

SPIDER EFFECTS ON PLANTHOPPER MORTALITY, DISPERSAL, AND SPATIAL POPULATION DYNAMICS

JAMES T. CRONIN,¹ KYLE J. HAYNES, AND FORREST DILLEMUTH

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

Abstract. Nonlethal (trait-mediated) effects of predators on prey populations, particularly with regard to prey dispersal, scarcely have been considered in spatial ecological studies. In this study, we report on the effects of spider predators on the mortality, dispersal, and spatial population dynamics of *Prokelisia crocea* planthoppers (Hemiptera: Delphacidae) in a prairie landscape. Based on a three-generation survey of host-plant patches (*Spartina pectinata*; Poaceae), the density of cursorial and web-building spiders declined significantly with increasing patch size (a pattern the opposite of that for the planthopper). Independent of patch size effects, an increase in the density of web-building and cursorial spiders had a negative effect on planthopper density in one of three generations each. Finally, the likelihood of extinction of local (patch) populations of planthoppers increased significantly with an increase in the density of web-building spiders. Planthoppers in small host-plant patches with high densities of web-building spiders were especially at risk of extinction. To evaluate whether spider effects on planthopper spatial dynamics were mediated by predation and/or spider-induced dispersal, we performed a field experiment in which host-plant patches were either caged or left open and received one of three spider density treatments (removal, ambient levels, or high = triple ambient levels). For the caged patches, there was a nonsignificant decline in planthopper recaptures with increasing spider density, suggesting that mortality effects of spiders on planthoppers were weak. In contrast, planthopper recaptures in open patches declined by 85% between the removal and high spider treatments. This significant decline was mostly attributed to spider-induced emigration. We conclude that, at high spider densities, spiders are likely to have a greater impact on planthopper densities through induced emigration than consumption. Because small cordgrass patches support high spider densities and favor high planthopper emigration rates, the nonlethal effects of spiders may play a very important role in determining critical patch size, source–sink properties of cordgrass patches, and the spatial distribution and spread of planthoppers.

Key words: dispersal; emigration; extinction; metapopulation; patch dynamics; planthoppers; *Prokelisia*; source–sink; *Spartina pectinata*; spatial distribution; tall-grass prairie; trait-mediated effects.

INTRODUCTION

Over the past several decades, theoretical models have provided a causal link between spatial subdivision and the stability of predator–prey interactions (reviewed in Hanski and Gilpin 1997, Tilman and Kareiva 1997, Hanski 1999, Hassell 2000). In these models, the possibility of coexistence was often strongly influenced by predator and prey dispersal abilities (e.g., Hastings 1977, Crowley 1981, McCauley et al. 1996). In one of the very few empirical evaluations of the effect of spatial subdivision on predator–prey dynamics, Amezcuca and Holyoak (2000) found that the persistence time of a ciliated protozoan prey and its heliozoan protist predator was substantially longer in a spatially subdivided, as compared to undivided, laboratory microcosm. Longer persistence times in the subdivided habitat were

attributed to, among other things, higher rates of dispersal of the prey than predator (promoting prey rescue effects).

Spatial studies of predator–prey interactions have focused only on the direct lethal (mortality) effects of predators on prey populations. Recent studies, however, have suggested that predators can also have important nonlethal (trait-mediated) effects on prey dispersal ability (for recent reviews of trait-mediated effects see Bolker et al. 2003, Dill et al. 2003, Werner and Peacor 2003). For example, increased predation risk can elicit the production of wings (Dixon and Agarwala 1999) or increase emigration rates of prey (e.g., Sih et al. 1992, Peckarsky 1996, Hakkalainen et al. 2001). Given the direct connection between dispersal rates and predator–prey stability, the impact of nonlethal predator effects potentially may be very significant. Predator density may strongly influence prey connectivity among patches if the effects of predation risk on emigration are not trivial relative to the effects of predation on prey mortality. Furthermore, emigra-

Manuscript received 5 September 2003; revised 1 December 2003; accepted 20 January 2004. Corresponding Editor: D. A. Spiller.

¹ E-mail: jcronin@lsu.edu

tion in response to predation risk may vary with features of the landscape (e.g., patch size, isolation, or the composition of the surrounding habitat [or matrix]) if predator distributions (and risk of predation) are landscape dependent.

The planthopper, *Prokelisia crocea* (Hemiptera: Delphacidae), is known to exhibit a mainland–island metapopulation structure in tall grass prairie landscapes (Cronin 2003a), but to date, nothing is known about the impact of generalist spider predators on their mortality, movement, and spatial population dynamics. Based on census data spanning three planthopper generations, we determined whether the among-patch distributions of three spider guilds (cursorial, sit-and-wait, or web-building spiders) were related to characteristics of host-plant patches (patch size, isolation, and matrix composition). We also assessed whether planthopper patch density or likelihood of extinction was related to spider guild density and patch characteristics. Finally, we performed a field experiment to quantify the effects of spider predators on the mortality and emigration of their planthopper prey. Spiders were released at three different densities onto planthopper-infested patches that were either caged (preventing both natural and predator-induced emigration from occurring) or open (allowing for both prey consumption and dispersal). Results from this study are used to reevaluate the mechanisms underlying the spatial population structure of *P. crocea* in light of its relationship with these abundant generalist predators.

METHODS

Life history

Prairie cordgrass, *Spartina pectinata* (Poaceae), is a common native plant species of hydric grasslands of North America (Hitchcock 1963). Reproduction in cordgrass is primarily via rhizomatous growth, which results in the formation of clonal patches of highly variable size (Cronin 2003a). The dominant herbivore of cordgrass is the specialist delphacid planthopper, *P. crocea* (Holder and Wilson 1992, Cronin 2003a, b, c). Planthoppers overwinter as first-instar nymphs, pass through five instars in the spring, and then mature into adults in early mid-June. *Prokelisia crocea* undergoes two distinct generations per year in the northern Great Plains (Cronin 2003a, b, c); the second generation of adults reach a peak in early August. Although adults are wing-dimorphic, >90% of the females and males are macropterous (Cronin 2003a).

The suite of natural enemies that attack *P. crocea* is typical of most other delphacids (Cronin and Strong 1994, Döbel and Denno 1994). In addition to egg parasitism by *Anagrus columbi* (Hymenoptera: Mymaridae) and nymphal–adult parasitism by an undescribed dryinid (Hymenoptera: Dryinidae), *P. crocea* is attacked by a large number of arthropod predators, particularly spiders (Cronin 2003b, c; J. T. Cronin, un-

published data). While no studies have previously reported information on spider mortality within this system, high rates of mortality have been reported for an analogous system in salt-marsh cordgrass (*S. alterniflora*) fed upon by *P. marginata* and *P. dolus* (e.g., Döbel and Denno 1994, Denno et al. 2002, Finke and Denno 2002).

Among-patch distribution of spiders and planthoppers

In a census program initiated in 1999, we have been monitoring planthopper and parasitoid (*A. columbi*) population abundances among 147 cordgrass patches within a single prairie fragment, Site 104 (Cronin 2003a, c). Site 104 is located adjacent to the Kelly's Slough National Wildlife Refuge 16 km west of Grand Forks, North Dakota, USA. For three generations (generations I and II in 2001, and generation I in 2002) we included the collection of spiders in the survey. The size (square meters), isolation, and the composition of the matrix surrounding each patch was quantified in the middle of the summer of each year (see Cronin 2003a, c for details). Patch isolation (*I*) was determined from the linear distance to, and size of, the nearest neighboring patch in each of four quadrats (NE, NW, SE, and SW). Larger values of *I* indicated greater patch isolation. The matrix was characterized as the proportion of a 3-m buffer surrounding the patch that was composed of mudflat. Emigration and immigration of *P. crocea* are significantly reduced when the matrix is composed of mudflat (Haynes and Cronin 2003).

During peak adult planthopper activity in each of the three generations, D-Vac samples (Rincon-Vitova, Ventura, California, USA; 5 s/sample using a 0.08-m² sampling head) were taken from each patch. The number of samples increased in proportion to patch size. For each patch, *P. crocea* adults were counted and spiders were identified to family. Because there were insufficient numbers for any one species to perform statistical analyses, spiders were pooled into foraging guilds as either sit-and-wait (Philodromidae and Thomisidae), web-building (Araneidae, Dictynidae, Linyphiidae, Tetragnathidae, and Theridiidae), or cursorial (Clubionidae, Salticidae, and Lycosidae [primarily *Pardosa modica*]) predators. Planthopper and spider counts were converted to densities (number/square-meter), and cordgrass stem densities were determined as described by Cronin (2003a).

From these census data, we addressed the following four questions. First, within each of the three census periods, did the three spider guilds differ in density per cordgrass patch? Second, did the densities of each spider guild vary with the landscape variables patch size, patch isolation, and the composition of the matrix surrounding a patch? Third, was planthopper density per patch significantly influenced by spiders (each guild as a separate variable), three landscape variables, and planthopper density in the previous generation? Final-

ly, was the likelihood of a planthopper extinction influenced by spider density (each guild as a separate variable), planthopper density, and the three landscape variables? Statistical procedures used to address these questions are described in Appendix A.

Spider impact experiment

In this field experiment, we quantified the effects of spiders on planthopper emigration and mortality over a 48-h period within discrete cordgrass patches. This study was conducted in two sites, Site 104 and Limehouse (1 km northeast of Site 104). For this study, we selected 48 circular cordgrass patches that were comparable in size ($0.26 \pm 0.014 \text{ m}^2$ [mean \pm 1 SE], range: 0.11–0.51 m^2) and at least 3 m from any neighboring cordgrass. Patches of this size and smaller constitute 12% of the cordgrass patches in these field sites. For each patch, we counted the total number of cordgrass stems (≥ 3 cm tall).

Planthoppers and all other arthropods were initially removed from each patch, and a 1-m buffer surrounding the patch, through repeated vacuuming with a D-Vac (Cronin 2003a). Arthropod-free patches were assigned to two fully crossed treatments: a caging treatment (cage, no cage) and a spider density treatment (removal, ambient levels, and high = triple ambient levels). Cages were constructed of a polyvinylchloride frame (0.5 m on a side and 1 m tall) and enclosed by mosquito netting. Given the short-term duration of this study, caging effects on arthropod survivorship were expected to be unimportant.

Prior to the application of the spider treatment, all patches were stocked at a constant density of two planthopper adult females per cordgrass stem. Planthoppers were collected with a sweep net from nearby cordgrass habitat and immediately transported on ice to the experimental patches. Within 10 minutes of their release, the planthoppers settled and began feeding on the phloem of cordgrass (Haynes and Cronin 2003). Male planthoppers were not included in the study because they were scarce relative to females and are less important to the spatial spread of the species (Cronin 2003a). The lack of males in experimental patches likely did not bias female movement patterns because mate searching is primarily a male trait in planthopper species (Langelotto and Denno 2001). This release density was moderate based on a four-year census of planthoppers among cordgrass patches (Cronin 2003a).

Thirty minutes after planthoppers were released, the spider treatment was implemented. Spiders were collected from nearby cordgrass patches (similar in size to the experimental patches) using a D-Vac with a 0.08- m^2 sampling head. For the ambient spider density treatment, the D-Vac head was placed at four points for 5 s each; the total area vacuumed was approximately equal to the size of the experimental patches. D-Vac samples were field sorted to eliminate vegetation, *P. crocea*, and all other non spider arthropods (on average,

≤ 12 nonspiders [≥ 1 mm total length] remained following this procedure; J. T. Cronin, unpublished data), and then the spiders were carefully released into the patches. The high spider treatment consisted of spiders obtained from three times the collection area of the ambient spider treatment (12 D-Vac samples). The experiment ran for 48 h, after which time, the contents of the patch were thoroughly vacuumed and the arthropods returned to the laboratory.

To confirm that the spider treatments effectively altered spider abundances at the beginning of the experiment, we applied the spider treatments to an additional 15 small, uncaged cordgrass patches (five replicates per treatment; designated “baseline density patches”). After 30 min, the baseline patches were D-Vacced as above and the spiders collected. For each experimental and baseline patch, the numbers of *P. crocea* adults and spiders (separated into three foraging guilds) were counted and converted to a density (numbers/square meter/patch).

Planthopper emigration from open cordgrass patches could have been exacerbated by the disturbance associated with the release and subsequent settlement of spiders. To evaluate whether this possibility was true, we visually counted all planthoppers in open cordgrass patches 30 min after their release and immediately prior to the release of spiders. Planthoppers also were recounted at 1 h and 8 h after release. A significant decline in planthopper counts between 30 min and 1 h would indicate a strong effect of the spider release on planthopper emigration (see Appendix A for description of the statistical analysis).

For each spider guild, an ANOVA test was used to determine whether the spider treatments (removal, ambient, and high) were effective in altering spider densities (numbers per square meter) 30 min after their release into the patches. The effects of spider treatment and caging (fixed main effects) on either the percentage of planthoppers recaptured (number recaptured/number released) or spider density (each guild treated separately) 48 h later were determined with ANOVA (see Appendix A). In this experiment, a decrease in planthopper recaptures with an increase in spider density can be attributed to predation alone in the caged patches and a combination of predation and predator-induced emigration (nonlethal effect) in the open patches. (Note that because planthopper densities were initially equal across the spider density treatments, a change in the percentage of planthoppers recaptured with increasing spider density in uncaged patches is likely attributable only to the overall negative effects of spider predators.) By subtracting the mean percentage of planthoppers recaptured in uncaged patches from caged patches (within each spider density treatment), we obtain an estimate of the mean percentage of planthoppers that emigrated from the patch (owing to both intrinsic and spider-induced emigration). If the difference in planthopper recaptures between the caged and uncaged

patches increases with spider density, this would indicate that planthopper emigration is spider dependent. Additional detail regarding these statistical analyses is presented in Appendix A.

RESULTS

Among-patch distribution of spiders and planthoppers

Based on our survey, web-building spiders were numerically the most dominant, averaging 45.1 ± 21.0 individuals/m² (mean \pm 1 SE, $n = 3$; mean of generation means). Cursorial spiders were second in abundance (16.9 ± 4.4 individuals/m²), followed by sit-and-wait spiders (10.3 ± 2.2 individuals/m²). The dominance of web builders was largely caused by the observed patterns of abundance in the first generation surveyed (2001-I): the density per patch of web builders was significantly higher than either the density of cursorial or sit-and-wait spiders (based on separate paired t tests and Bonferroni-corrected P values; $P < 0.001$; Appendix B).

Of the three landscape features, only patch size significantly influenced the distribution of spider predators. For cursorial and web-building spiders, densities declined significantly with increasing patch size (Fig. 1; statistics in Appendix C). Patch size explained 22% and 20% of the among-patch variation in densities of these two guilds, respectively. For each spider guild, density within a patch varied significantly among generations ($P \leq 0.011$ for all tests; Appendix C). However, densities per patch of the same guild were not well correlated between generations ($R < 0.30$ for all comparisons).

For all three generations, planthopper density significantly increased with patch size and the proportion of the matrix that was mudflat ($P \leq 0.036$ for all tests; Appendix D). The effect of patch size on planthoppers is the opposite of that for the spiders; consequently, spiders and planthoppers tended to be negatively correlated (Appendix E). Independent of patch size, an increase in the density of web-building and cursorial spiders had a negative effect on planthopper density in one of three generations each (web builders in 2001-II: $P = 0.017$; cursorial spiders in 2002-I: $P = 0.020$; Appendix D). However, based on a comparison of standardized regression coefficients, the effect of spiders was 4.2 and 2.2 times less than the effect of patch size on planthopper densities in those years, respectively. Spider and matrix effects on planthopper density were approximately equal.

Planthopper populations in cordgrass patches went extinct at a rate of $18.5 \pm 2.9\%$ /generation. The likelihood of extinction increased with an increase in the abundance of all three spider guilds, but only for the web-building spiders was this effect significant ($P = 0.002$; Appendix F). On average, patches in which local planthopper populations went extinct had 51.9 ± 10.0

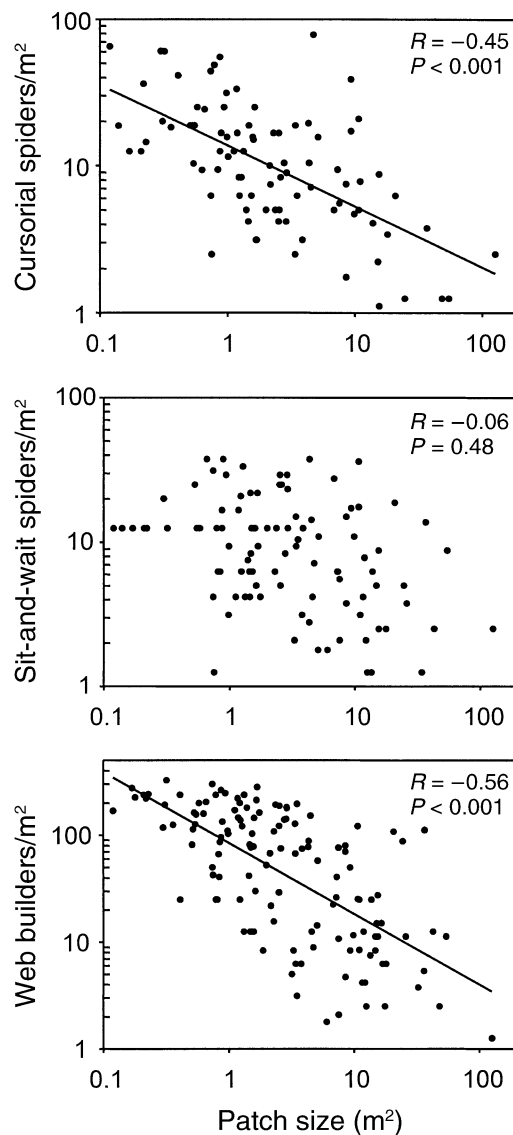


FIG. 1. The relationship between patch size (m²) and the density of spiders (no./m²) from three different foraging guilds (log-log plot). Data are presented for only one representative generation (2001-I). For significant correlations ($P \leq 0.05$), a least-squares regression line is presented.

vs. only 32.0 ± 3.2 web builders/m²; a 38% difference in density. Planthopper extinctions were also significantly more frequent in smaller and less isolated patches and there was a significant web builder \times patch size interaction ($P = 0.013$; Appendix F). The significant interaction likely derived from the very high extinction rate for small patches with high web builder densities relative to all other combinations of these variables (Fig. 2).

Spider impact experiment

Thirty minutes after spider manipulations were implemented, we found significant differences among spi-

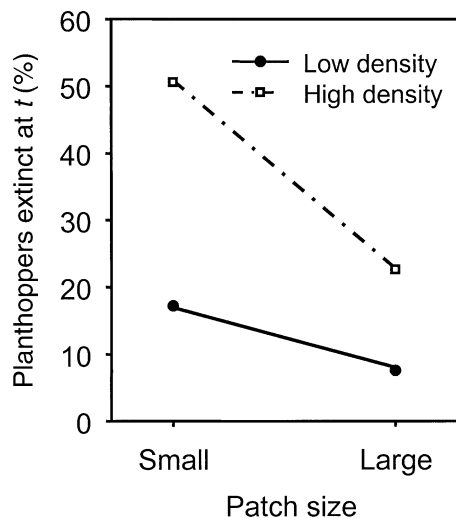


FIG. 2. The percentage of local planthopper populations that went extinct during the three-generation census period with respect to patch size and web-building spider density. The median size of patches and density of web builders served as the dividing point between small and large patches and between low and high densities of web builders, respectively.

der treatments for all spider guilds (separate one-way ANOVAs for each guild; all comparisons, $P < 0.001$; see Appendix B). On average, densities in the spider removal patches were 79% lower than in the ambient-spider patches, and the ambient-spider patches were 58% lower than the high-spider patches. Comparably sized cordgrass patches from the Site 104 survey (i.e., those $\leq 0.51 \text{ m}^2$) had total spider densities that were 16% higher than in the ambient-spider treatment, but the difference was not significant (based on patches from all three generations combined; $t_{36} = 1.46$, $P = 0.076$; Appendix B). At the end of the study (48 h), distinctions among spider-density treatments were still evident. For cursorial spiders, web builders, and all spiders combined, densities were significantly lower in the spider removal patches than the high-spider patches (separate mixed-model ANCOVAs, $P \leq 0.039$). However, there were no significant differences in densities of sit-and-wait spiders among spider treatments ($F_{2,31} = 2.04$, $P = 0.195$). Densities from the start to the end of the experiment (48 h) declined by an estimated 9.1% for cursorial spiders, 25.0% for sit-and-wait spiders, 27.3% for web builders, and 22.1% for all spiders combined (based on a comparison between baseline-ambient density and uncaged-ambient density patches). Because there was no significant difference in densities between caged and uncaged patches at the end of the experiment for all three spider guilds ($P \geq 0.55$), these losses cannot be attributed to emigration from patches.

Spider densities in the high spider treatment were within the range of densities found in our three-generation survey of spiders in natural patches. Based on the midpoint between the initial (estimated indepen-

dently from the baseline density patches) and final spider densities 48 h later, there was an estimated total of 479.4 ± 52.7 spiders/ m^2 /patch in the high spider treatment. Of the natural patches that were comparable in size to our experimental patches ($n = 33$), 21% had total spider densities equal to or greater than those in the high experimental treatment (Appendix B).

The release of spiders onto experimental cordgrass patches did not result in an immediate emigratory response by planthoppers. Based on the uncaged cordgrass patches, planthopper populations declined to an average of 83% of their initial release numbers after 30 min (Fig. 3). Planthopper populations further declined by only 4% during the first half hour after spiders were released into those patches. The change in density between these two time periods was statistically insignificant (repeated-measures ANOVA, $F_{1,21} = 3.35$, $P = 0.081$) and independent of spider release density ($F_{2,21} = 1.55$, $P = 0.235$). Only after 8 h was there evidence for an effect of spider treatment on planthopper losses per patch, and it was only between the removal and high spider treatments (Tukey's hsd, $P = 0.007$). We note here that 30 min after their release, the sit-and-wait and web-building spiders were quite sedentary, whereas the cursorial spiders were exhibiting movement behaviors associated with prey search (based on 10-min observations of each experimental patch).

After 48 h, the percentage of released planthoppers that were recaptured in the experimental cordgrass patches was strongly affected by both the spider and caging treatments (Fig. 4; statistics in legend). Planthopper densities were on average 1.5–6.9 times higher on caged than uncaged patches, and decreased significantly with increasing spider density. Among spider density treatments, all pairwise comparisons were sig-

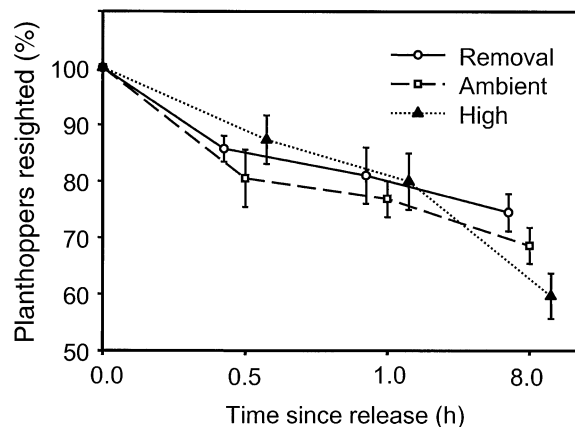


FIG. 3. The percentage of planthoppers in uncaged experimental patches that were visually detected at 0.5, 1.0, and 8.0 h after release. Percentage means ($\pm 1 \text{ SE}$) are reported for each spider treatment (removal, ambient, and high density). Spiders were added to the patches immediately after the counts at 0.5 h.

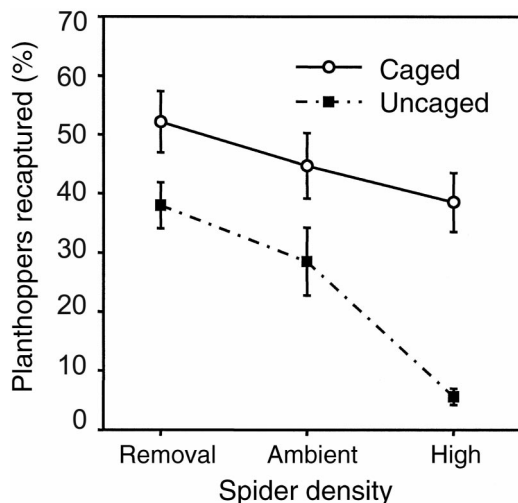


FIG. 4. The percentage of released planthoppers (± 1 SE) that were recaptured 48 h later with respect to spider and caging treatments. Based on a mixed-model ANCOVA, spider treatment ($F_{2,33} = 15.36$, $P < 0.001$), caging ($F_{1,33} = 40.59$, $P < 0.001$), and spider \times caging interaction ($F_{2,33} = 4.98$, $P = 0.013$) significantly affected recapture rates. Patch size (covariate) and release date (block effect) did not significantly influence planthopper recaptures (patch size, $F_{1,33} = 0.02$, $P = 0.880$; release date, $F_{7,33} = 2.16$, $P = 0.065$).

nificantly different (Tukey's hsd, $P < 0.001$) except between the removal and ambient density treatments ($P < 0.122$). There was also a significant nonadditive effect of caging and spider density treatments on planthopper recaptures (Fig. 4): the caging effect became significantly more pronounced with an increase in spider density. Most notably, there was a very small percentage of planthoppers recaptured in open patches that had high spider densities.

In the caged patches (planthopper emigration excluded), there was a gradual, but nonsignificant decline in planthopper recaptures as spider density increased (Fig. 4; one-way ANOVA; $F_{2,19} = 1.80$, $P = 0.193$), suggesting that mortality effects on planthopper abundance were of minor importance during this two-day experiment. In contrast, there was a significant decline in the percentage recaptured as spider density increased in the open patches ($F_{2,19} = 34.74$, $P < 0.001$). The effect was due primarily to the difference between the high-spider patches and the ambient and removal spider patches (Tukey's hsd, $P < 0.001$). The mean difference in planthopper recaptures between the caged and uncaged patches (i.e., the total percentage of planthoppers emigrating) increased significantly with spider density (based on a comparison of 95% CIs about the means for the removal and high spider treatment patches), suggesting that planthopper emigration increased with spider density (Fig. 5).

DISCUSSION

Predatory and nonlethal effects of spiders

Predatory arachnids are an abundant and integral component of many terrestrial food webs (e.g., Döbel

and Denno 1994, Spiller and Schoener 1994, Schmitz 1998, 2003, Snyder and Wise 2001) and have been shown to contribute significantly to the suppression of pests in agroecosystems (e.g., Agnew and Smith 1989, Riechert and Bishop 1990, Lang 2003). In prairie cordgrass patches, spiders averaged >70 individuals/m², but densities varied considerably in time and in space.

Our study suggests that a change in spider abundance has a greater nonlethal (trait-mediated) than predatory (direct-mortality) effect on the abundance of planthoppers among host-plant patches. Within caged patches, there was no evidence of a significant decline in planthopper recaptures with increasing spider density, suggesting that mortality effects of spiders on planthoppers were weak. In comparison, planthopper recaptures in open patches declined by 85% between the removal and high spider treatments. We attribute much of this steep, significant decline to predator-induced planthopper emigration, a nonlethal effect (at least in the short term; Fig. 4). Spider-induced planthopper emigration was density dependent, but an increase in the rate of emigration (in this case by twofold), was only evident in the treatment with high spider densities: ~ 500 total spiders/m² (Fig. 5). Such high densities of spiders do occur in nature, but are generally restricted to the numerous small cordgrass patches. We conclude that at high spider densities, spiders are likely to have a greater impact on the rate of planthopper loss (on a per-day basis) due to emigration than predator consumption. Whether spider-induced emigration by the planthoppers occurred in response to the perceived risk of pre-

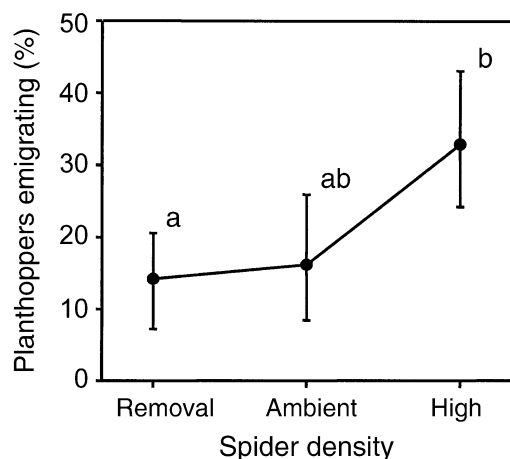


FIG. 5. The effect of spider treatment on planthopper emigration. Mean percentages emigrating for each spider treatment level were determined as the difference in the percentage of planthoppers recaptured between caged and uncaged patches (see Fig. 4). Error bars are 95% confidence intervals determined from 1000 bootstrapped estimates of the mean difference between caged and uncaged patches (Efron and Tibshirani 1993). The 95% confidence intervals that do not overlap zero indicate that emigration losses are nontrivial. Means with different letters are significantly different (i.e., 95% confidence intervals do not overlap).

dation (as assumed in most studies of this sort; e.g., Beckerman et al. 1997, Schmitz et al. 1997, Schmitz 1998) or was simply a generalized response to the disturbance effects of any arthropod is unknown; however, the implications for the spatial population dynamics of the planthopper would be the same regardless of the underlying mechanism initiating emigration. Other studies have detected strong negative effects of spiders on *Prokelisia* planthopper abundances (e.g., Döbel and Denno 1994, Denno et al. 2002, 2003, Finke and Denno 2002), but none of them have attempted to separate the lethal from nonlethal effects of these predators. Given that total spider densities in this other system often exceed 500 individuals/m², it seems very plausible that nonlethal effects of spiders may be of considerable importance to the spatial population dynamics of *Prokelisia* species.

Results of this study with *P. crocea* corroborate the conclusions from both aquatic and terrestrial studies that nonlethal effects may significantly add to or override direct mortality effects on prey populations (reviewed in Werner and Peacor 2003). For example, by using spiders with and without their chelicera glued together, Beckerman et al. (1997) were able to demonstrate that spiders had little influence on grasshopper density, but strongly influenced habitat use by the grasshoppers. The risk of spider predation caused a dietary shift from grasses to forbs. Beckerman et al. (1997; see also Schmitz et al. 1997, Schmitz 1998) were also able to demonstrate that the spider-induced shift in grasshopper diet had a cascading effect on the host plants; i.e., in the face of spider predation risk, grasses received lower levels of grasshopper damage than in the absence of spider risk. Whereas behaviorally mediated trophic cascades are evident in a number of other systems (see Schmitz et al. 2000), we currently do not know whether prairie cordgrass benefits from predator-induced planthopper emigration. In an analogous system, Denno et al. (2002, 2003) found no evidence in the field of top-down trophic cascades among spiders, *Prokelisia* planthoppers, and saltmarsh cordgrass. In their studies, intraguild predation by spiders was thought to attenuate the top-down effects of these predators.

Predator-induced emigration has been reported in a number of species in addition to *P. crocea* (e.g., Sih et al. 1992, Peckarsky 1996, Hakkarainen et al. 2001). How predator-induced emigration impacts the regional population dynamics of *P. crocea* is an important consideration, especially in light of the theoretical significance of predator/prey dispersal to population stability and persistence (e.g., Hastings 1977, Crowley 1981, McCauley et al. 1996). Previous studies of ours suggest that emigrant *P. crocea* are fully capable of colonizing new cordgrass patches following their escape from predators. First, >90% of *P. crocea* adults are macropterous and capable of nontrivial flight (Cronin 2003a). Second, the colonization of patches by emi-

grants is not limited by isolation distances up to 50 m, the maximum separation between patches in our prairie field sites (Cronin 2003a). Thus, all else being equal, patch connectivity for *P. crocea* is likely to be greater when spider densities are high than when spider densities are low. Consequently, the spatial population structure for the prairie planthopper may also vary in a fundamental way in the face of differing spider densities: at low densities the ensemble of local planthopper populations may fit a classical metapopulation structure, whereas at high densities the local planthopper populations may coalesce into a single patchy population (see Harrison and Taylor 1997, Thomas and Kunin 1999).

Presently, we have no information on the potential trade-offs associated with the emigration from a patch when planthoppers are at risk to predation. Emigration costs may be incurred through dispersal mortality (e.g., Ward et al. 1998, Hanski et al. 2000, Conradt et al. 2001), the expenditure of energy in flight that otherwise could be utilized for reproduction (e.g., Zera et al. 1998), or the loss of time for a time-limited forager (Driessen and Hemerik 1992). If costs exist, predator-induced emigration may be nonlethal only in the short term.

Planthopper–spider spatial dynamics

Comparatively little work has been conducted on the interactions between arachnids and their prey at the landscape level. Most of the available studies have focused on predatory spider mites and their prey (e.g., Walde 1994, Ellner et al. 2001, Nachman 2001) including the seminal work by Huffaker (1958). In general, these studies have revealed unstable local dynamics, predator-driven extinctions of prey, and long term regional (metapopulation) persistence of subdivided populations.

The three-generation survey of cordgrass patches indicates that spiders may play an important role in the spatial distribution of their planthopper prey. Web-building and cursorial spiders, the two most abundant spider guilds, were unevenly distributed among cordgrass patches. Densities of both spider guilds were negatively correlated with patch size, a pattern the opposite of that for the planthopper (Cronin 2003a). One possible explanation for why small patches have greater densities of web-building and cursorial spiders than large patches is because of the close proximity of all occupants to different vegetation/habitat types. Increased vegetational complexity or diversity may provide access to other prey species, or provide refuge from their own predators (McNett and Rypstra 2000, Finke and Denno 2002). Therefore, smaller patches, with a greater perimeter : area ratio, would have a proportionately greater influx of spiders than larger patches. If this were true, then we might expect spider densities to be higher at the edge than in the interior of large cordgrass patches. However, a census of the

distribution of spiders within large patches revealed that edge densities were only marginally higher than interior densities (J. T. Cronin and K. J. Haynes, *unpublished data*). Other factors that may vary with patch size and affect spider abundances, e.g., thatch accumulation, microclimate, or avian predators, have not been explored.

The lack of a patch isolation effect on spider guild densities was not surprising given that the majority of these spiders are likely generalists. Evidence for a generalist lifestyle is indicated by the occurrence of all members of the three guilds in moderate abundances in brome and native grass habitat, and from feeding trials in the laboratory with several of the most common spider species from each foraging guild (J. T. Cronin and K. J. Haynes, *unpublished data*). Spiders were scarcely observed in mudflats (J. T. Cronin and K. J. Haynes, *unpublished data*); therefore it was somewhat unexpected that spider densities within cordgrass patches were not dependent upon the composition of the surrounding matrix. In comparison to spider predators, the density distribution of the planthopper's primary parasitoid, *A. columbi*, was independent of patch size, and an increasing function of patch isolation and the proportion of the matrix that was mudflat (Cronin 2003c).

Our census data further suggest that spiders may play a significant role in the extinction of local patch populations of *P. crocea*. Although we cannot ascribe a causal link with these data, an increase in web-builder density per patch (numerically the dominant spider guild) was associated with an increased likelihood of planthopper extinction. Planthopper populations in small patches were particularly prone to extinction (Fig. 2). Several factors likely contributed to the high rate of extinction in these smaller patches. First, one of the strongest patterns in the spatial distribution of *P. crocea* is that patch densities are positively correlated with patch size (Cronin 2003a). Second, in the absence of arthropod predators, the emigration rate for *P. crocea* is inversely related to patch size (Cronin 2003a). These two characteristics of small patches are expected biogeographic patterns that likely result in high extinction rates (e.g., Burkey 1997, Kindvall 1999, Crone et al. 2001). Finally, spiders likely exacerbate the extinction risk faced by small populations because smaller patches also support higher densities of both web-building and cursorial spiders. Through their effects primarily on planthopper emigration, and secondarily on planthopper mortality, these spiders may render it highly unlikely that small patches are able to support viable planthopper populations without immigration; i.e., spiders may be causing small patches to function as population sinks. Therefore, nonlethal effects, such as the influence of spiders on *P. crocea* emigration, may moderate the critical patch size needed to sustain a planthopper population, influence the patch

incidence function, and limit the spatial spread of planthoppers.

Given the arguments above, it is most likely that spiders exert the greatest influence on the local dynamics of planthopper populations in smaller rather than larger cordgrass patches. Patches below the median size comprise <1% of the total cordgrass area within any one of our several field sites. Because these smaller patches also support lower densities of *P. crocea* (Cronin 2003a), they may be construed as being unimportant to the population dynamics of this species. In fact, we have presented data previously that suggests *P. crocea* has a mainland-island metapopulation structure and that large mainland patches (>4 ha) serve as sources of immigrants for smaller cordgrass patch sinks (Cronin 2003a). Following this logic, spiders may play a more influential role in the spatial distribution and spread of planthoppers than in the regional temporal dynamics of the planthoppers. However, this assessment may be premature. Large cordgrass patches do support spiders that clearly can depress local prey populations (see Fig. 4). It is also the case that organisms in sink populations can exert a significant effect on regional dynamics and persistence (e.g., Amezcuca and Holyoak 2000, Doak 2000, Gundersen et al. 2001). For example, Crone et al. (2001) found that small ephemeral subpopulations of field voles had elevated emigration rates prior to extinction and that those emigrants contributed significantly to the persistence of the whole metapopulation. Furthermore, Amezcuca and Holyoak (2000) found that prey immigration from source to sink subpopulations may have weakened the coupling between predator and prey dynamics and contributed to the increase in regional persistence. In the tall grass prairie, it has been hypothesized that small cordgrass patches are richer in nutrients than larger patches (Cronin 2003a) and that offspring derived from those small patches may be more fecund, vagile, and have higher survivorship than offspring derived from larger patches (see also Doak 2000). Emigrants from these patches may contribute much more to the regional population than their numbers would indicate—a prospect that is currently under investigation.

In conclusion, we agree with Schmitz's (1998) assessment that nonlethal effects of predators may be an important and overlooked process determining community-level interactions. We would add that because many of the prey's traits under the influence of predators are dispersal related (e.g., emigration rate, movement speed, wing production, and morphology), nonlethal effects of predators may play a very important role in the spatial ecology of predator-prey interactions. In our study, an increase in spider density appears to have a stronger impact on planthopper emigration than on their survivorship. The nonlethal effects of spiders may play an important role in determining the source-sink properties of cordgrass patches and influencing the spatial distributions and temporal dynamics

of its prey. Clearly, more studies are needed in this fertile area.

ACKNOWLEDGMENTS

Special thanks to Michael Draney for identifying our spiders, and the Biology Department at the University of North Dakota for sharing their facilities with us during this investigation. The following people assisted with this project: M. Bryant, G. Collins, J. Constible, J. Cutrera, K. Euliss, M. Szymanski, and A. Widdell. K. Tompkins of the U.S. Fish and Wildlife Service granted us permission to work at the Kelly's Slough National Wildlife Refuge and H. Johnson kindly allowed us access to his land. Finally, K. Baum, D. Finke, C. Gratton, P. Hamback, D. Spiller, and an anonymous reviewer provided valuable comments on previous drafts of the manuscript. This work was supported by Louisiana State University, a Board of Regents Fellowship (K. J. Haynes), and The National Science Foundation (DEB-9973789 and DEB-0211359 to J. T. Cronin).

LITERATURE CITED

- Agnew, C. W., and J. W. Smith, Jr. 1989. Ecology of spiders (Araneae) in a peanut agroecosystem. *Environmental Entomology* **18**:30–42.
- Amezcuca, A. B., and M. Holyoak. 2000. Empirical evidence for predator–prey source–sink dynamics. *Ecology* **81**:3087–3098.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences (USA)* **94**:10735–10738.
- Bolker, B., M. Holyoak, V. Křivan, L. Rowe, and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* **84**:1101–1114.
- Burkey, T. V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria and protozoa communities as model ecosystems. *American Naturalist* **150**:568–591.
- Conradt, L., T. J. Roper, and C. D. Thomas. 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos* **95**:416–424.
- Crone, E. E., D. Doak, and J. Pokki. 2001. Ecological influences on the dynamics of a field vole metapopulation. *Ecology* **82**:831–843.
- Cronin, J. T. 2003a. Movement and spatial population structure of a prairie planthopper. *Ecology* **84**:1179–1188.
- Cronin, J. T. 2003b. Patch structure, oviposition behavior, and the distribution of parasitism risk. *Ecological Monographs* **73**:283–300.
- Cronin, J. T. 2003c. Matrix heterogeneity and planthopper–parasitoid interactions in space. *Ecology* **84**:1506–1516.
- Cronin, J. T., and D. R. Strong. 1994. Parasitoid interactions and their contribution to the stabilization of Auchenorrhyncha populations. Pages 400–428 in R. F. Denno and T. J. Perfect, editors. *Planthoppers: their ecology and management*. Chapman and Hall, New York, New York, USA.
- Crowley, P. H. 1981. Dispersal and the stability of predator–prey interactions. *American Naturalist* **118**:673–701.
- Denno, R. F., C. Gratton, H. Döbel, and D. L. Finke. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* **84**:1032–1044.
- Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* **83**:1443–1458.
- Dill, L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* **84**:1151–1157.
- Dixon, A. F. G., and B. K. Agarwala. 1999. Ladybird-induced life-history changes in aphids. *Proceedings of the Royal Society of London Series B Biological* **266**:1549–1553.
- Doak, P. 2000. Habitat patchiness and the distribution, abundance, and population dynamics of an insect herbivore. *Ecology* **81**:1842–1857.
- Döbel, H. G., and R. F. Denno. 1994. Predator–planthopper interactions. Pages 325–399 in R. F. Denno and T. J. Perfect, editors. *Planthoppers: their ecology and management*. Chapman and Hall, New York, New York, USA.
- Driessen, G., and L. Hemerik. 1992. The time and egg budget of *Leptopilina clavipes*, a parasitoid of larval *Drosophila*. *Ecological Entomology* **17**:17–27.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.
- Ellner, S. P., E. McCauley, B. E. Kendall, C. J. Briggs, P. R. Hosseini, S. N. Wood, A. Janssen, M. W. Sabelis, P. Turchin, R. M. Nisbet, and W. W. Murdoch. 2001. Habitat structure and population persistence in an experimental community. *Nature* **412**:538–543.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* **83**:643–652.
- Gundersen, G., E. Johannesen, H. P. Andreassen, and R. A. Ims. 2001. Source–sink dynamics: how sinks affect demography of sources. *Ecology Letters* **4**:14–21.
- Hakkarainen, H., P. Ilmonen, V. Koivunen, and E. Korpimäki. 2001. Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. *Oecologia* **126**:355–359.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, New York, New York, USA.
- Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* **81**:239–251.
- Hanski, I., and M. Gilpin. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology*. Academic Press, San Diego, California, USA.
- Hassell, M. P. 2000. *The spatial and temporal dynamics of host–parasitoid interactions*. Oxford University Press, New York, New York, USA.
- Hastings, A. 1977. Spatial heterogeneity and the stability of predator–prey systems. *Theoretical Population Biology* **12**:37–48.
- Haynes, K. J., and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* **84**:2856–2866.
- Hitchcock, A. S. 1963. *Manual of the grasses of the United States*. Dover Publications, New York, New York, USA.
- Holder, M. W., and S. W. Wilson. 1992. Life history and descriptions of the immature stages of the planthopper *Prokelisia crocea* (Van Duzee) (Homoptera: Delphacidae). *Journal of the New York Entomological Society* **100**:491–497.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia* **27**:343–383.
- Kindvall, O. 1999. Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *Journal of Animal Ecology* **68**:172–185.
- Lang, A. 2003. Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia* **134**:144–153.
- Langellotto, G. A., and R. F. Denno. 2001. Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. *Ecology* **82**:1870–1878.

- McCauley, E., W. G. Wilson, and A. M. de Roos. 1996. Dynamics of age-structured predator-prey populations in space: asymmetrical effects of mobility in juvenile and adult predators. *Oikos* **76**:485–497.
- McNett, B. J., and A. L. Rypstra. 2000. Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecological Entomology* **25**:423–432.
- Nachman, G. 2001. Predator-prey interactions in a non-equilibrium context: the metapopulation approach to modeling “hide-and-peek” dynamics in a spatially explicit tritrophic system. *Oikos* **94**:72–88.
- Peckarsky, B. L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology* **77**:1888–1905.
- Riechert, S. E., and L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology* **71**:1441–1450.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* **151**:327–342.
- Schmitz, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters* **6**:156–163.
- Schmitz, O. J., A. P. Beckerman, and K. M. O’Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78**:1388–1399.
- Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* **155**:141–153.
- Sih, A., L. B. Kats, and R. D. Moore. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. *Ecology* **73**:1418–1430.
- Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. *Ecology* **82**:1571–1583.
- Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. *Ecology* **75**:182–196.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* **68**:647–657.
- Tilman, D., and P. Kareiva. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Walde, S. J. 1994. Immigration and the dynamics of a predator-prey interaction in biological control. *Journal of Animal Ecology* **63**:337–346.
- Ward, S. A., S. R. Leather, J. Pickup, and R. Harrington. 1998. Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *Journal of Animal Ecology* **67**:763–773.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**:1083–1100.
- Zera, A. J., J. Potts, and K. Kobus. 1998. The physiology of life-history trade-offs: experimental analysis of a hormonally induced life-history trade-off in *Gryllus assimilis*. *American Naturalist* **152**:7–23.

APPENDIX A

Statistical procedures for the among-patch survey of the distribution of spiders and planthoppers and the spider impact experiment are available in ESA’s Electronic Data Archive: *Ecological Archives* E085-064-A1.

APPENDIX B

Spider guild densities in the three-generation survey and spider impact experiment are reported in ESA’s Electronic Data Archive: *Ecological Archives* E085-064-A2.

APPENDIX C

Statistical results from separate repeated-measures ANOVAs for the effect of patch size, isolation, and proportion mudflat on the density of spiders in each of three foraging guilds are available in ESA’s Electronic Data Archive: *Ecological Archives* E085-064-A3.

APPENDIX D

The results from a backward stepwise regression analysis for the effect of spider guild density, landscape factors, spider guild density \times patch size interaction, and planthopper density at $t - 1$ on current planthopper density are provided in ESA’s Electronic Data Archive: *Ecological Archives* E085-064-A4.

APPENDIX E

The correlation (and associated P value) between planthopper and spider density in each of three planthopper generations is provided in ESA’s Electronic Data Archive: *Ecological Archives* E085-064-A5.

APPENDIX F

The results from backward stepwise logistic regression analyses for the effect of cursorial, sit-and-wait, and web-building spiders, planthopper density, three landscape variables, and the interaction between patch size and the density of each spider guild on the likelihood of a local planthopper extinction are provided in ESA’s Electronic Data Archive: *Ecological Archives* E085-064-A6.