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The Effects of Dispersal and Predator Density on Prey Survival in an Insect-Red Clover Metacommunity

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Abstract

Trophic interactions are often studied within habitat patches, but among-patch dispersal of individuals may influence local patch dynamics. Metacommunity concepts incorporate the effects of dispersal on local and community dynamics. There are few experimental tests of metacommunity theory using insects compared to those conducted in microbial microcosms. Using connected experimental mesocosms, we varied the density of the leafhopper *Agallia constricta* Van Duzee (Homoptera: Cicadellidae) and a generalist insect predator, the damsel bug (*Nabis* spp., Heteroptera: Nabidae), to determine the effects of conspecific and predator density and varying the time available to dispersal among mesocosms on predation rates, dispersal rates, and leafhopper survival. Conspecific and damsel bug density did not affect dispersal rates in leafhoppers, but this may be due to leafhoppers' aversion to leaving the host plants or the connecting tubes between mesocosms hindering leafhopper movement. Leafhopper dispersal was higher in high-dispersal treatments. Survival rates of *A. constricta* were also lowest in treatments where dispersal was not limited. This is one of the first experimental studies to vary predator density and the time available to dispersal. Our results indicate that dispersal is the key to understanding short-term processes such as prey survival in predator-prey metacommunities. Further work is needed to determine how dispersal rates influence persistence of communities in multigenerational studies.

Key words: dispersal, metacommunity, survival, Cicadellidae, Nabidae

Trophic interactions of insects are often studied in local communities (Beckerman et al. 1997, Schmitz et al. 1997, Schmitz 2003), but dispersal among communities may be important to local dynamics. Metacommunity concepts incorporate dispersal among local communities and how dispersal affects biodiversity and species interactions, such as predation, parasitism, herbivory, and competition (Leibold et al. 2004, Holyoak et al. 2005). There is a well-developed body of theory for metacommunities, but there are relatively few experimental tests of dispersal on insect predator-prey interactions (but see Kareiva 1987; Demptser et al. 1995; Bowne and Bowers 2004; Cronin and Haynes 2004; Cronin 2007, 2009; Bergerot et al. 2010; Costa et al. 2013; Start and Gilbert 2016).

Dispersal rates of individuals moving among habitat patches determine the extent to which predator and prey dynamics are coupled in patchy landscapes. Dispersal of both predators and their prey may stabilize predator-prey dynamics (Holt 2002, Briggs and Hoopes 2004), but higher levels of predator dispersal may uncouple these dynamics due to overexploitation of prey (Holyoak and Lawler 1996b). At low predator dispersal rates, prey may escape in space from predators by colonizing empty habitat patches (Holyoak and Lawler 1996b, Costa et al. 2013). If predators are able to

colonize patches with abundant prey, however, an increased numerical response by the predator and a subsequent population crash after prey are overexploited may result (Holyoak and Lawler 1996b, Kneitel and Miller 2003, Kondoh 2003).

Intermediate dispersal rates are predicted to increase the persistence time of both predators and their prey due to greater recolonization of vacant patches than at low dispersal rates if dispersal rates are low enough that predators cannot overexploit their prey (Brown and Kodric-Brown 1977, Crowley 1981, Nachman 1987, Holyoak and Lawler 1996b). This has been shown in microbial communities provided that dispersal-limited species are able to colonize new habitat patches (Holyoak and Lawler 1996a, b; Loreau and Mouquet 1999; Mouquet and Loreau 2002; Kneitel and Miller 2003; Cadotte and Fukami 2005; Hauzy et al. 2007).

Metacommunity persistence is difficult to study in larger organisms due to longer generation times (but see Bonsall et al. 2002, 2005; Bull et al. 2006). However, persistence may be studied by quantifying the movements of predators and prey among habitat patches and their effects on prey survival. This provides insights into mechanisms of metacommunity dynamics operating within generations. Individual-based explanations for short-term metacommunity

dynamics include processes, such as predation (Bonsall et al. 2002, 2005; Bull et al. 2006), herbivory (Matthiessen et al. 2007), and habitat selection (Resetarits 2005, Binckley and Resetarits 2007). The factors influencing dispersal among habitat patches are important to understand as dispersal among habitat patches is thought to be required for long-term metacommunity persistence (Holyoak et al. 2005).

Our aims in this study were to determine the effects of varying conspecific densities of the leafhopper *Agallia constricta* Van Duzee (Homoptera: Cicadellidae) and densities of a leafhopper predator, the damsel bug (Heteroptera: Nabidae, *Nabis* spp.), on *A. contricta* dispersal rates and survival in connected sets of mesocosm cages that regulated the time available for insect dispersal. First, we determined if density-dependent dispersal occurred in *A. constricta* in the absence of predation, as documented in many other taxa, such as birds, mammals, and insects (Denno and Peterson 1995, Fonseca and Hart 1996, Matthysen 2005). Specifically, we predicted greater dispersal among local communities in high-density or high-dispersal treatments compared with low-density or low-dispersal treatments. Second, we determined the effect of varying dispersal treatments and predator density on the dispersal rates of *A. constricta*. We predicted that leafhopper dispersal rates would be greatest in the high-dispersal and low-predator density treatments if differential dispersal rates occurred between insect predators and prey. We further predicted that leafhopper survival would be greatest in the low-predator density and intermediate levels of dispersal in accordance with metacommunity theory.

Materials and Methods

Study Species

Insects were collected from clover and soybean fields at the Miami University Ecology Research Center, Oxford, OH, USA, during the summer of 2008. *A. constricta* is a generalist leafhopper that consumes several families of plants, including legumes and grasses (LaHue 1936, Black 1944, Nielson 1968). *A. constricta* is present at our study site from June to September, but it is most abundant in late July and early August (Schroeder 2007).

Damsel bugs are generalist predators that prey on multiple insect families including aphids, plant bugs, and leafhoppers (Lattin 1989, Östman and Ives 2003). They are diurnal predators who actively forage for their prey using chemoreception and vibrations (Donahoe and Pitre 1977; Irwin and Shepard 1980; Braman and Yeargan 1989, 1990; Schotzko and O'Keeffe 1989; Freund and Olmstead 2000). Damsel bugs are common predators in many agricultural systems (Irwin and Shepard 1980; Braman and Yeargan 1989,

1990; Schotzko and O'Keeffe 1989). *Nabis americoferus* (Carayon) (Hemiptera: Nabidae) and *N. roseipennis* Reuter both occur at our study site, but it was not possible to differentiate between the species in the field. Therefore, we randomly collected both of the species from the field for use in our experiments. Previous work has indicated that any confounding effects of species are likely negligible (Östman and Ives 2003).

Experimental Mesocosms

All experiments were conducted outdoors in arrays of caged pots of red clover (*Trifolium pratense* L.) during June to September 2008 at the Miami University Ecology Research Center. Cylindrical cages were constructed using 'no-see-um netting' covering a wire frame (28 cm × 40 cm [depth by height]) and a pot of red clover (30 cm × 10 cm [depth by height]) grown from the seed (Fig. 1). To remove any arthropods present on clover, pots were sprayed with organic pyrethrin insecticide before placing experimental insects in the mesocosms. After spraying, cages were placed in an open field with full sun. Pyrethrin insecticides degrade rapidly in sunlight with half-lives not exceeding 3 h (Antonious 2004). After 2 d, less than 0.05 μg of pesticide residue remains on 1 g of plant leaves (Antonious 2004).

After 2 d, experimental leafhoppers were introduced to cages. Each cage contained a local community of clover, leafhoppers, and predators, and three cages were linked by dispersal to create a metacommunity. The cages were connected using rectangular, vinyl rain gutter downspouts with the sides removed and lined with 'no-see-um' netting. Tubes were 10 cm × 50 cm (width by length), and dispersal was controlled by closing the ends of the tubes.

Preliminary observations were conducted to ensure that leafhoppers and damsel bugs would move through the connecting tubes. Before the start of the experiment, leafhoppers were introduced into a connecting tube and observed over the course of an hour. The leafhoppers would either walk or hop along the length of the tube. After 1 h, a single damsel bug was added to the tube. Leafhoppers would hop to the ceiling of the tube as the damsel bug approached and then walk quickly away from the damsel bug toward the ends of the tube.

The three levels of the dispersal treatment were based on the time the connecting tubes were open: a low level with tubes open 5% of the time per wk, or 8 h; an intermediate level with the tubes open 30% per wk, or 48 h; and a high dispersal level with the tubes open 100% of the time. The 5% dispersal treatment represented the low end of metapopulation dispersal where each mesocosm was predicted to behave as an isolated local patch, the 30% dispersal treatment represented the high end of where metacommunity dynamics are expected to occur among local patches, and the 100% dispersal treatment represented a single, large, patchy community
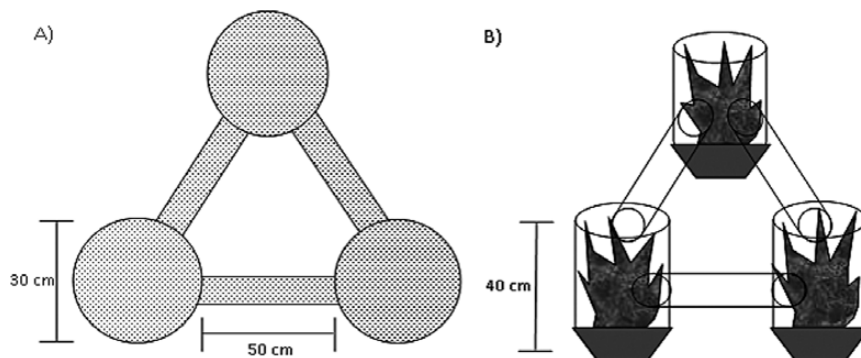

Fig. 1. Diagram of experimental unit from two views (A) above and (B) ground level. Each circle or cylinder represents a community connected by tubing to allow dispersal of insects among communities. A pot of red clover was placed in each cylinder.

(cf. Holyoak and Lawler 1996a). We randomly assigned periods when tubes were open to movement so that different replicates were open at different times during the experiment.

Preliminary Experiment

To quantify leafhopper movement among mesocosms, leafhoppers in different mesocosms were dusted with a different color of fluorescent powder. A preliminary experiment was conducted to determine if damsel bugs prefer to prey on a particular color of powder. A total of 25 *A. constricta* were dusted with red, blue, or yellow fluorescent powder and added to single-chamber mesocosms containing a single pot of red clover. A control treatment with no powder was also used. Five replicates were used for each treatment. Damsel bugs were food-deprived for 2 d and were then added to the mesocosms 1 d after the leafhoppers. Mesocosms were vacuum-sampled with a modified portable vacuum (BioQuip Products, Rancho Dominguez, California) 1 d after damsel bugs were added, and the number of surviving leafhoppers was counted. One replicate in both the yellow and blue powder treatments was not included in the analysis due to the damsel bug dying during the experiment. Before the analysis, data were square-root transformed. Results were analyzed using a general linear model in SPSS (IBM Corp. 2017). There was no difference in the number of leafhoppers consumed among the color treatments and the control ($F = 0.751$; df = 3, 14; $P = 0.540$). Damsel bugs were not dusted with different colored powder to avoid altering *A. constricta's* behavioral response to predators.

Dispersal Experiments

To determine the effect of prey density and dispersal treatment on dispersal and survival rates of *A. constricta*, three dispersal treatments (5, 30, and 100%) were crossed with two different densities of leafhoppers per mesocosm (25 or 50). Four replicate metacommunities of each treatment were used for a total of 72 cages and 24 metacommunities. Only two mesocosms were stocked with leafhoppers to determine if leafhopper colonization rates of an empty mesocosm differed among density or dispersal treatments. Leafhoppers were dusted with either red or yellow fluorescent powder to quantify movements among communities. Each community was sampled with a suction-sampler 1 d after the damsel bugs were introduced and every 2 d thereafter. Surviving leafhoppers were counted and returned to the community where they were sampled. The experiment was only conducted for 5 d because of the inclement weather caused by the remnants of Hurricane Ike moving through the Oxford area. A single 50-leafhopper, 5% dispersal replicate and a single 50-leafhopper, 30% dispersal replicate did not have tubes opened as a result of the experiment being terminated earlier than expected; however, tube-open times were randomly assigned across replicates, so this should not have biased the results among treatments.

We also tested the effect of dispersal treatments on *A. constricta* survival probabilities and dispersal rates in the presence of predation. For this experiment, we used a fixed density of 50 leafhoppers per local community, and we replicated the dispersal levels as in the previous experiment. One mesocosm was intentionally left empty at the beginning to serve as a refuge from predation. Leafhoppers were dusted with either blue or red fluorescent powder to quantify movements among cages. One day later, either one or two damsel bugs were added to each of the two mesocosm cages containing leafhoppers, for a total of either two or four per metacommunity. We used only female damsel bugs in this experiment. Female damsel bugs are more voracious than males (Lingren et al. 1968, Donahoe and Pitre 1977, Propp 1982, Ma et al. 2005). The females are likely energy maximizers for reproduction, whereas males may spend less time foraging to find mates (Schoener 1971).

Each mesocosm was sampled with a suction sampler 1 d after the damsel bugs were introduced and every 2 d thereafter. Surviving leafhoppers and damsel bugs were returned to the mesocosm from which they were sampled. If a dead damsel bug was found during sampling, it was replaced to maintain a constant predator density throughout the course of the 7-d experiment.

Statistical Analyses

Poisson regression was used to determine the effect of conspecific density and dispersal treatment on dispersal rates of *A. constricta* in the absence of predation. Both main effects were tested along with their interaction. Dispersal was analyzed as the total number of leafhoppers that moved among mesocosms in each treatment over the course of the experiment. Poisson regression was also used to determine the effect of damsel bug density and dispersal treatment on leafhopper dispersal rates (glm function, R Development Core Team 2009). Both main effects were tested along with their interaction.

The roles of predation and dispersal in leafhopper survival were modeled using failure-time analysis (Fox 2001). It is possible that some leafhoppers may have escaped capture by finding refuge in the clover despite our extensive sampling efforts. Failure-time analysis allows for the possibility that some leafhoppers may not be recovered alive or dead during a sampling period (right-censored data), which occurred in 2% of the total of 2,400 leafhopper counts. The exact time of an animal's death is often not known in empirical studies. The interval in which death (failure) occurred is often all that is known. Leafhopper survival under different treatment factors of predation (0, 1, or 2 damsel bugs) and dispersal rate (5, 30, and 100%) were recorded after 1, 3, 5, and 7 d so that the time to mortality can be treated as a distribution of failure times. We expected that leafhopper mortality would not occur at a constant rate as food-deprived damsel bugs were expected to have high feeding rates at the beginning of the experiment and then level off as they became satiated or as prey encounter rates decreased. The predictor variables of predation and dispersal will influence these rates, a pattern that is suited to using nonparametric life-table analysis (Kalbfleisch and Prentice 1980, PROC LIFETEST, SAS Institute 2003). Failure-time analysis has been used to measure predation rates over time in intertidal communities (Petraitis 1998), and the survival probability of grasshoppers in response to spider presence (Danner and Joern 2003).

Results

In the absence of predation, <5% (2–16 leafhoppers) of the total leafhoppers within each replicate moved among the mesocosms in all treatments, except in the 25 leafhoppers/100% dispersal treatment, where 18 of the 200 (9%) total leafhoppers moved among local patches. There was no effect of leafhopper density on leafhopper dispersal rate (Poisson regression, Wald's $Z = 0.44$; $P = 0.66$). There was no detectable density-dependent dispersal of leafhoppers among patches in the absence of predation. There was a significant effect of dispersal treatment on the dispersal rate of leafhoppers with a greater number of leafhoppers dispersing in the 100% dispersal treatment compared with the 30 and 5% dispersal treatments ($Z = 3.11$; $P = 0.0019$). There was no interaction between density and dispersal treatment. There was also no difference among treatments in survival time of *A. constricta* in the absence of predation ($\chi^2 = 1.8637$; df = 5; $P = 0.8677$, Table 1, Fig. 2).

Table 1. Survival probabilities (±SE) and mean (±SD) *A. constricta* surviving per day in response to varied isolation and leafhopper density

Dispersal	Density	Time	Survival probability(±SE)	Mean *A. constricta* (±SD)
5	25	24	0.891 ± 0.022	22.25 ± 1.3
		72	0.851 ± 0.025	21.25 ± 2.3
5	50	24	0.946 ± 0.012	47.00 ± 1.3
		72	0.891 ± 0.016	44.38 ± 3.1
30	25	24	0.945 ± 0.016	23.63 ± 1.1
		72	0.891 ± 0.025	21.50 ± 2.3
30	50	24	0.949 ± 0.011	47.50 ± 1.1
		72	0.870 ± 0.017	43.63 ± 3.0
100	25	24	0.918 ± 0.019	22.75 ± 1.4
		72	0.840 ± 0.026	21.00 ± 1.2
100	50	24	0.922 ± 0.013	46.00 ± 1.2
		72	0.870 ± 0.017	64.88 ± 1.7

'Dispersal' is the percentage of time per week that connecting tubes were open to movement. 'Density' is the density of leafhoppers per mesocosm. 'Time' is the hours since the experiment commenced.
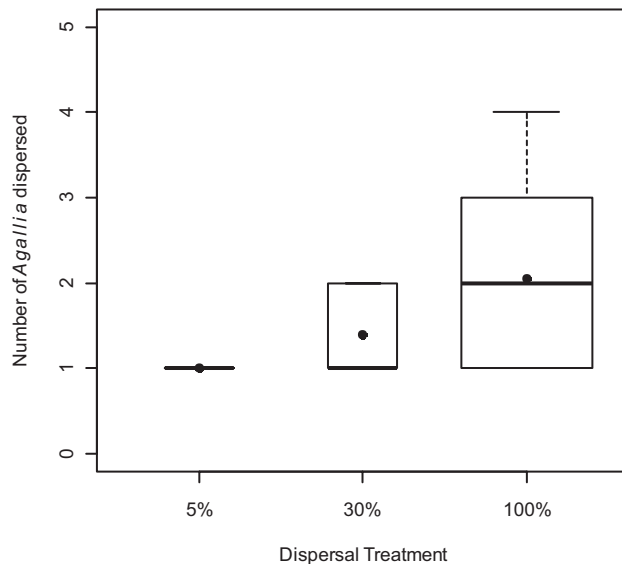

Fig. 2. The number of *Agallia constricta* that dispersed among mesocosms in the three dispersal treatments in the absence of predation. The edges of the boxes represent the 25th and 75th percentiles, the dark circle indicates the mean, the dark line indicates the median, and the whiskers represent the highest and lowest number of leafhoppers eaten, excluding outliers. Box widths are proportional to the square root of the number of leafhoppers that dispersed in each treatment.

Damsel bug density had no effect on leafhopper movements among mesocosms ($Z = -0.566$; $P = 0.57$). However, dispersal did have a significant effect on leafhopper movement with more leafhoppers dispersing in the 100% dispersal treatment compared with the 5 and 30% treatments ($Z = 2.22$; $P = 0.027$). There was no interaction between dispersal treatment and damsel bug density. Less than 5% of the leafhoppers (1–12 leafhoppers) moved among local communities in all treatments. We only observed three instances of damsel bugs moving among communities.

A. constricta had a higher survival probability in the 1-damsel bug/5% dispersal treatment compared to the 1-damsel bug/100% dispersal treatment ($\chi^2 = 8.86$; df = 1; $P = 0.0029$, Table 2, Fig. 3).

Leafhoppers also had higher survival probabilities in the 1-damsel bug/5% dispersal treatment than in the 2-damsel bug/30% dispersal treatment ($\chi^2 = 9.41$; df = 1; $P = 0.0022$, Table 2, Fig. 3) and the 2-damsel bug/100% dispersal treatment ($\chi^2 = 4.75$; df = 1; $P = 0.0293$, Table 2, Fig. 3).

Discussion

Leafhopper density did not affect dispersal rates among mesocosms, but leafhoppers moved among mesocosms more in the 100% dispersal treatment compared with the 5 and 30% treatments. Despite high conspecific densities and the opportunity to disperse among mesocosms, leafhoppers moved infrequently among habitat patches. Densities of *A. constricta* can be as high as 108 leafhoppers m^{-2} in the field with a mean of 35 leafhoppers m^{-2} (Schroeder 2007). This is equivalent to a mean of 2.56 leafhoppers per mesocosm, which have an area of 0.073 m^2. Therefore, densities in the mesocosms were 10–20 times greater than the observed field densities for the 25- and 50-leafhopper density treatments, respectively, yet movement among patches was still infrequent.

A meta-analysis by Denno and Peterson (1995) determined that declining host-plant quality is the main factor influencing emigration in sap-feeding insects. All local habitat patches in our mesocosms were of similar quality, and there was no evidence of 'hopper burn', a yellowing of plant leaves resulting from leafhopper feeding. Hopper burn results in stunted growth, delayed maturation, and loss of yield (Kindler et al. 1973, Wilson et al. 1979). It is not known if *A. constricta* causes hopper burn, but Haynes and Crist (2009) suggested that potato leafhoppers (Homoptera: Cicadellidae, *Empoasca fabae*) may be more associated with reductions in plant biomass than *A. constricta*.

Leafhoppers may also be averse to leaving host plants within mescosoms, or connecting tubes may not have been conducive to hopping modes of movement by leafhoppers. Insects show an aversion to leaving suitable habitat patches by exhibiting exploratory behavior along the patch edge or by not approaching the patch edge (Schtickzelle and Baguette 2003, Bowler and Benton 2005, Baguette and Van Dyck 2007, Fahrig 2007, Stasek et al. 2008, Cronin 2009, Costa et al. 2013). We did not observe *A. constricta*'s behavior as it approached the connecting tubes, but once leafhoppers entered a connecting tube, they may not have crossed the tube due to the tubes' length, small diameter, or perceived increased risk of mortality (Schtickzelle and Baguette 2003). Therefore, it is important to determine the scale at which leafhoppers perceive landscape features, such as the patch edge, and assess the risks of approaching and crossing the edge (Cronin 2003, Haynes and Cronin 2003, Schtickzelle and Baguette 2003, Bowler and Benton 2005, Baguette and Van Dyck 2007, Fahrig 2007, Stasek et al. 2008).

We predicted that *A. constricta* would have the highest dispersal rates in the single damsel bug, 100% dispersal treatment. As predicted, leafhoppers did have the greatest dispersal rates in the 100% dispersal treatment, though dispersal rates were generally low with <5% of each local leafhopper population dispersed among mesocosms. Low dispersal rates among mesocosms may have occurred because leafhoppers had limited opportunities to jump or fly to escape from predation and thus remained sedentary to escape predation. Damsel bugs search for prey both visually and chemically (Freund and Olmstead 2000), and they may have been able to locate leafhoppers more efficiently after leafhoppers left the host plant. Leafhoppers will often walk or hop to escape from predation (Larsen et al. 1992). Dispersal tubes between the sides of mesocosms required leafhoppers to walk or hop horizontally between mesocosms; if tubes had connected the tops of mesocosms, flying, or vertical hopping movements might be facilitated between cages. As a

Table 2. Survival probabilities (±SE) and mean (±SD) *A. constricta* surviving per day in response to varied isolation and damsel bug density

Dispersal	Density	Time	Survival probability (±SE)	Mean *A. constricta* (±SD)
5a	1	24	0.427 ± 0.024	20.63 ± 6.2
		72	0.261 ± 0.022	11.50 ± 5.8
		120	0.149 ± 0.018	7.88 ± 2.5
		168	0.0551 ± 0.012	4.13 ± 3.1
5a,b	2	24	0.400 ± 0.025	19.25 ± 6.7
		72	0.153 ± 0.018	7.88 ± 4.1
		120	0.100 ± 0.016	4.75 ± 3.0
		168	0.0634 ± 0.013	2.88 ± 2.2
30a,b	1	24	0.359 ± 0.024	18.00 ± 5.1
		72	0.228 ± 0.021	11.38 ± 4.6
		120	0.151 ± 0.018	8.00 ± 6.0
		168	0.0563 ± 0.012	3.38 ± 2.8
30b	2	24	0.370 ± 0.024	18.75 ± 5.0
		72	0.119 ± 0.016	6.38 ± 2.3
		120	0.046 ± 0.011	2.75 ± 1.3
		168	0.0214 ± 0.0074	1.38 ± 1.1
100b	1	24	0.354 ± 0.024	17.88 ± 9.9
		72	0.150 ± 0.018	7.38 ± 3.6
		120	0.0528 ± 0.012	3.00 ± 3.0
		168	0.0363 ± 0.010	2.25 ± 2.4
100b	2	24	0.373 ± 0.024	18.75 ± 6.3
		72	0.193 ± 0.020	9.75 ± 4.7
		120	0.0727 ± 0.013	3.88 ± 3.6
		168	0.0337 ± 0.0091	1.63 ± 2.8

'Dispersal' is the percentage of time per week that connecting tubes were open to movement. 'Density' is the density of damsel bugs per mesocosm. 'Time' is the hours since the experiment commenced. Different letters after dispersal treatments indicate a significant difference in survival probability ($P < 0.05$).
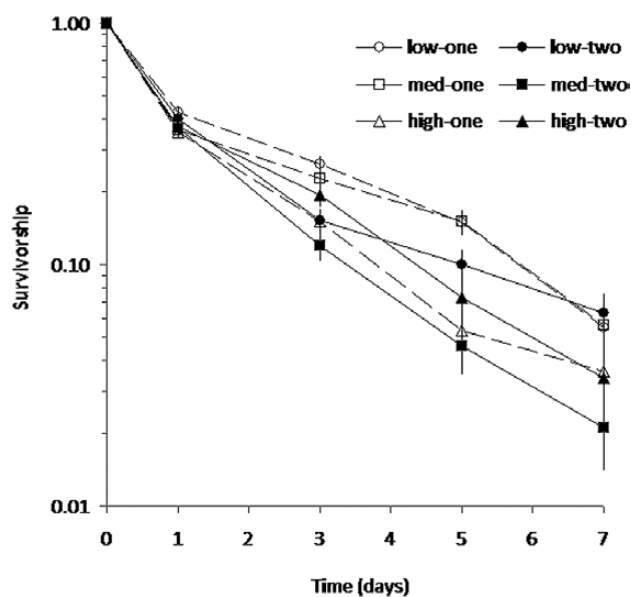

Fig. 3. Survival probability of *A. constricta*. The y-axis is plotted on a logarithmic scale. 'Low', 'med', and 'high' represent 5, 30, and 100% dispersal treatments, respectively. 'One' and 'two' represent one and two damsel bugs added per mesocosm.

result, leafhoppers may have also chosen to remain sedentary to escape predation rather than moving among habitat patches (Östman and Ives 2003), which is observed in planthoppers exposed to predation by spiders (Finke and Denno 2002, 2006).

Contrary to our predictions, damsel bug density had no effect on the dispersal rates of leafhoppers. Previous studies show that predator or parasitoid density does (Hauzy et al. 2007, Bowler et al. 2013) or does not (French and Travis 2001) influence prey dispersal. Parasitoid dispersal rates may increase as the parasitoid:host ratio increases, resulting in a decreased competition with the conspecifics (French and Travis 2001). Adult damsel bug densities peak at 1 bug m^{-2} at our field site (Stasek et al. unpublished data). Therefore, damsel bugs in the two-predator treatments might have increased their dispersal rates to avoid encounters with the conspecifics.

It was also predicted that the prey would have lower survival probabilities in habitat patches with two damsel bugs than those with only one damsel bug. The combined effect of the two damsel bugs preying on *A. constricta* resulted in slightly higher predation rates but did not double the predation rates found in the single damsel bug treatment (Table 2). As a result, leafhoppers may have been unable to escape predation in all treatments, resulting in a similar survival probability among dispersal treatments. Predator interference is another factor that would lower per predator feeding rates (Arditi and Akçakaya 1990), but other experiments in our study system showed no evidence of predator interference or cannibalism (Stasek 2009).

A. constricta had a higher survival probability in the 1-damsel bug/5% dispersal treatment compared with the 1-damsel bug/100% dispersal treatment, the 2-damsel bug/ 100% dispersal treatment, and the 2-damsel bug/30% dispersal treatment. Leafhoppers in the 100% dispersal treatment were predicted to have lower survival probabilities than the 5 and 30% dispersal treatments. We expected the damsel bug to move freely among communities in the 100% treatment and consume their leafhopper prey. However, we observed only three instances of damsel bugs moving among habitat patches in all of our trials. Because we did not mark damsel bugs individually to avoid altering *A. constricta*'s behavior, it is possible that damsel bugs may have moved among habitat patches at greater rates than we observed. Leafhoppers may have also emigrated from habitat

patches at greater rates than we observed, thus increasing their encounter rates with damsel bugs. Damsel bugs are voracious predators and may have consumed immigrating leafhoppers before we observed the interpatch movements.

There was no difference between the 5 and 30% dispersal treatments on leafhopper survival in the single damsel bug treatment, contrary to our predictions. We predicted that the 30% dispersal treatment would have the greatest survival time because a greater proportion of leafhoppers would disperse to other local communities to escape predation than in the 5% dispersal treatment, and damsel bugs would not be able to follow leafhoppers once the tubes were closed (Brown and Kodric-Brown 1977, Crowley 1981, Nachman 1987, Holyoak and Lawler 1996b). This was likely due to the fact that there was no difference in dispersal rates of leafhoppers between the 5 and 30% dispersal treatments.

Most experimental metacommunity studies use prototozoans to assess persistence due to their short generation times (Holyoak and Lawler 1996a,b; Forbes and Chase 2002; Kneitel and Miller 2003; Cadotte and Fukami 2005; Cadotte 2006; Hauzy et al. 2007). However, it is important to understand the short-term behaviors that influence dispersal among local patches, such as predation risk (Resetarits 2005), habitat quality (Binckley and Resetarits 2007), patch arrangement (Bull et al. 2006), number of habitat patches (Bonsall et al. 2002, 2005), and connectivity (Matthiessen et al. 2007, Start and Gilbert 2016). This study is one of the first experiments to manipulate dispersal rates of predators and prey on prey survival in insects. Our results demonstrated that neither conspecific nor predator density had an effect on dispersal rates, while dispersal treatment did affect dispersal rates of leafhoppers with 100% treatment having a greater number of leafhoppers moving among habitat patches. This suggests that dispersal is key to understanding short-term persistence in predator-prey metacommunities. Dispersal rates expressed per generation could be 2–3 times larger in longer term, multigenerational experiments. Further work is needed to determine the factors which facilitate or hinder dispersal of predators and their prey in metacommunities and how predator numerical response and dispersal rates vary in response to prey patches.

Future experiments should focus on varying both predator and prey densities as well as dispersal rates to determine the factors influencing predation rates of predators within generations. Variation in intraspecific and interspecific dispersal rates has only been conducted in a few studies (Bernstein 1984, French and Travis 2001, Hauzy et al. 2007). *A. constricta* densities in the field vary dramatically over the course of spring and summer with a peak density occurring in late July and early August at our study site (Schroeder 2007). The numerical and functional responses of damsel bugs may also vary as *A. constricta* abundance changes, and damsel bugs may disperse more or less in response to the changing *A. constricta* densities.

Acknowledgments

References Cited

Antonious, G. F. 2004. Residues and half-lives of pyrethrins on field-grown pepper and tomato. J. Environ. Sci. Health. B. 39: 491–503.

Arditi, R., and H. R. Akçakaya. 1990. Underestimation of mutual interference of predators. Oecologia. 83: 358–361.

Baguette, M., and H. Van Dyck. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landsc. Ecol. 22: 1117–1129.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proc. Natl. Acad. Sci. U.S.A. 94: 10735–10738.

Bergerot, B., R. Julliard, and M. Baguette. 2010. Metacommunity dynamics: decline of functional relationship along a habitat fragmentation gradient. PLoS One. 5:1–6.

Bernstein, C. 1984. Prey and predator emigration responses in the acarine system *Tetranychus urticae-Phytoseiulus persimilis*. Oecologia. 61: 134–142.

Binckley, C. A., and W. J. Resetarits, Jr. 2007. Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. Oecologia. 153: 951–958.

Black, L. M. 1944. Some viruses transmitted by Agallian leafhoppers. Proc. Am. Philos. Soc. 88: 132–144.

Bonsall, M. B., D. R. French, and M. P. Hassell. 2002. Metapopulation structures affect persistence of predator-prey interactions. J. Anim. Ecol. 71: 1075–1084.

Bonsall, M. B., J. C. Bull, N. J. Pickup, and M. P. Hassell. 2005. Indirect effects and spatial scaling affect the persistence of multispecies metapopulations. Proc. Biol. Sci. 272: 1465–1471.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. Camb. Philos. Soc. 80: 205–225.

Bowler, D. E., S. Yano, and H. Amano. 2013. The non-consumptive effects of a predator on spider mites depend on predator density. J. Zoology. 289: 52–59.

Bowne, D. R., and M. A. Bowers. 2004. Interpatch movements in spatially structured populations: a literature review. Landsc. Ecol. 19: 1–20.

Braman, S. K., and K. V. Yeargan. 1989. Intraplant distribution of three *Nabis* species (Hemiptera: Nabidae), and impact of *N. roseipennis* on green cloverworm populations in soybean. Environ. Entomol. 18: 240–244.

Braman, S. K., and K. V. Yeargan. 1990. Phenology and abundance of *Nabis americoferus*, *N. roseipennis*, and *N. rufusculus* (Hemiptera: Nabidae) and their parasitoids in alfalfa and soybean. J. Econ. Entomol. 83: 823–830.

Briggs, C. J., and M. F. Hoopes. 2004. Stabilizing effects in spatial parasitoid-host and predator-prey models: a review. Theor. Popul. Biol. 65: 299–315.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology. 58: 445–449.

Bull, J. C., N. J. Pickup, M. P. Hassell, and M. B. Bonsall. 2006. Habitat shape, metapopulation processes and the dynamics of multispecies predator-prey interactions. j. Anim. Ecol. 75: 899–907.

Cadotte, M. W. 2006. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. Ecology. 87: 1008–1016.

Cadotte, M. W., and T. Fukami. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. Ecol. Lett. 8: 548–557.

Costa, A., A. Min, C. K. Boone, A. P. Kendrick, R. J. Murphy, W. C. Sharpee, K. F. Raffa, and J. D. Reeve. 2013. Dispersal and edge behavior of bark beetles and predators inhabiting red pine plantations. Agric. For. Entomol. 15: 1–11.

Cronin, J. T. 2003. Matrix heterogeneity and planthopper-parasitoid interactions in space. Ecology. 84: 1506–1516.

Cronin, J. T. 2007. From population sources to sieves: the matrix alters host-parasitoid source-sink structure. Ecology. 88: 2966–2976.

Cronin, J. T. 2009. Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. Ecology. 90: 196–207.

Cronin, J. T., and K. J. Haynes. 2004. An invasive plant promotes unstable host-parasitoid patch dynamics. Ecology. 85: 2772–2782.

Crowley, P. H. 1981. Dispersal and the stability of predator-prey interactions. Am. Nat. 118: 673–701.

Danner, B. J., and A. Joern. 2003. Resource-mediated impact of spider predation risk on performance in the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). Oecologia. 137: 352–359.

Dempster, J. P., D. A. Atkinson, and M. C. French. 1995. The spatial population dynamics of insects exploiting a patchy food resource: II. Movements between patches. Oecologia. 104: 354–362.

Denno, R. F., and M. A. Peterson. 1995. Density-dependent dispersal and its consequences for population dynamics, pp. 113–130. In N. Cappuccino and P.W. Price (eds.), Population dynamics: new approaches and synthesis. Academic Press, New York, NY, USA.

Donahoe, M. C., and H. N. Pitre 1977. *Reduviolus roseipennis* behavior and effectiveness in reducing numbers of *Heliothis zea* on cotton. Environ. Entomol. 6: 872–876.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Funct. Ecol. 21: 1003–1015.

Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology. 83: 643–652.

Finke, D. L., and R. F. Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia. 149: 265–275.

Fonseca, D. M., and D. D. Hart 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos. 75: 49–58.

Forbes, A. E., and J. M. Chase 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos. 96: 433–440.

Fox, G. A. 2001. Failure-time analysis: emergence, flowering, survivorship, and other waiting times, pp. 235–266. In S.M. Scheiner and J. Gurevitch (eds.), Design and analysis of ecological experiments, 2nd ed. Oxford University Press, New York, NY, USA.

French, D. R., and J. M. J. Travis. 2001. Density-dependent dispersal in host-parasitoid assemblages. Oikos. 95: 125–135.

Freund, R. L., and K. L. Olmstead. 2000. Role of vision and antennal olfaction in habitat and prey location by three predatory heteropterans. Environ. Entomol. 29: 721–732.

Hauzy, C., F. D. Hulot, A. Gins, and M. Loreau. 2007. Intra- and interspecific density-dependent dispersal in an aquatic prey-predator system. J. Anim. Ecol. 76: 552–558.

Haynes, K. J., and T. O. Crist. 2009. Insect herbivory in an experimental agroecosystem: the relative importance of habitat area, fragmentation, and the matrix. Oikos. 118: 1477–1486.

Haynes, K. J., and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. Ecology. 84: 2856–2866.

Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. Ecol. Res. 17: 261–273.

Holyoak, M., and S. P. Lawler. 1996a. Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. Ecology. 77: 1867–1879.

Holyoak, M., and S. P. Lawler. 1996b. The role of dispersal in predator-prey metapopulation dynamics. J. Anim. Ecol. 65: 640–652.

Holyoak, M., M. A. Leibold, N. Mouquet, R. D. Holt, and M. F. Hoopes, 2005. Metacommunities: a framework for large-scale community ecology, pp. 1–31. In M. Holyoak, M.A. Leibold, and R.D. Holt (eds.), Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, IL, USA.

IBM Corp. 2017. IBM SPSS Statistics for Windows, Version 25.0. IBM Corp. Armonk, NY.

Irwin, M. E., and M. Shepard 1980. Sampling predaceous hemiptera on soybeans, pp. 505–531. In M. Kogan and D. Herzog (eds.), Sampling methods in soybean entomology. Springer, New York, NY, USA.

Kalbfleisch, J. D., and R. L. Prentice, 1980. The statistical analysis of failure time data. Wiley, New York, NY, USA.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. Nature. 326: 388–390.

Kindler, S. D., W. R. Kehr, R. L. Ogden, and J. M. Schalk. 1973. Effect of potato leafhopper injury on yield and quality of resistant and susceptible alfalfa clones. J. Econ. Entomol. 66: 1298–1302.

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. Am. Nat. 162: 165–171.

Kondoh, M. 2003. Habitat fragmentation resulting in overgrazing by herbivores. j. Theor. Biol. 225: 453–460.

LaHue, D. W. 1936. An annotated list of the Bythoscopinae of Indiana (Cicadellidae, Homoptera). Proc. Indiana Acad. Sci. 45: 310–314.

Larsen, K. J., S. E. Heady, and L. R. Nault. 1992. Influence of ants (Hymenoptera: Formicidae) on honeydew excretion and escape behaviors in a Myrmecophile, *Dalbulus quinquenotatus* (Homoptera: Cicadellidae), and its congeners. J. Insect Sci. 5: 109–122.

Lattin, J. D. 1989. Bionomics of the Nabidae. Annu. Rev. Entomol. 34: 383–400.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7: 601–613.

Lingren, P. D., R. L. Ridgway, and S. L. Jones, 1968. Consumption by several common arthropod predators of eggs and larvae of two *Heliothis* species that attack cotton. Ann. Entomol. Soc. Am. 61: 613–618.

Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. Am. Nat. 154: 427–440.

Ma, J., Y. Z. Li, M. Keller, and S. X. Ren. 2005. Functional response and predation of *Nabis kinbergii* (Hemiptera: Nabidae) to *Plutella xylostella* (Lepidoptera: Plutellidae). Insect Sci. 12: 281–286.

Matthiessen, B., L. Gamfeldt, P. R. Jonsson, and H. Hillebrand. 2007. Effects of grazer richness and composition on algal biomass in a closed and open marine system. Ecology. 88: 178–187.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography. 28: 403–416.

Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. Am. Nat. 159: 420–426.

Nachman, G. 1987. Systems analysis of acarine predator-prey interactions. II. The role of spatial processes in system stability. J. Anim. Ecol. 56: 267–281.

Nielson, M. W. 1968. The leafhopper vectors of phytopathogenic viruses (Homoptera, Cicadellidae) taxonomy, biology, and virus transmission. U S Dep. Agric. Tech. Bull. 1382: 1–386.

Östman, Ö., and A. R. Ives. 2003. Scale-dependent indirect interactions between two prey species through a shared predator. Oikos. 102: 505–514.

Petraitis, P. S. 1998. Timing of mussel mortality and predator activity in sheltered bays of the Gulf of Maine, USA. J. Exp. Mar. Biol. Ecol. 231: 47–62.

Propp, G. D. 1982. Functional response of *Nabis americoferus* to two of its prey, *Spodoptera exigua* and *Lygus hesperus*. Environ. Entomol. 11: 670–674.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org.

Resetarits, W. J., Jr. 2005. Habitat selection behaviour links local and regional scales in aquatic systems. Ecol. Lett. 8: 480–486.

SAS Institute. 2003. SAS for Windows, Release 9.1. SAS Institute, Cary, NC.

Schmitz, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. Ecol. Lett. 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.

Schoener, T. W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2: 369–404.

Schotzko, D. J., and L. E. O'Keeffe. 1989. Comparison of sweep net, d-vac, and absolute sampling, and diel variation of sweep net sampling estimates in lentils for pea aphid (Homoptera: Aphididae), nabids (Hemiptera: Nabidae), lady beetles (Coleoptera: Coccinellidae), and lacewings (Neuroptera: Chrysopidae). J. Econ. Entomol. 82: 491–506.

Schroeder, B. J. 2007. Effects of landscape structure on generalist and specialist insect herbivores. M.S. thesis. Miami University, Oxford, OH, USA.

Schtickzelle, N., and M. Baguette. 2003. Behavioral responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. J. Anim. Ecol. 72: 533–545.

Start, D., and B. Gilbert. 2016. Host–parasitoid evolution in a metacommunity. Proc. R. Soc. B. 283: 1–8.

Stasek, D. J. 2009. Population responses of a generalist insect predator and its prey to patch characteristics in forage crops. Ph.D. dissertation, Miami University, Oxford, OH, USA.

Stasek, D. J., C. Bean, and T. O. Crist. 2008. Butterfly abundance and movements among prairie patches: the roles of habitat quality, edge, and forest matrix permeability. Environ. Entomol. 37: 897–906.

Wilson, M. C., J. K. Stewart, and H. D. Vail. 1979. Full season impact of the alfalfa weevil, meadow spittlebug, and potato leafhopper in an alfalfa field. J. Econ. Entomol. 72: 830–834.