (>1 ha cordgrass patch) or heterogeneous (a collection of small discrete cordgrass patches positioned in concentric circles around a release point) landscape. Recaptures per square meter (note log scale) are reported for each landscape type (mean ± 1 SE $n = 5$). Lines are fitted by least-squares regression for all five replicates combined and represent the fit of the data to a simple Gaussian diffusion model. Homogeneous landscape: $R^2 = 0.95$, $P < 0.001$; heterogeneous landscape: $R^2 = 0.75$, $P < 0.001$.

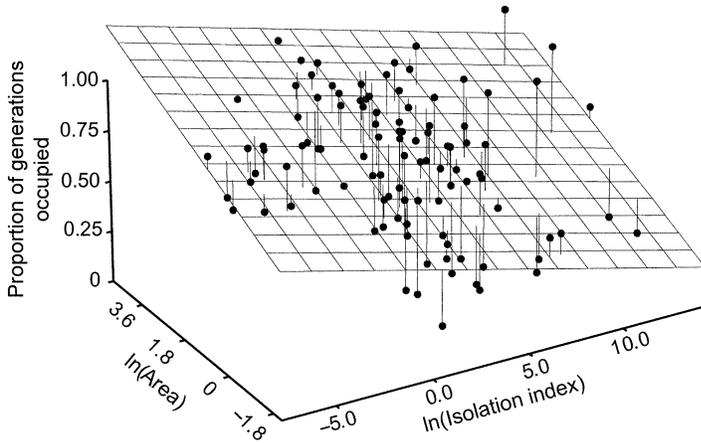


FIG. 5. The effect of patch size (area originally measured in square meters) and isolation on the proportion of generations in which the patch was occupied. Based on multiple least-squares regression, occupancy rates significantly increased with increasing patch size ($t = 5.25, P < 0.001$) and decreased with increasing patch isolation ($t = 3.74, P < 0.001$). For the overall model, $R^2 = 0.261, n = 105, P < 0.001$.

0.008) and recolonization rates increased ($\chi^2 = 7.05, df = 2, P = 0.029$) (Fig. 6A). Patch-isolation effects on turnover rates were less clear. Patches of intermediate isolation were most prone to extinction ($\chi^2 = 8.73, df = 2, P = 0.013$), and the trend toward decreasing recolonization rates with increasing isolation was not significant ($\chi^2 = 4.05, df = 2, P = 0.132$) (Fig. 6B).

The correlation in *P. crocea* egg densities between patches separated by <10 m averaged only $R = 0.26$ among four planthopper generations (Fig. 7). As the distance between patches increased, the correlation coefficient decreased significantly (least-squares regression, $R^2 = 0.76, n = 9, P = 0.002$). Overall, these results indicated that local populations within a prairie were weakly synchronous at <10 m and almost completely asynchronous at 50 m and beyond. In contrast, there was a high degree of synchrony among the three regional prairie fragments (mean $R: 0.73 \pm 0.05; n = 3$).

DISCUSSION

Planthopper movement among patches

A pervasive feature of the prairie landscape is the patchiness of cordgrass. Patches vary widely in size, but the extent of their isolation is relatively small (<50 m). Small patches not only had a higher rate of emigration loss but also received fewer immigrants than

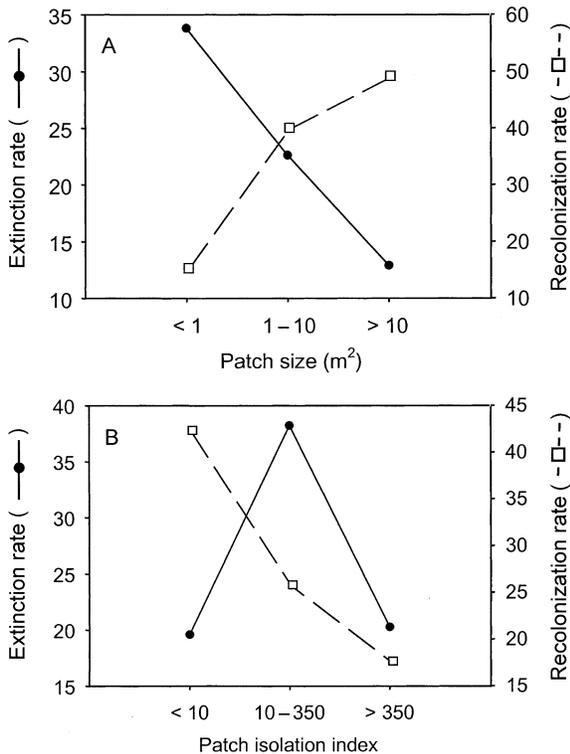


FIG. 6. Per-generation turnover rates among cordgrass patches with respect to (A) patch size and (B) patch isolation. Extinction rate was the percentage of patches occupied in generation $t - 1$ that were vacant at generation t , and recolonization rate was the percentage of patches that were vacant at $t - 1$ and occupied at t . Percentages were based on the five planthopper generations combined.

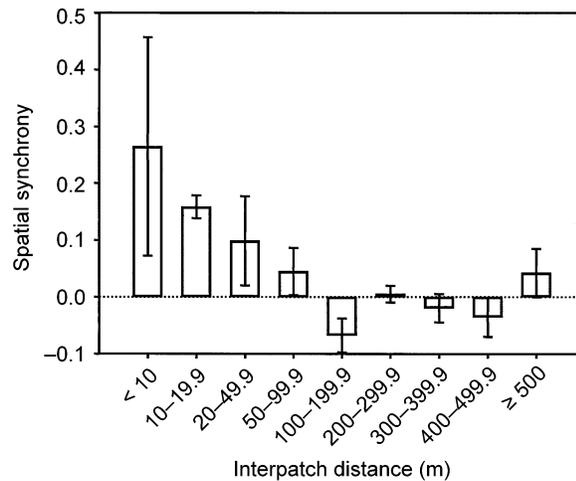


FIG. 7. Strength of spatial synchrony (correlation coefficient) in *P. crocea* egg densities among cordgrass patches within a distance category. The mean ± 1 SE from four generations are reported.

large patches. This suggests that small patches may be too easy to lose and too hard to find to sustain a viable planthopper population (e.g., MacGarvin 1982, Karieva 1985). Interestingly, the relationship between patch size and emigration was nonlinear: medium-sized patches had a loss rate that was significantly lower than the rate for small or large patches. One possible explanation for this pattern is that as these monoclonal cordgrass patches mature and enlarge, their nutritional quality may decline or their resistance to herbivory may increase (e.g., Hanzawa and Kalisz 1993, Kearsley and Whitham 1998), thus favoring higher rates of emigration.

Emigration from a cordgrass patch also increased linearly with planthopper density. In my field sites, planthopper patch densities varied by more than three orders of magnitude (*unpublished data*), suggesting that this density-dependent process will have a strong impact on planthopper movement. As with other insect species that exhibit density-dependent emigration (e.g., Herzig 1995, Kratz 1996), this process is predicted to homogenize the planthopper's density distribution among host patches (promote spatial synchrony) and increase the frequency of occupied patches (Sæther et al. 1999). Furthermore, patch size is expected to strongly influence this density-dependent process because not only do larger patches have higher densities than smaller patches (Appendix F), but also emigration is a complex function of patch size (Fig. 3). The latter effect may vitiate a homogeneous density distribution.

In spite of the expectations of biogeographic theory and existing empirical data (Hanski 1999: Table 9.1), planthopper immigration did not decline with increasing isolation. The lack of an isolation effect, however, was contrary to the results from my diffusion study that indicated an exponential decay in recaptures over a range of just 12 m. This contradiction may be explained by the difference in the duration of the two studies, 24 h in the diffusion study and 7 d in the immigration study. Complete remixing of planthoppers may have taken place in seven days time, whereas a shorter time scale may have revealed isolation effects on immigration. Relatively high connectivity among cordgrass patches is likely promoted by high macropredation rates in this species (>90%; *unpublished data*); the expected consequences of which are increased spatial synchrony among patches and reduced persistence of the population at the regional scale (Reeve 1988, Allen et al. 1993, Hanski 1999).

Finally, I found strong evidence to suggest that the rate and pattern of spatial spread differed for planthoppers moving within or among cordgrass patches. Planthopper redistribution within pure cordgrass was well described by a simple diffusive process, but in a heterogeneous habitat composed of host and nonhost vegetation there was evidence of a higher-than-expected number of recaptures at long distances (leptokurtosis). Leptokurtosis, commonly found in the dis-

persal curves of a number of insect species (Karieva 1983, Cronin et al. 2000), was likely the underlying explanation for the 2.5 times greater rate of spatial spread among, than within, cordgrass patches. Few other studies have reported landscape dependent rates of spatial spread (but see Crist et al. 1992, Hannunen and Ekbom 2001). Recently, Vandermeer and Carvajal (2001) demonstrated that different dispersal rates (owing to matrix heterogeneity) can have fundamentally different effects on metapopulation persistence.

Additional factors thought to affect herbivore dispersal include the presence of predators (e.g., Lima and Dill 1989, Kratz 1996), heterogeneity in matrix composition (e.g., Roland et al. 2000, Ricketts 2001), and plant quality (e.g., Thomas and Singer 1987, Denno and Roderick 1992). Studies in my laboratory have revealed that high densities of arthropod predators in patches favor high planthopper emigration rates (*unpublished data*), and that denser and taller matrix vegetation types favor both high rates of emigration and immigration (K. J. Haynes and J. T. Cronin, *unpublished manuscript*). Neither of these factors is as important as planthopper density and patch size in influencing planthopper dispersal. The effect of plant quality on planthopper movement is currently under investigation, but as mentioned above, may play a significant role in the relationship between patch size and emigration.

Planthopper distribution in space

The above conclusions lead to the following predictions regarding the natural distribution of planthoppers. Because large patches receive more immigrants and lose fewer individuals to emigration, large patches are expected to support large planthopper populations and have a low probability of extinction. Small patches, with high emigration rates and low immigration rates, should exhibit the opposite pattern. Finally, patch isolation is expected to have little effect on patch population size.

The majority of these spatial predictions were upheld. Planthopper occurrence or density in a patch in the previous generation was the most important determinant of present-day planthopper abundances. After factoring out this temporal correlation in abundances, planthopper distributions were also found to be significantly influenced by patch size. Large patches tended to have greater planthopper densities and were more likely to be occupied than small patches. The smallest 25% of the patches ($\leq 0.87 \text{ m}^2$) were 2.5 times less likely to be occupied than the largest 25% of the patches ($\geq 7.25 \text{ m}^2$). These small patches are at such risk to extinction that they may never sustain a population for more than a few generations; i.e., they represent population sinks (e.g., Berggren et al. 2001). In contrast, the large mainland patches never went extinct during this study. Isolation effects on density were scarce within generations, but were evident in the analysis of

patch occupancies compiled for the duration of the study. The greater spatial scale of the census as compared to the immigration experiment (630 m vs. 45 m, respectively) may explain the occurrence of an isolation effect in the former and not the latter study. Overall, patch geography explained 26% of the variation in planthopper spatial distributions (see Fig. 5). Accounting for matrix heterogeneity and the presence of predators almost doubled the explanatory power of this model (K. J. Haynes and J. T. Cronin, *unpublished manuscript*). Other landscape-level studies have also revealed the myriad factors, in addition to geographic variables, that influence the spatial distribution of species; excellent examples include the Glanville fritillary (reviewed in Hanski 1999), bush crickets (Kindvall 1996, Kindvall et al. 1998, Berggren et al. 2001), and whirligig beetles (Svensson 1998, 1999).

Spatial population structure

Dispersal experiments and census data combine to provide a very powerful approach with which to characterize the spatial structure of a population (see Hanski 1999 for examples). The structure of a subdivided population falls along a continuum in terms of patch structure and dispersal ability, ranging from independent subpopulations with low interpatch dispersal to an ensemble of subpopulations connected by high rates of migration (Harrison and Taylor 1997, Thomas and Kunin 1999). Metapopulations fall near the middle of this continuum and represent a frame of reference for evaluating the spatial structure of the *P. crocea* population. Hanski (1999) identified four conditions that define a true metapopulation. The first condition is that local patches must be able to support discrete breeding populations of *P. crocea*. This appears to be true because a planthopper population can be sustained for at least seven generations on cordgrass patches in isolation (*unpublished data*).

The second condition for metapopulation structure is that all patch populations have a high risk of extinction. My census revealed that an average of 21% of the cordgrass patches went extinct each generation. The cause for extinction could not be determined from this study, but does not appear to be due to high rates of parasitism or resource depletion (Cronin 2003a). The extinction rate declined significantly with increasing patch size, and was zero for the large mainland patches. Finally, although most spatially explicit population models assume that extinction rates are independent of isolation (Hanski 1999), I found the highest rates for patches of intermediate isolation. I do not yet know the cause for this unusual pattern, but it is currently under investigation. Overall, these patterns of extinction suggest a mainland-island population structure (see also Harrison 1991, Berendonk and Bonsall 2002).

Recolonization of patches following an extinction event is the third condition of a metapopulation. Of the cordgrass patches that went extinct in a given plant-

hopper generation, one-fourth were recolonized one generation later and one-half were recolonized within two generations. Per-generation recolonization rates increased with patch size and tended to decrease with patch isolation. On average, recolonization and extinction rates were roughly equivalent (26% vs. 21%), and were within the range of the rates found in other studies (e.g., Harrison et al. 1988, Hanski et al. 1995). The patterns of recolonization and extinction fit within the rubric of metapopulation theory (Hanski 1999).

The final condition is that local patch dynamics should be sufficiently asynchronous that wholesale regional extinction is unlikely. Local populations of *P. crocea* were quite uncorrelated in space, even at close distances (<10 m). Asynchronous spatial dynamics among cordgrass patches occurs despite high and density-dependent emigration rates. Among regions, planthopper populations were much more synchronous (mean $R = 0.74$). Given an isolation of ≥ 3.4 km, it is unlikely that synchrony is brought about by high rates of dispersal among regions. Demographic stochasticity in small local populations may favor a weak correlation among neighboring patches within a prairie, whereas the averaging of planthopper densities across a broader scale (sweep samples were taken from a much larger area) may mitigate these effects (Thomas and Hanski 1997). The large-scale spatial synchrony among regions is likely attributed to spatially correlated weather conditions (see Hanski and Woiwod 1993, Thomas and Hanski 1997). Although there is no general criterion for the level of asynchrony necessary for long-term metapopulation persistence, the very low correlations in densities among patches suggests that at this scale, this system meets the criterion of spatial asynchrony.

In conclusion, these data suggest that the structure of the planthopper population is of the island-mainland form (see also Harrison 1991, Berendonk and Bonsall 2002), although it does not fit perfectly within this construct because movement among patches is high. I would concur with Harrison and Taylor (1997) and Thomas and Kunin (1999) that a classical (Levins) metapopulation structure is generally the exception rather than the rule for fragmented populations, and that a broad array of structures is possible. For *P. crocea*, I would anticipate that mainland dynamics likely dominate the system (e.g., Harrison et al. 1988, Harrison 1991, Hanski 1999): the largest 5% of the patches account for a total of 89% of all the cordgrass habitat in Site 104. The contribution from small patches is further trivialized by the tendency of planthoppers to be underrepresented in those patches (i.e., densities are lower in small as compared to large patches). Given the spatial structure of this population, island extinctions and recolonizations may not be as important to population persistence as are the processes taking place within the mainland patches (Harrison and Taylor 1997). On the other hand, the spatial spread of *P. crocea* is likely to be strongly dependent upon population

turnover in these island patches. This study underscores the importance of characterizing the movement and spatial structure of populations as a principal step in evaluating the contribution of regional, relative to local, processes in affecting the persistence of subdivided populations (see also Clinchy et al. 2002).

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APPENDIX A

The distribution of sizes for all cordgrass patches located within Site 104 is presented in ESA's Electronic Data Archive: *Ecological Archives* E084-026-A1.

APPENDIX B

Evidence that fluorescent powders do not adversely affect planthopper survivorship or dispersal ability is available in ESA's Electronic Data Archive: *Ecological Archives* E084-026-A2.

APPENDIX C

A description of a simple and heterogeneous diffusion model used to predict planthopper redistribution in space is provided in ESA's Electronic Data Archive: *Ecological Archives* E084-026-A3.

APPENDIX D

The census procedure and analyses of planthopper distributions in nature are provided in ESA's Electronic Data Archive: *Ecological Archives* E084-026-A4.

APPENDIX E

The fit of a simple Gaussian diffusion model to the redistribution of female planthoppers in a homogeneous or heterogeneous landscape is provided in ESA's Electronic Data Archive: *Ecological Archives* E084-026-A5.

APPENDIX F

A table of statistical tests for the effect of patch size, isolation, and planthopper abundance on planthopper distributions over five generations is provided in ESA's Electronic Data Archive: *Ecological Archives* E084-026-A6.