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Stage-specific predation on *Lygus hesperus* affects its population stage structure

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Abstract

Evidence suggests that prey can vary in their susceptibility to predation depending on their developmental stage. Stage-dependent predation is of particular importance to integrated pest management, because it is often a particular developmental stage of a pest that causes the majority of the damage to the crop. An understanding of stage-dependent biocontrol is therefore important for predicting the ultimate impact of herbivore populations. In this article, we addressed this issue by focusing on the stage structure of *Lygus hesperus* Knight (Heteroptera: Miridae) populations in cotton as related to the density of a specific generalist predator. We first demonstrated in a field experiment that *Geocoris* spp. adults suppressed *L. hesperus* eggs and/or early instars (first through third), but did not suppress fourth through fifth instars or adult *L. hesperus*. We then demonstrated that this stage-specific predation translated into season-long shifts in the stage structure of *L. hesperus* populations in cotton fields. Using weekly sweep counts across 21 separate cotton fields, we found a negative correlation between season-long *Geocoris* spp. densities and season-long densities of *L. hesperus* nymphs. In contrast, there was no such correlation between *Geocoris* spp. and *L. hesperus* adults. Taken together, these results suggest that *Geocoris* spp. predators influence the stage structure of *L. hesperus* populations in cotton, which in turn has the potential to affect patterns of cotton square damage and sampling bias when monitoring *L. hesperus* populations.

Introduction

Parasitism or predation pressure can influence the stage structure of a prey population when certain life stages of prey are more susceptible than others (Murdoch et al., 1987). Correspondingly, when certain developmental stages of a pest inflict a higher per capita level of damage to the crop, top-down effects on prey stage structure can translate into changes in long-term patterns of plant damage (Zink & Rosenheim, 2005). Generalist predators are considered effective biocontrol agents, because they often attack a wide range of developmental stages within their prey species; however, the rates of predation can vary dramatically across the developmental stages of a particular prey (Dyer & Gentry, 1999). Therefore, a proper characterization of stage-dependent susceptibility in prey is essential for predicting the population dynamics and control of a given pest species (Murdoch & Briggs, 1996; Grabenweger, 2003).

Lygus hesperus Knight (Heteroptera: Miridae) is a major pest of cotton throughout the San Joaquin Valley of California, CA, USA, responsible for large reductions in yields (Falcon et al., 1971; Leigh et al., 1988; Rosenheim et al., 2006). However, *L. hesperus* also shows ontogenetic shifts in overall feeding behavior, with different life stages causing different levels of damage to host plants (Ellsworth, 2000; Rosenheim et al., 2004; Zink & Rosenheim, 2005). Both *L. hesperus* adults and nymphs feed on developing cotton buds, injecting pectin-digesting salivary enzymes that cause cotton plants to abscise buds from fruiting branches (Strong & Kruitwagen, 1968; Strong, 1970; Cline & Backus, 2002). *Lygus hesperus* nymphs, however, may represent a particular problem for integrated pest management (IPM) in cotton, because they can inflict great damage to cotton flower buds while remaining relatively undetected in sweep net samples relative to *L. hesperus* adults (Zink & Rosenheim, 2004, 2005). Therefore, understanding the factors that influence *L. hesperus* stage structure

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(i.e., the ratio of nymphs to adults) should help to improve the effectiveness of IPM for *L. hesperus* in cotton.

In this article, we argue that previously documented differences in *L. hesperus* stage structure across cotton fields (Zink & Rosenheim, 2004) are influenced by the culling of *L. hesperus* eggs and nymphs (but not adults) by *Geocoris* spp. predators (Heteroptera: Miridae). It is generally recognized that populations of the generalist predator *Geocoris* spp. (big-eyed bugs) have the greatest potential to suppress *L. hesperus* populations in California cotton fields (University of California, 1996). Prey-selection experiments, for example, have revealed that *Geocoris punctipes* Say prefers *L. hesperus* over several other commonly encountered prey options (Hagler & Cohen, 1991). In field cage experiments, *Geocoris pallens* Stal produced clear suppression of *L. hesperus* nymphal populations, although the results for *L. hesperus* adults were inconclusive (Leigh & Gonzalez, 1976). Other work has also suggested that the effect of *Geocoris* spp. predation may be most pronounced on *L. hesperus* nymphs; Hagler et al. (1992) uncovered very low levels of *L. hesperus* egg antigen in the guts of *Geocoris* spp., suggesting that *Geocoris* spp. may not be eating *L. hesperus* eggs or female adults.

To resolve these questions surrounding stage-dependent predation by *Geocoris* spp., we conducted a field experiment that simultaneously examined the effects of *Geocoris* spp. predators on *L. hesperus* nymphs and adults. We also examined the population-level effect of this stage-specific suppression of *L. hesperus* by taking weekly samples of *L. hesperus* and *Geocoris* spp. nymphs and adults across 21 separate unsprayed cotton fields. To rule out the possibility of alternative predators affecting *L. hesperus* population structure, we also counted the numbers of *Nabis* spp. (Heteroptera: Nabidae) and *Zelus renardii* Kolenati (Heteroptera: Reduviidae) in these weekly samples. Together these two experiments address the potential role that *Geocoris* spp. is likely to play in cotton IPM through shaping the overall stage structure of *L. hesperus* populations.

Materials and methods

For our field experiment, we used large bags of insect netting to enclose the top six nodes of individual plants of upland cotton *Gossypium hirsutum* L. (Malvaceae). Twenty-four plants were chosen from each of two rows (48 plants total) of unsprayed cotton at the West Side field station, CA, USA on 7 August 2006. Before enclosing the plant, we searched and removed all predators and all visible *L. hesperus* (these were particularly abundant at the early-instar stages). We did not remove *L. hesperus* eggs and most likely missed some first instars of *L. hesperus*, as these stages are extremely difficult to see on the plant. Therefore, our treatments were performed across a natural distribution of eggs and a reduced but non-zero density of first-instar nymphs. We used a 2 × 2 factorial design, manipulating *Geocoris* spp. (present vs. absent) and *L. hesperus* stage (second–third instar nymphs vs. adults) for a total of 12 replicates per treatment. For the *Geocoris* spp. treatment, we added one male adult and one female adult, collected on the same day from a cotton field at the Shafter Research Station. *Lygus hesperus* were collected from alfalfa fields on the University of California Davis campus on 6 August and kept in a cooler for 24 h. For the adult *L. hesperus* treatment, we added two adult *L. hesperus* (one male and one female), and for the nymph *L. hesperus* treatment, we added one second–instar nymph and one third-instar nymph.

The number of *Geocoris* spp. and *L. hesperus* nymphs and adults were counted for all plants after 1 week (on 14 August 2006). Previous work suggested that, over the course of a week, the second- to third-instar nymphs that were added to the cages would grow to fourth–fifth instars. In our analyses, we examined the survival of adult *L. hesperus* with and without *Geocoris* spp. present as well as the survival of fourth- to fifth-instar *L. hesperus* nymphs with and without *Geocoris* spp. present. We were also able to compare the survival of first- to third-instar *L. hesperus* nymphs in sleeves with and without *Geocoris* spp. added, as these individuals were originally present in the natural background of *L. hesperus* eggs and first-instar nymphs that we did not remove.

The second study, involving season-long field correlations, was conducted in both conventional and organic fields of upland cotton, *G. hirsutum*, throughout the San Joaquin Valley, CA, USA, from late June through September. None of the fields were sprayed during the entire sampling period. The sampling protocol involved repeated sampling at weekly intervals in each of 10 fields in 1993 and 11 fields in 1994. The number of *L. hesperus* nymphs and adults were recorded for each sweep sample (irrespective of sex or instar). In addition, we recorded the numbers of nymphs and adults of *Geocoris* spp. predators, a mix of *G. pallens* (most common) and *G. punctipes* (Say) (often around 20%). To rule out the possibility of alternative predators affecting *L. hesperus* population structure, we also counted numbers of *Nabis* spp. and *Zelus renardii*. In our samples, '*Nabis*' was a mix of *Nabis alternatus* Parshley (most common) and *Nabis americoferus* Carayon (much less common).

All samples, consisting of 8–10 runs of 50 sweeps each, were taken in 1 day and averaged to get a weekly value for a field. These weekly averages were then averaged across all weeks sampled to obtain a season-long value. We returned to the same subset of the field for each week of the entire season so that this season-long average was representative of dynamics within a particular portion of a field. Because the individual sweeps were not conducted in the same exact spot each week, we used weekly means (rather than individual sweep samples within a week) as our sampling unit. When examining the correlation between predators and *L. hesperus*, we used the season-long values (averages of weekly values) to obtain a conservative estimate of overall *L. hesperus* suppression. Samples were taken across 6–15 weeks, depending on the field, a period that is long enough to include between one and two complete *L. hesperus* generations.

Due to the limited nature of our season-long correlative data set (i.e., 21 fields), and the recognition that there may be several predators that affect *L. hesperus*, we allocated our statistical power ($\alpha = 0.05$) to specifically test the hypothesis that *Geocoris* spp. was correlated with *L. hesperus* stage structure. We took this approach, because we knew from previous work that *Geocoris* spp. was clearly the most likely candidate for *L. hesperus* biocontrol (University of California, 1996). However, in recognizing that *Geocoris* spp. may not be the only explanation for variation in *L. hesperus* stage structure, we allocated an additional α ($= 0.05$) to test the hypothesis that other predators such as *Nabis* and *Zelus* spp. may have an effect on *L. hesperus*.

Results

Using a 2 × 2 factorial analysis of variance (ANOVA), the manipulative experiment revealed that the *Geocoris* spp. treatment reduced the densities of early-instar nymphs (first through third: F = 5.18, P = 0.028; n = 48; Figure 1). The same ANOVA revealed that both the *L. hesperus* treatment and the interaction term were non-significant (P = 1.0 and P = 0.572, respectively). Therefore, it appears that these early-instar nymphs were originally present as naturally occurring background eggs and first instars in all 48 plants, independent of treatment, at the beginning of the experiment. The *Geocoris* spp. treatment had no effect on the densities of later-instar nymphs (the nymph treatment that grew to fourth and fifth over the duration of the experiment: F = 0.000, P = 1.0; n = 48; Figure 1). In this same ANOVA, the *L. hesperus* treatment was highly significant ($P<0.0001$) and the interaction term was non-significant (P = 0.669). The *Geocoris* spp. treatment had no effect on *L. hesperus* adults in this experiment (F = 0.318, P = 0.575; n = 48; Figure 1). In this same ANOVA, the *L. hesperus* treatment was highly significant ($P<0.0001$) and the interaction term was non-significant (P = 0.575).

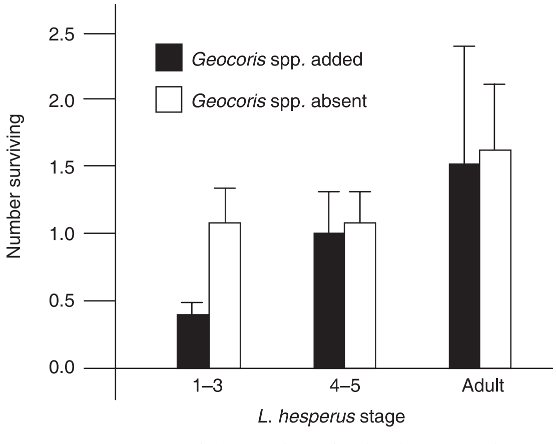

Figure 1 Means + SE of the number of individual *Lygus hesperus* surviving, with and without *Geocoris* spp. predators in the field cage experiment.

Field-level correlations showed season-long differences in the relative number of *L. hesperus* nymphs and adults, resulting in a spread of the proportion of nymphs that ranged from 33 to 71% nymphs. Across both years, there was a negative correlation between the season-long density of *Geocoris* spp. (nymphs plus adults) and the density of *L. hesperus* nymphs (R = –0.470, P = 0.032; n = 21; Figure 2A). This negative correlation also held when focusing on *Geocoris* spp. nymphs alone (R = –0.483, P = 0.026) or *Geocoris* spp. adults alone (R = –0.419, P = 0.059). There was no correlation between the season-long density of *Geocoris* spp. (nymphs plus adults) and *L. hesperus* adults (R = –0.051, P = 0.827; n = 21; Figure 2B). Similarly, there was no correlation between *L. hesperus* adults and *Geocoris* spp. nymphs alone (R = –0.156, P = 0.499) or *Geocoris* spp. adults alone (R = 0.038, P = 0.871).

Together, these relationships resulted in a significant negative correlation between *Geocoris* spp. density (nymphs plus adults) and the fraction of all *L. hesperus* individuals in a given field that were nymphs (i.e., stage structure: R = –0.488, P = 0.025; n = 21; Figure 2C). An angular transformation of this percentage data (arcsine of square root of percentage) revealed identical R- and P-values. This negative correlation also held when focusing on *Geocoris* spp. nymphs alone (R = –0.428, P = 0.053; n = 21) or *Geocoris* spp. adults alone (R = –0.495, P = 0.023; n = 21). A multivariate model of the relationship between *Geocoris* spp. and the number of *L. hesperus* nymphs including year was marginally non-significant (P = 0.06), suggesting that year-to-year variation may influence *L. hesperus* population dynamics over and above variation due to *Geocoris* spp.

When examining the effects of alternative predators, there was no correlation between the density of *Nabis* spp. (adults plus nymphs) or the density of *Z. renardii* (adults plus nymphs) and the number of *L. hesperus* nymphs in

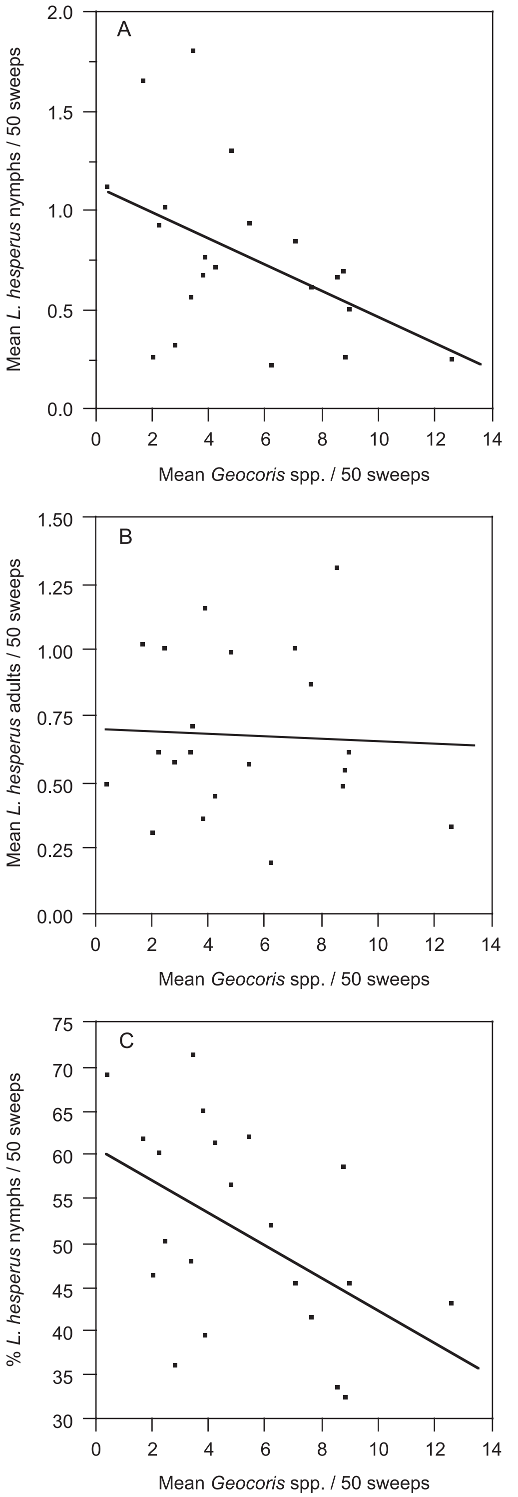

Figure 2 Correlations between season-long densities of *Geocoris* spp. (adults plus nymphs) and season-long densities of *Lygus hesperus* (A) nymphs, (B) adults, and (C) percentage of nymphs [where percentage = nymphs/(adults + nymphs)] across fields.

season-long sweep counts (r = –0.164, P = 0.477 and r = –0.076, P = 0.742, respectively; n = 21). This same lack of relationship existed when examining correlations between total number of *Nabis* or total number of *Z. renardii* and the densities of *L. hesperus* adults (r = 0.076, P = 0.743 and r = –0.231, P = 0.313, respectively; n = 21). In previous observations, we have specifically observed *Z. renardii* adults attacking and eating *L. hesperus* adults, so we also looked for a correlation between the season-long densities of *L. hesperus* adults and that of *Z. renardii* adults. There does appear to be a marginally non-significant negative relationship between the two, reflecting our observations and expectations (r = –0.420, P = 0.058; n = 21).

Discussion

Our manipulative experiment revealed that, within mesh enclosures, the earliest life stages of *L. hesperus* are susceptible to predation by *Geocoris* spp. In this same experiment, we found no such relationship with late-instar *L. hesperus* nymphs or adults. A second experiment used field correlations to examine the effects of stage-dependent predation on population stage structure. These season-long correlations suggested that *Geocoris* spp. nymphs and adults are a major influence on the season-long stage structure of *L. hesperus* populations in cotton fields via the suppression of *L. hesperus* nymphs, but not adults. Similarities of adult *L. hesperus* densities across cotton fields are most likely due to a high dispersal rate, which allows adults to continually colonize the fields that we sampled (including those areas in which *Geocoris* spp. are consistently culling *L. hesperus* nymphs). Even when *Geocoris* spp. densities are high, *L. hesperus* adults probably escape predation due to their large body size, as shown in other species that shift susceptibility across development (De Roos et al., 2003).

It is less clear that predators other than *Geocoris* spp. are having a significant impact on the stage structure of *L. hesperus* populations. In particular, we found no evidence that *Nabis* spp. are an important predator of *L. hesperus* nymphs or adults (Perkins & Watson, 1972). However, our finding that *Z. renardii* adults are marginally correlated with season-long densities of *L. hesperus* adults in cotton fields matched our observations (on more than one occasion) of *Z. renardii* adults eating *L. hesperus* adults. In addition to the possibility that predators other than *Geocoris* spp. are affecting *L. hesperus* population structure, it may be that the non-consumptive effects of *Geocoris* spp. on *L. hesperus* are contributing to the correlations found in this study. While our manipulative experiment clearly showed an effect of direct consumption, it is possible that *Geocoris* spp. predators cause the numbers of *L. hesperus* nymphs to decline through facultative dispersal by *L. hesperus* nymphs or, more likely, avoidance of plants with *Geocoris* spp. by egg-laying *L. hesperus* females. Future work will need to examine these potential effects of predators on *L. hesperus* foraging and oviposition.

In future work, it will be important to consider the specific foraging arena used by *Geocoris* spp., as it relates to aspects of cotton plant architecture. For example, other work has revealed that *Geocoris* spp. tend to forage in the middle nodes of cotton plants (Wilson & Gutierrez, 1980); this corresponds with the plant stratum that harbors the majority of square production. Early nymphal stages of *L. hesperus* are more likely to spend time in the concealed areas of squares (Rosenheim et al., 2004), so it is possible that these early-instar nymphs have a high encounter rate with *Geocoris* spp. Alternatively, these smaller nymphs may be more likely to escape capture by other predators by using concealed foraging locations, as has been demonstrated for *L. hesperus* eggs that escape predation by *Anaphes iole* due to aspects of host-plant structure (Udayagiri & Welter, 2000). Future work should consider the influence of alternative predators of *L. hesperus* as well as alternative prey of *Geocoris* spp., which feeds on a very wide range of prey species (Crocker & Whitcomb, 1980).

Overall, the natural history of the *Lygus–Geocoris* system conforms to theoretical assumptions dictating that stage-specific predation will influence stage structure. Specifically, (i) *L. hesperus* populations contain highly mobile adults that are likely to move in and out of the host-plant crop (Bancroft, 2005), and (ii) *Geocoris* spp. appear to be eating the less mobile stage of *L. hesperus* nymphs that remain in the field, independent of adult *L. hesperus* dispersal (Leigh & Gonzales, 1976). What is the long-term impact of this ability of *Geocoris* spp. to influence and stabilize the stage structure of *L. hesperus* on square retention and damage in cotton plants? Recent work has shown that later instars of *L. hesperus* can cause square shed that is comparable to that of adult *L. hesperus* (Zink & Rosenheim, 2005). Therefore, it is possible that higher *Geocoris* spp. densities will increase square retention through the reduction of *L. hesperus* nymphs. This effect may be a challenge to detect, however, as *L. hesperus* nymphs (particularly the early instars) are both more difficult to catch in a sweep net relative to adults and less frequently counted by field scouts (Zink & Rosenheim, 2004). Therefore, *Geocoris* spp. seems to play a particularly important role, by suppressing a *L. hesperus* stage that is both damaging and hard to detect through the standard sampling methods. We suggest that because *Geocoris* spp. plays an important role in cotton biocontrol, future work should focus on helping growers modify their decisions about controlling *L. hesperus* by incorporating *Geocoris* spp. abundance.

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