Relative dispersal ability of a key agricultural pest and its predators in an annual agroecosystem

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HIGHLIGHTS

▶ Large-scale mark-capture experiments were conducted using protein markers.
▶ Relative dispersal abilities of an agricultural pest and its predators was measured.
▶ The dispersal ability of the pest fell near the average dispersal of its predators.
▶ *Lygus* did not escape its predators by out-dispersing them.

GRAPHICAL ABSTRACT
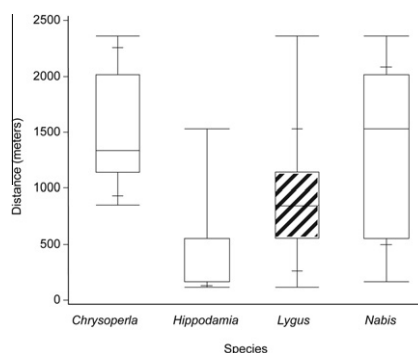
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ABSTRACT

In predator–prey interactions, a widely held view is that prey species have higher dispersal rates relative to their predators and are thereby able to escape from predation by colonizing habitats before their predators. Despite major implications for predator–prey interactions, community assembly, and biological control, this view has rarely been tested, and measuring relative dispersal abilities is often complicated by colonizing predators and prey originating from different locations. In California's San Joaquin Valley, the periodic harvest of alfalfa presents an opportunity to measure dispersal of a key generalist pest, *Lygus* spp., relative to a suite of its generalist predators. We performed a large-scale mark-capture study by marking a mature alfalfa field containing *Lygus* and its predators with an aerial application of a protein marker. The alfalfa was then harvested by the grower, prompting a dispersal event. At several times following harvest, surrounding cotton fields were sampled at known distances from the marked field to quantify movement by *Lygus* and its predators. Contrary to the general view, our data do not suggest that *Lygus* routinely out-disperses its suite of predators. Instead, the mean dispersal distance for *Lygus* fell near the average dispersal distances of its predators. Implications for biological control are discussed in light of these results, and the importance of predators' trophic strategy is stressed.

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1. Introduction

The importance of dispersal in the persistence of predator–prey interactions has long been recognized in the theoretical literature (Holyoak and Lawler, 1996; Kareiva, 1990; Taylor, 1990). Early models (reviewed in Taylor, 1990) demonstrated that if prey disperse into newly-available habitats without predators, they can escape control. Free of predators and without food limitation, these prey populations experience unrestrained population growth, which is checked only after colonization by predators or the

depletion of resources. Inherent in these models is the commonly held, but largely untested, assumption that prey have high dispersal rates relative to those of their predators. Differential dispersal has been demonstrated theoretically to be necessary for persistence of predator prey interactions in a metapopulation context (Hauzy et al., 2010; Taylor, 1990). It also underlies early empirical studies of the effects of spatial heterogeneity on predator prey interactions, where habitat patchiness promoted outbreaks of pests (Kareiva, 1987; Roland, 1993).

Despite theoretical evidence that differences in the relative dispersal ability of prey and their predators is important, empirical studies are rare. In terrestrial systems, empirical studies almost exclusively derive from research with insect hosts and their parasitoids (reviewed by Cronin and Reeve, 2005). In natural systems, the movement of parasitoids relative to their hosts (and relative to their competitors) has been investigated to understand patterns of species coexistence (Elzinga et al., 2007; Hopper, 1984; Roland and Taylor, 1997; van Nouhuys and Hanski, 2002). However, because these studies generally do not definitively identify the origins of migrants, movement distances cannot be directly quantified. Additionally, as noted by Cronin and Reeve (2005), these studies assess parasitoid movement using observations of the distribution of parasitized hosts. Parasitoids that disperse beyond the distribution of their dispersing hosts are not observed, and parasitoid dispersal ability may be underestimated using this method (Darrouzet-Nardi et al., 2006).

In aquatic systems, the dispersal of predators and their prey have been examined empirically on a landscape-scale to understand the drivers of community assembly (Hein and Gillooly, 2011; Shulman and Chase, 2007). These studies have demonstrated the importance of both dispersal and resource limitation in community assembly. Hein and Gillooly (2011) found that both predators and prey were dispersal limited, but did not explicitly state whether prey species out-dispersed predator species (or visa-versa). They also highlighted that the importance of dispersal limitation can change over time, suggesting that it is important to consider the transient state of these systems.

In annual agroecosystems, frequent disturbances create a system of patches continually in a transient state. Over the course of a growing season, annual crops change in their availability and suitability, necessitating frequent colonization and recolonization by pests and their predators (Wiedenmann and Smith, 1997; Wissinger, 1997). In such systems, early colonization of new crops by predators has been demonstrated both theoretically (Bianchi et al., 2009; Ives and Settle, 1997) and empirically (Landis and van der Werf, 1997; Settle et al., 1996) to be a key feature in their ability to suppress pest populations. As in early predator–prey models, these studies make the key assumption that pests have already colonized the patch; the early colonization by predators merely reduces the time lag between pest establishment and predator colonization (but see Settle et al., 1996). In these studies, predators and prey are not necessarily assumed to be emigrating from the same source (Bianchi et al., 2010, 2009) and dispersal events may not occur at the same time. Thus, it remains unclear how the relative dispersal abilities of predators and their prey affect their colonization abilities and subsequent interactions.

The periodic hay harvest of alfalfa (Medicago sativa L.) presents an opportunity to simultaneously study movement of a community of arthropods (Hossain et al., 2000; Pearce and Zalucki, 2005; Schaber et al., 1990), including plant bugs in the genus Lygus (Hemiptera: Miridae), which are important agricultural pests, and their suite of predators. Several species of Lygus often co-occur in California's San Joaquin Valley and are managed the same way in terms of agricultural systems. Thus, in this study we will refer to a combination of Lygus hesperus Knight and Lygus elisus Van Duzee simply as 'Lygus' (See Supplementary Data Appendix A for species'

frequencies for species' frequencies). Lygus feeds on a broad array of crops grown in California's San Joaquin Valley and displays a preference for several common crops, including alfalfa. Alfalfa is a perennial crop and a preferred host, and Lygus is thought to overwinter in alfalfa or colonize alfalfa fields early in the growing season. Large populations build up in alfalfa, peaking by the late spring (Sevacherian and Stern, 1975). The monthly harvest of alfalfa is thought to displace Lygus, and emigrants may serve as a major source of Lygus colonists for young cotton (Gossypium hirsutum L.) plantings. In cotton Lygus are major pests and can cause economic damage even at low densities (Rosenheim et al., 2006).

In addition to harboring Lygus, alfalfa typically contains a rich community of predators (Hossain et al., 2000), including several generalist insect predators that are potential control agents for Lygus, including damsel bugs (Nabis spp.; Perkins and Watson, 1972), big-eyed bugs (Geocoris spp.), and lacewings (Chrysoperla spp.; Hagler, 2011). Despite this suite of predators, the biological control of Lygus in most crops appears to be relatively weak. An understanding of the relative dispersal ability of Lygus and its predators may provide insight into the biological control of this important pest. If Lygus' dispersal ability is high relative to its predators, then one possible mechanism explaining why this pest is under poor control is that it escapes its predators in space.

Until recently, it has been technically difficult to estimate the relative dispersal abilities of pests and their predators on a scale relevant to crop colonization. Movement of populations of small arthropods has traditionally been studied using mark-release-recapture techniques. In most studies, insects are reared in the lab or collected en masse, marked in the lab, released back into the field at a central location, and then recaptured at known time and distance intervals. The need to mark individual insects limits the size of the population that can be marked, reducing the likelihood of detecting rare long-distance dispersal events. Additionally, as emigrants radiate out from a point source, marked individuals are spread over a progressively larger area as the distance from the release point increases resulting in an area dilution effect. To maintain high capture efficiency and minimize the area dilution effect, most movement experiments have been conducted on relatively small scales. The development of protein markers (Hagler and Jones, 2010; Jones et al., 2006), which are inexpensive and easy to obtain, make it possible to apply markers over a large area in the field with conventional spray equipment, creating a large population of marked individuals. Additionally, this method marks the entire arthropod community within the sprayed area, allowing for the movement of more than one species to be quantified simultaneously.

Using protein marking, we performed a large-scale mark-capture experiment to quantify the relative dispersal abilities of Lygus, an economically important pest in cotton, and its key predators. We marked alfalfa fields and studied the movement of Lygus and its predators following the monthly hay harvest of the alfalfa. These dispersal events likely represent a common situation in the agricultural landscape, where a high-quality habitat becomes rapidly unsuitable and acts as a source of colonists to suitable habitats in the surrounding landscape.

2. Materials and methods

2.1. Study system

Experiments were conducted on three commercial farms in California's San Joaquin Valley: (i) at Buttonwillow Land and Cattle (35°25′31.79″N and 119°24′42.08″W) in May 2006; (ii) at J.G. Boswell Company (35°56′4.75″N and 119°34′23.90″W) in June 2007; and (iii) at Bowles Farming Company (37°7′32.51″N and 120°45′7.58″W) in June 2008. We will first describe elements

common to all experiments (Sections 2.2 and 2.3), and then provide details specific to each experiment (Section 2.4). Each site consisted of an alfalfa field adjacent to a continuous stretch of young cotton. To minimize the complicating effects of habitat type on movement rates (Ovaskainen, 2004), we only measured colonization into continuous stretches of cotton fields. Cotton is an annual crop and does not support a community of overwintering insects, so the density of *Lygus* builds over the cotton growing season. Conversely, the *Lygus* population in alfalfa, a perennial crop, is more stable over the year. We conducted this study early in the cotton growing season, when cotton was beginning to produce flower buds and become a suitable host for *Lygus* but the resident community was still small, to increase the prevalence of marked individuals in our samples. The likelihood that a sample included marked individuals was higher early in the growing season, as *Lygus* that leave alfalfa were dispersing into a small recipient *Lygus* population.

2.2. Mark-capture method

To describe the movement of *Lygus* and its predators resulting from the harvest of alfalfa, we conducted large-scale mark-capture studies using protein marking (Hagler, 1997; Jones et al., 2006). Insect communities in commercial alfalfa fields were marked in the field using crude food proteins: bovine casein (applied as cow's milk; Kirkland Signature, Seattle, WA) or chicken egg albumin (as chicken egg whites; Egg Starts®, Kirkland Signature, Seattle, WA). Marks were applied aerially by a crop duster. The efficacy of these markers in field applications has previously been confirmed (Hagler and Jones, 2010), and was evaluated here by testing individuals collected from the marked alfalfa field (Table 1). Within 24 h of marking, the alfalfa field was harvested by the grower, prompting a dispersal event. Surrounding cotton fields were sampled for marked insects at fixed distances measured from the edge of the harvested alfalfa field 1 day after harvest, and this sampling was repeated at least once on a later day. Collected insects were sorted in the lab, and adult *L. hesperus*, *L. elisus*, *Geocoris* spp., *Chrysoperla carnea* spp. (Stephens), *Hippodamia convergens* Guérin-Méneville, and *Nabis* spp. were identified and sexed (for relative abundance see Table 2). 'Nabis' consisted of *Nabis alternatus* Parshley (most common in this system) and *Nabis americoferus* Carayon (much less common). *C. carnea* spp. is a complex of species whose systematics remain unresolved (M. Tauber and K. Tauber, Personal communication). *Geocoris* spp. is a combination of *Geocoris pallens* Stål and *Geocoris punctipes* (Say).

2.3. Detecting marked individuals

Collected insects were analyzed for the presence of both egg albumin protein and milk casein protein using protein-specific enzyme-linked immunosorbent assays (ELISA) described by Hagler and Jones (2010). The amount of protein detected by the ELISA is reported as a continuous optical density (OD) score, and a threshold must be chosen to classify individuals as marked or unmarked. It is important to choose a threshold that minimizes classification errors that can create erroneous patterns in the data set, by first characterizing the distribution of OD scores for the unmarked and marked populations. False positives (unmarked individuals misclassified as marked) are especially problematic in dispersal studies, where they can inflate estimates of long-distance dispersal (Sivakoff et al., 2011). To estimate the distribution of OD scores, we collected control individuals from both the alfalfa and cotton fields before the mark was applied, and then used the control OD scores to estimate the distribution of the unmarked population. We collected individuals from the alfalfa field after it was sprayed with the protein mark, but before the field was cut to establish the distribution of OD scores for the marked population. We characterized the OD distributions separately for each of our focal species. Following Sivakoff et al. (2011) we set a threshold for each species that was associated with a very low (approximately 1 in 1000) false positive rate. Individuals were classified as marked or unmarked using the chosen threshold, and the number of marked individuals was adjusted to account for the false positive rate. For details on the unmarked and marked OD distributions, chosen thresholds, associated false positive rates, and method of correcting for false positives, see Appendix B. To determine the extent of aerial drift of the applied marking solution, we also collected samples from cotton fields surrounding the sprayed alfalfa field after we applied the protein marker solution but before the sprayed field was harvested.

2.4. Experimental design

2.4.1. Experiment 1
On May 29, 2006, a 29.14 ha flowering alfalfa field was sprayed with a 5% milk solution, applied aerially by a commercial crop duster. Within 24 h of marking, the alfalfa field was harvested by the grower. One day after harvest (May 30, 2006) we sampled contiguous cotton fields to the east of the marked field. Samples were collected at eight distances from the eastern edge of the harvested alfalfa field: 10, 50, 100, 150, 200, 400, 600, and 800 m. Samples were collected using an aerial sweep net along transects that ran parallel to the edge of the harvested field. Sampling was repeated 7 days after harvest on June 5, 2006, with additional samples collected at 1000 and 1200 m from the harvested field. A sample consisted of 200 m of sweeping, and at least ten samples were collected at each distance.

2.4.2. Experiment 2
On May 30, 2007 we sprayed the 16.19 northernmost ha of a 119-ha alfalfa field with a 20% egg white solution. The field was cut by the grower the following day. In this landscape we had a large continuous stretch of cotton to the north of the sprayed field, and samples were collected 1, 5, and 12 days (June 1, 5, and 12) after harvest at 10, 50, 100, 200, 400, 800, 1300, 1600, 2400, 3200, 4000, and 4800 m from the northern edge of the focal alfalfa field. Samples were collected using a handheld vacuum (STIHL®, Andreas Stihl Ag & Co. KG, Waiblingen, Germany) instead of sweep nets to increase sampling efficiency. On each sampling day, and at each distance, we took 10 samples, with each sample defined as 200 m of suction sampling with the vacuum at full force.

2.4.3. Experiment 3
On June 18, 2008, the insect community in a 5.67 ha section of an 32.78 ha alfalfa field was marked using a solution of 40% cow's milk and 20% chicken egg whites. The sprayed alfalfa field was harvested on June 20, prompting a dispersal event. Surrounding cotton

Table 1
Marking efficiency of the milk and egg marks for the 2007 and 2008 experiments, measured as the proportion of marked individuals collected from the marked alfalfa field before it was harvested. In 2007, only the egg mark was used. No marking efficiency data were collected for the 2006 experiment.

Year	Species	Egg	Milk
2007	Geocoris spp.	0.61 (11 of 18)	N/A
	Hippodamia convergens	0.65 (17 of 26)	N/A
	Lygus spp.	0.76 (38 of 50)	N/A
	Nabis spp.	1.00 (24 of 24)	N/A
2008	Chrysoperla carnea spp.	1.00 (6 of 6)	0.67 (4 of 6)
	Geocoris spp.	0.32 (48 of 152)	0.15 (23 of 152)
	Hippodamia convergens	1.00 (39 of 39)	0.72 (28 of 39)
	Lygus spp.	0.97 (154 of 159)	0.41 (65 of 159)
	Nabis spp.	1.00 (24 of 24)	0.83 (20 of 24)

Table 2
Lygus spp. and cotton predators collected and marked in cotton. Mean distance flown estimates and standard errors (in meters) corrected for sampling intensity, sampling area, and false positive rate.

Species	2006			2007			2008		
	Number Collected	Number Marked of those Collected	Mean Distance Flown (meters) ± SE	Number Collected	Number Marked of those Collected	Mean Distance Flown (meters) ± SE	Number Collected	Number Marked of those Collected	Mean Distance Flown (meters) ± SE
Chrysoperla carnea spp.	na*	na	na	na*	na	na	1233	12	1637 ± 136
Geocoris spp.	2600	57	774 ± 56	1257	20	3158 ± 301	1099	2	NA
Hippodamia convergens	213	6	684 ± 107	409	0	na	631	11	1037 ± 177
Lygus spp.	32	1	na	198	0	na	1066	24	1157 ± 114
Nabis spp.	48	0	na	409	7	4516 ± 421	213	27	1637 ± 101

fields to the south and west of the sprayed area were sampled for marked insects at 50, 100, and 200 m and at 50, 100, 200, 500, 800, 1100, 1500, 2000, and 2350 m to the north (upwind of the sprayed area). Samples were collected 1, 3, and 5 days after harvest, and on each day, at each distance, we took 14–60 samples (median = 15). Similar to 2007, samples were collected using a handheld vacuum, with a single sample defined as 200 m of suction sampling with the vacuum at full force. While samples were collected in three cardinal directions, only samples collected to the north of the sprayed areas were used in the analysis, as a result of downwind drift of the protein mark.

2.5. Statistical analysis

The differences in experimental design between the 3 years prompted us to analyze each experiment separately. For each experiment, we performed a randomization test (Resampling stats for excel 2007© statistics.com LLC, Arlington, VA) to determine if species differ in their mean dispersal ability. An analysis of variance (ANOVA) using the original data, where species identity of marked individuals was the treatment and the response variable was the distance traveled by each marked individual was used to estimate an F statistic. The F statistic from this ANOVA was then compared to the distribution of F statistics generated from resampling the data 10,000 times. The number of cases that were greater than or equal to the original F statistic were counted. This number was divided by 10,000 to produce an approximate P-value for the randomization test. To explore whether particular pairs of species differed in their mean dispersal distance, we repeated the process with the relevant subset of the observations.

2.6. Mean distance flown

To estimate mean distance traveled for each species, movement estimates were adjusted to correct for the differences in area of the sampled annuli and for the number of samples taken at each distance (e.g. Fletcher, 1974). The total number of marked individuals in the ith annulus would then be proportional to the density of marked individuals multiplied by the area of the annulus:

$$\frac{n_i}{m_i}(r_{2i}^2 - r_{1i}^2) \tag{1}$$

where, for the ith annulus, r_{1i} is the inner radius and r_{2i} is the outer radius, n_i is the total number of marked individuals, and m_i is the number of samples collected. The relative frequency (i.e. the proportion of the total dispersing marked population in the ith annulus) is:

$$f_i = \frac{n_i}{m_i}(r_{2i}^2 - r_{1i}^2) \bigg/ \sum_i \frac{n_i}{m_i}(r_{2i}^2 - r_{1i}^2) \tag{2}$$

The mean distance flown (MDF) is then estimated:

$$\text{MDF} = \sum_i \hat{f}_i \frac{1}{2}(r_{2i} + r_{1i}) = \sum_i f_i \bar{r}_i \tag{3}$$

where $\bar{r}_i = 1/2(r_{2i} + r_{1i})$ \hfill (4)

Given the likely ability of C. carnea and H. convergens to disperse farther than our furthest sampling location, the measures of mean distance flown are minimum estimates. The correction tends to increase mean dispersal distance estimates, because it weighs more heavily the few individuals that were recaptured at the greatest distances from the alfalfa field, where dispersing individuals are expected to be diluted in space.
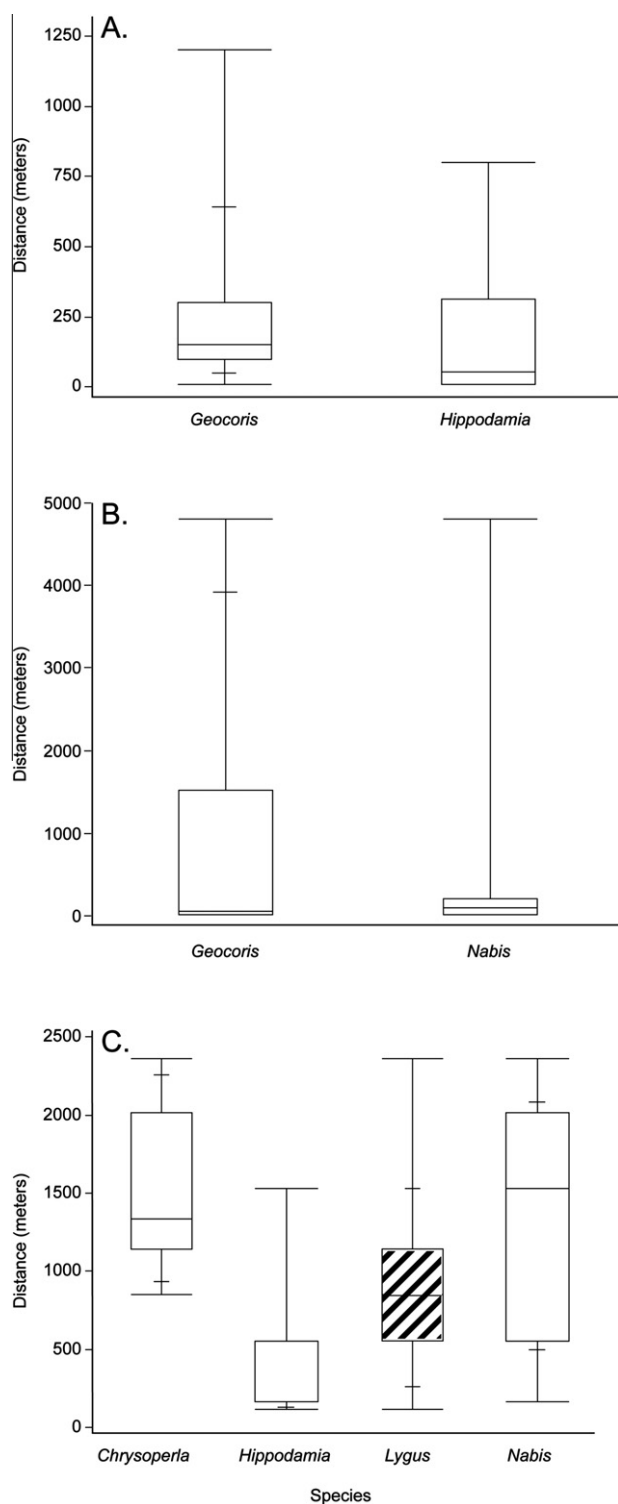
Fig. 1. Box plot displaying differences in species' movement in the (A) 2006, (B) 2007, and (C) 2008 experiments. The whiskers on the box plot indicate the quantiles. The box with the crosshatching indicates *Lygus*, the pest species. The other species are predators.

3. Results

Positive control samples confirmed the field efficacy of the milk and egg marks, although marking efficiency varied across years and target insect (Table 1). Experiments conducted in 2006 and 2007 generated dispersal estimates for some of the predator species. In 2006, we collected marked individuals of the predators *Geocoris* spp. (captures ranged from 10 to 1200 m, Appendix C) and *H. convergens* (captures ranged from 10 to 800 m, Appendix C), in addition to a single marked *Lygus* that was collected 800 m away from the edge of the marked alfalfa field. The randomization test (using the predators) indicated that there was no significant difference in the mean dispersal distances between these predators ($P = 0.13$; Fig. 1A). In 2007 we collected marked individuals of the predators *Geocoris* spp. (captures ranged from 10 to 4800 m, Appendix C) and *Nabis* spp. (captures ranged from 10 to 4800 m, Appendix C). As in 2006, the randomization test for the 2007 data indicated that there was no significant difference in the mean dispersal distances between these predators ($P = 0.90$; Fig. 1B).

Only the 2008 experiment provided data to allow a direct comparison between *Lygus* movement and that of its natural enemies, it appears that *Lygus'* mean dispersal distance falls between those of its predators (captures ranged from 50 to 2350 m, Fig. 1C, Table 2). In 2008, there were insufficient captures of marked individuals of *Geocoris* spp. (number marked = 2, captured at 50 and 1500 m), and these data were excluded from further analysis. The randomization test indicated that there was a significant difference in the dispersal distances across all species ($P < 0.001$). Pairwise contrasts revealed that on average *H. convergens* dispersed significantly shorter distances (captures ranged from 50 to 1500 m) than *Lygus* ($P = 0.034$), *Nabis* ($P = 0.0011$), and *C. carnea* ($P = 0.0004$). *Nabis* (captures ranged from 100 to 2350 m) and *C. carnea* (captures ranged from 800 to 2350 m) dispersed significantly farther than *Lygus* ($P = 0.017$ and $P = 0.002$, respectively), and there was no significant difference between the mean dispersal distance for *Nabis* and *C. carnea* ($P = 0.41$). Raw dispersal data for all marked individuals can be found in Appendix C.

Dispersal estimates using MDF were inconsistent between years for *Geocoris* and *Nabis* (Table 2). *H. convergens* mean dispersal estimates were similarly low in both 2006 and 2008 (684 ± 107 m vs. 1037 ± 177 m, respectively) compared to the other arthropods tested, whereas *Geocoris* dispersal estimates were quite different across years (774 ± 56 m vs. 3158 ± 301 m, respectively). This difference may be due to the very different lengths of the recapture transects for 2006 (1200 m) versus 2007 (4800 m). When the 2007 distances were limited to samples within 1300 m (the closest transect distance to 1200 m), the MDF for *Geocoris* was 1208 ± 83 m. *Nabis* movement estimates were also quite different in 2007 versus 2008 (4516 m vs. 1637 m, respectively), but the 2007 estimate was heavily influenced by a single long-distance movement event (Fig. 1B).

4. Discussion

The results from the mark-capture experiment demonstrate differences in the average distances *Lygus* and its predators dispersed. Recaptures of marked individuals moving from alfalfa into cotton suggest that *Lygus* does not out-disperse its suite of generalist predators. *Lygus* had an intermediate mean dispersal distance compared to its complex of generalist predators. In 2008, *Lygus'* mean dispersal was estimated to be greater than that for *H. convergens* but less than that for *Nabis* or *C. carnea*. Of the predators included in this study, *Geocoris* and *Nabis* are thought to be effective predators on eggs and early instars of *Lygus* (Hagler, 2011; Leigh and Gonzalez, 1976; Zink and Rosenheim, 2008). *C. carnea* and *H. convergens* will feed on *Lygus* nymphs in experimental settings (Hagler, 2011), but are not generally thought to be important predators of *Lygus* (Leigh and Gonzalez, 1976). While direct comparisons with *Geocoris* are not possible, comparing means dispersal distance across experiments suggests that *Lygus* does not disperse farther than either of its two main predators, *Geocoris* and

Nabis. Our results suggest that the reason why *Lygus* is not effectively controlled by its predators is not because it out-disperses them.

The large majority of studies examining the relative dispersal of insects have focused on the movement of parasitoids and their hosts (e.g. references in Cronin and Reeve, 2005; Elzinga et al., 2007). As discussed by Darrouzet-Nardi et al. (2006), a key challenge to interpreting these studies, which infer parasitoid movement through patterns of host parasitism, is that parasitoid movement cannot be ascertained without the host having first moved to the recapture site. Thus, these studies may underestimate the extent to which natural enemies are capable of dispersing farther than their hosts. A few studies do suggest that parasitoids may often be more mobile than their hosts. Darrouzet-Nardi et al. (2006) found the mean dispersal distance of the parasitoid *Platygaster californica* to be 4.5 m, while an earlier study estimated the average distance travelled by their female midge host, *Rhopalomyia californica*, to be 1.7 m (Briggs and Latto, 2000). Jones et al. (1996) performed a mark-release-recapture study of a tephritid fly, *Terellia ruficauda*, and four of its parasitoids. In that study, dispersal was measured directly using recaptured marked individuals, avoiding the challenges associated with estimating movement from parasitized hosts. All parasitoids moved farther than their host (Jones et al., 1996). Small-scale studies can provide key insights into local population dynamics, but may be less relevant to colonization processes that involve longer-distance movement events.

Few studies have examined the movement of prey relative to their predators at large spatial scales, despite calls for increased research in this area (Cronin and Reeve, 2005). In a seminal study, Cronin et al. (2000) quantified the long-distance dispersal of the beetle *Thanasimus dubius*, an important predator of the southern pine beetle, *Dendroctonus frontalis*. Using mark-release-recapture data fit with a heterogeneous diffusion model, Cronin et al. (2000) estimated that the radius containing 95% of dispersing *T. dubius* individuals was 5.1 km. They compared the pattern and range of movement of the predator to that of *D. frontalis,* whose 95% radius was estimated in Turchin and Thoeny (1993) to be 2.3 km, and concluded that predators were dispersing farther than their prey. Cronin et al. (2000) used estimated differences in the dispersal ability of the predator and its prey to address the formation of discrete *D. frontalis* infestations in a homogeneous landscape, as modeled by Mimura and Murray (1978). Just as Cronin et al. (2000) used their experimental results to inform theory, the biological control theoretical literature can be enriched with knowledge of relative dispersal abilities. As an example, optimal farmscape design of annual agroecosystems to enhance biological control would differ depending on the relative dispersal abilities of pests and their natural enemies. If pests routinely out-disperse their natural enemies, then strategies that enhance colonization of natural enemies (including augmentative releases, intercropping, etc.) will be important. Alternatively, if natural enemies out-disperse their prey, then different strategies, including potentially clumping of fields of a particular crop to create huge monocultures, may reduce pest densities (Segoli and Rosenheim, 2012).

In determining what species will be an effective predator, it is important to consider not only a predator's dispersal ability, but also its trophic strategy. For specialist predators, it seems reasonable to suggest that the most effective predators would be those that demonstrate similar dispersal ability to their prey, as this would avoid both of two adverse scenarios: (i) the prey out-disperses its predators and thus escapes from control, and (ii) the predator out-disperses its prey, and as a result lacks the food resources needed to sustain its population. The idea that specialist predators have dispersal abilities similar to those of their prey has been suggested in discussions of specialist species' responses to climate change (Berg et al., 2010). Generalist predators may be successful as early colonists, even if they out-disperse one of their prey species, because they may be able to subsist on alternate prey and build up large populations that subsequently suppress later-developing pest populations (Settle et al., 1996). We hypothesize that omnivorous predators, which can sustain their populations using plant-based resources, may have the largest advantage of all in temporary agroecosystems, as they may be able to sustain themselves when their prey are rare or completely absent, i.e. during the establishment of a new crop. *C. carnea* (Limburg and Rosenheim, 2001), *H. convergens* (Pemberton and Vandenberg, 1993), *Nabis* spp. (Stoner, 1972), and *G. punctipes* (Stoner, 1970) all use food resources provided by the cotton plant, feeding on extrafloral nectar and, in some cases, directly on plant tissues. In the absence of prey, plant resources increased the longevity of these predators. To our knowledge, these hypotheses linking trophic strategy to the evolution of dispersal behaviors have yet to be investigated formally.

The relative scale of *Lygus* movement found in our study, MDF = 1157 m, supports the inferences made by Carrière et al. (2006) who suggested that source populations up to 1500 m away have the potential to affect the population density of *Lygus* in a focal cotton field. Our results suggest that *Lygus'* dispersal ability is much greater than estimated by Bancroft (2005). Bancroft (2005) examined the movement of *Lygus* using a traditional mark-release-recapture study in a small field plot (samples were taken at distances up to 30 m away from a central release point) and found the mean dispersal distance to be 4.6 m/day, with 98% of the population dispersing less than 15.6 m/day in cotton, based on diffusion estimates. The difference in scale of investigation is likely the reason behind the differing conclusions with regards to *Lygus'* dispersal ability. Dispersal estimates in that study may have been lower because marked individuals were released in the middle of alfalfa and cotton fields that consisted of mature stands of vigorous host plants, habitats that are considered suitable for *Lygus* feeding and reproduction. In contrast, in our study, the host crop was harvested, and *Lygus* seeking feeding opportunities were forced to leave the field, potentially promoting longer distance movement. Schellhorn et al. (2008) also observed accelerated colonization rates by male *Diadegma semiclausum* parasitoids following plowing, as compared to movement behavior in undisturbed habitats.

Our study is limited by several issues common to large-scale experiments. Foremost among these is a lack of replication. Our objective in this study was to describe the colonization processes for mobile insects in large-scale commercial agriculture, implying that we needed to work at a large spatial scale. We conducted our experiments over three years in commercial farms where we had no control over the configuration of fields. As a result, the scale and sampling design of each experiment varied, and we were unable to make formal comparisons across years. Additionally, most of our sampling in cotton occurred in a single direction, preventing us from exploring hypotheses related to directional dispersal or the effects of the predominant wind direction. Despite these shortcomings, we suggest that the general insight gained from our study, that our focal pest species exhibited intermediate mean dispersal distances compared to its suite of generalist predators, will add to knowledge of spatial predator–prey interactions and biological control. Indeed, this general result reinforces the view emerging from recent studies of dispersal by parasitoids and their hosts (Elzinga et al., 2007; van Nouhuys and Hanski, 2002). Finally, as in most long-distance dispersal studies, our study suffers from small recapture sample sizes. These recapture rates would likely be improved if we used traps baited with semiochemicals (as in Cronin et al., 2000), but these have yet to be developed in our system. Alternatively, successful dispersal studies often recapture individuals in specialized habitats, as in the aquatic mesocosms used by

Hein and Gillooly (2011), but this is difficult to do in our system when working with generalist species.

5. Conclusions

The primary result of our study is that a harvest-triggered long-distance dispersal event, which is a central feature of ephemeral agroecosystems, did not result in *Lygus* out-dispersing its complex of generalist predators. This suggests that limited predator dispersal is not the primary mechanism explaining why *Lygus* is under poor biological control. *Lygus* is a key pest in cotton and other crops, and further work must be done to understand the population dynamics and dispersal of this important generalist pest. Our understanding of relative movement would be enriched by a larger data set that could fully characterize the dispersal curves for the predators and their prey. Additionally, it will be important to determine how the relative dispersal abilities of predators and prey might vary in heterogeneous instead of homogeneous patch types.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocontrol.2012.09.008.

References

Bancroft, J.S., 2005. Dispersal and abundance of *Lygus hesperus* in field crops. Environmental Entomology 34, 1517–1523.

Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A., Ellers, J., 2010. Adapt or disperse: understanding species persistence in a changing world. Global Change Biology 16, 587–598.

Bianchi, F.J.J.A., Schellhorn, N.A., Buckley, Y.M., Possingham, H.P., 2010. Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression. Ecological Applications 20, 2322–2333.

Bianchi, F., Schellhorn, N.A., van der Werf, W., 2009. Predicting the time to colonization of the parasitoid *Diadegma semiclausum*: the importance of the shape of spatial dispersal kernels for biological control. Biological Control 50, 267–274.

Briggs, C.J., Latto, J., 2000. The effect of dispersal on the population dynamics of a gall-forming midge and its parasitoids. Journal of Animal Ecology 69, 96–105.

Carrière, Y., Ellsworth, P.C., Dutilleul, P., Ellers-Kirk, C., Barkley, V., Antilla, L., 2006. A GIS-based approach for areawide pest management: the scales of *Lygus hesperus* movements to cotton from alfalfa, weeds, and cotton. Entomologia Experimentalis Et Applicata 118, 203–210.

Cronin, J.T., Reeve, J.D., 2005. Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. Proceedings of the Royal Society B: Biological Sciences 272, 2225–2235.

Cronin, J.T., Reeve, J.D., Wilkens, R., Turchin, P., 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. Oikos 90, 127–138.

Darrouzet-Nardi, A., Hoopes, M.F., Walker, J.D., Briggs, C.J., 2006. Dispersal and foraging behaviour of *Platygaster californica*: hosts can't run, but they can hide. Ecological Entomology 31, 298–306.

Elzinga, J.A., van Nouhuys, S., van Leeuwen, D.J., Biere, A., 2007. Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape. Basic and Applied Ecology 8, 75–88.

Fletcher, B.S., 1974. The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni*. V. The dispersal of adults. Australian Journal of Zoology 22, 189–202.

Hagler, J.R., 1997. Field retention of a novel mark-release-recapture method. Environmental Entomology 26, 1079–1086.

Hagler, J.R., 2011. An immunological approach to quantify consumption of protein-tagged *Lygus hesperus* by the entire cotton predator assemblage. Biological Control 58, 337–345.

Hagler, J.R., Jones, V.P., 2010. A protein-based approach to mark arthropods for mark-capture type research. Entomologia Experimentalis Et Applicata 135, 177–192.

Hauzy, C., Gauduchon, M., Hulot, F.D., Loreau, M., 2010. Density-dependent dispersal and relative dispersal affect the stability of predator–prey metacommunities. Journal of Theoretical Biology 266, 458–469.

Hein, A.M., Gillooly, J.F., 2011. Predators, prey, and transient states in the assembly of spatially structured communities. Ecology 92, 549–555.

Holyoak, M., Lawler, S.P., 1996. The role of dispersal in predator–prey metapopulation dynamics. Journal of Animal Ecology 65, 640–652.

Hopper, K.R., 1984. The effects of host-finding and colonization rates on abundances of parasitoids of a gall midge. Ecology 65, 20–27.

Hossain, Z., Gurr, G.M., Wratten, S.D., 2000. Effects of harvest on survival and dispersal of insect predators in hay lucerne. Biological Agriculture & Horticulture 17, 339–348.

Ives, A.R., Settle, W.H., 1997. Metapopulation dynamics and pest control in agricultural systems. American Naturalist 149, 220–246.

Jones, T.H., Godfray, H.C.J., Hassell, M.P., 1996. Relative movement patterns of a tephritid fly and its parasitoid wasps. Oecologia 106, 317–324.

Jones, V.P., Hagler, J.R., Brunner, J.F., Baker, C.C., Wilburn, T.D., 2006. An inexpensive immunomarking technique for studying movement patterns of naturally occurring insect populations. Environmental Entomology 35, 827–836.

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

Kareiva, P., 1990. Population-dynamics in spatially complex environments – theory and data. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 330, 175–190.

Landis, D.A., van der Werf, W., 1997. Early-season predation impacts the establishment of aphids and spread of beet yellows virus in sugar beet. Entomophaga 42, 499–516.

Leigh, T.F., Gonzalez, D., 1976. Field cage evaluation of predators for control of *Lygus hesperus* Knight on cotton. Environmental Entomology 5, 948–952.

Limburg, D.D., Rosenheim, J.A., 2001. Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). Environmental Entomology 30, 595–604.

Mimura, M., Murray, J.D., 1978. On a diffusive prey-predator model which exhibits patchiness. Journal of Theoretical Biology 75, 249–262.

Ovaskainen, O., 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. Ecology 85, 242–257.

Pearce, S., Zalucki, M.P., 2005. Does the cutting of lucerne (*Medicago sativa*) encourage the movement of arthropod pests and predators into the adjacent crop? Australian Journal of Entomology 44, 219–225.

Pemberton, R.W., Vandenberg, N.J., 1993. Extrafloral nectar feeding by ladybird beetles (Coleoptera, Coccinellidae). Proceedings of the Entomological Society of Washington 95, 139–151.

Perkins, P.V., Watson, T.F., 1972. *Nabis alternatus* as a predator of *Lygus hesperus*. Annals of the Entomological Society of America 65, 652-&.

Roland, J., 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia 93, 25–30.

Roland, J., Taylor, P.D., 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386, 710–713.

Rosenheim, J.A., Steinmann, K., Langellotto, G.A., Zink, A.G., 2006. Estimating the impact of *Lygus hesperus* on cotton: the insect, plant, and human observer as sources of variability. Environmental Entomology 35, 1141–1153.

Segoli, M., Rosenheim, J.A., 2012. Should increasing the field size of monocultural crops be expected to exacerbate pest damage? Agriculture, Ecosystems, and Environment 150, 38–44.

Schaber, B.D., Harper, A.M., Entz, T., 1990. Effect of swathing Alfalfa for hay on insect dispersal. Journal of Economic Entomology 83, 2427–2433.

Schellhorn, N.A., Bellati, J., Paull, C.A., Maratos, L., 2008. Parasitoid and moth movement from refuge to crop. Basic and Applied Ecology 9, 691–700.

Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A.S., Sartanto, P., 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77, 1975–1988.

Sevacherian, V., Stern, V.M., 1975. Movement of *Lygus* bugs between alfalfa and cotton. Environmental Entomology 4, 163–165.

Shulman, R.S., Chase, J.M., 2007. Increasing isolation reduces predator:prey species richness ratios in aquatic food webs. Oikos 116, 1581–1587.

Sivakoff, F.S., Rosenheim, J.A., Hagler, J.R., 2011. Threshold choice and the analysis of protein marking data in long-distance dispersal studies. Methods in Ecology and Evolution 2, 77–85.

Stoner, A., 1970. Plant feeding by a predaceous insect, *Geocoris punctipes*. Journal of Economic Entomology 63, 1911–1915.

Stoner, A., 1972. Plant feeding by *Nabis*, a predaceous genus. Environmental Entomology 1, 557–558.

Taylor, A.D., 1990. Metapopulations, dispersal, and predator prey dynamics – an overview. Ecology 71, 429–433.

Turchin, P., Thoeny, W.T., 1993. Quantifying dispersal of Southern pine beetles with mark recapture experiments and a diffusion model. Ecological Applications 3, 187–198.

van Nouhuys, S., Hanski, I., 2002. Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. Journal of Animal Ecology 71, 639–650.

Wiedenmann, R.N., Smith, J.W., 1997. Attributes of natural enemies in ephemeral crop habitats. Biological Control 10, 16–22.

Wissinger, S.A., 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biological Control 10, 4–15.

Zink, A.G., Rosenheim, J.A., 2008. Stage-specific predation on *Lygus hesperus* affects its population stage structure. Entomologia Experimentalis et Applicata 126, 61–66.