Intraguild predation of *Orius tristicolor* by *Geocoris* spp. and the paradox of irruptive spider mite dynamics in California cotton

Jay A. Rosenheim*

Department of Entomology, University of California, One Shields Avenue, Davis, CA 95616, United States

Received 12 May 2004; accepted 15 September 2004

Abstract

It is paradoxical when a community of several natural enemies fails to control a pest population when it can be shown experimentally that single members of the natural enemy community are effective control agents when tested individually. This is the case for spider mites, *Tetranychus* spp., in California cotton. Spider mites exhibit irruptive population dynamics despite that fact that experiments have shown that there are at least four predators (*Galendromus occidentalis*, *Frankliniella occidentalis*, *Orius tristicolor*, and *Geocoris* spp.) that, when tested singly, can suppress mite populations. One possible explanation for the paradox is intraguild predation, wherein one predator consumes another. Here, I evaluate the hypothesis that intraguild predation is a strong interaction among spider mite predators. I report manipulative field experiments, focal observations of freely foraging predators in the field, and population survey data that suggest that the minute pirate bug *O. tristicolor*, is subject to strong predation by other members of the predator community, and in particular by *Geocoris* spp. These results, combined with the results of prior work, suggest that pervasive intraguild predation among spider mite predators may explain the pest status of *Tetranychus* spp. in cotton.

Keywords: Intraguild predation; Predator–predator interactions; Herbivore population suppression; Spider mites; *Orius tristicolor*; *Geocoris pallens*; *Geocoris punctipes*; *Tetranychus* spp.; *Chrysoperla* spp.; *Nabis* spp.; *Zelus renardii*

1. Introduction

There are many potential reasons why herbivorous arthropod populations might fail to be regulated by their natural enemies (Evans and Schmidt, 1990; Messenger et al., 1976; Stiling, 1993). The failure of biological control becomes paradoxical, however, when manipulative experimentation demonstrates that single members of the natural enemy community can, in isolation, produce effective suppression of the herbivore population, whereas the full, unmanipulated predator community fails to generate herbivore suppression (e.g., Rosenheim, 2001; Snyder and Wise, 2001). These cases violate our general expectation that increasing natural enemy species diversity should lead to progressive declines in herbivore equilibrium density (Riechert and Bishop, 1990; Riechert and Lawrence, 1997; Snyder and Ives, 2003; Snyder et al., 2004; Sunderland, 1999). In some cases, antagonistic interactions between natural enemies, including intraguild predation, wherein one predator consumes another, may explain why natural enemy communities generate weaker suppression of herbivore populations than do single members of the same natural enemy community (Rosenheim, 1998).

California cotton is host to a three species complex of spider mites in the genus *Tetranychus* (Acari: Tetranychidae), including *Tetranychus pacificus* McGregor, *Tetranychus turkestani* Ugarov and Nikolski, and *Tetranychus urticae* Koch, that exhibit irruptive population dynamics (University of California, 1996). Although spider mite outbreaks may be triggered by the use of broad-spectrum insecticides for the control of other pests...
(e.g., Schoenig and Wilson, 1992), even in the absence of insecticide use spider mites can outbreak and defoliate cotton plants. The irritant dynamics of spider mite populations is paradoxical, because experimentation suggests that at least four groups of predators that are common in cotton can produce effective suppression of spider mites when tested singly: (1) the predatory mite Galedromus occidentalis (Nesbitt) (Acari: Phytoseiidae), the western flower thrips Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae), the minute pirate bug Orius tristicolor (White) (Hemiptera: Anthocoridae), and the big-eyed bugs Geocoris pallens Stål and Geocoris punctipes (Say) (Hemiptera: Lygaeidae) (Colfer et al., 2003; R.G. Colfer, pers. comm.; see also Wilson et al., 1991).

Could the failure of biological control by the full predator community be a reflection of intraguild predation? We know that the predators of spider mites can be arranged in a size-based ‘ladder’ of intraguild predation (Fig. 1; see also Schoenig and Wilson, 1992), and recent work has demonstrated that some of these predator–prey interactions can be strong. Colfer et al. (2003) demonstrated experimentally that Orius and Geocoris suppress populations of Galendromus below densities at which they can contribute to mite suppression. In large field plots, these interactions appear to prevent Galendromus populations from becoming established in cotton, even when they are artificially released early in the season under conditions of high prey availability and low densities of hemipteran predators (Colfer et al., 2004). Frankliniella can also consume the eggs of Galendromus and other predatory mites (Faraji et al., 2002; Janssen et al., 2002, 2003), although they do not appear to contribute to the suppression of G. occidentalis in California cotton (Colfer et al., 2003). Nothing is known about factors that might reduce the ability of Frankliniella to suppress mite populations; they appear to be important biological control agents very early in the season, but decline in abundance later as cotton is colonized by other predators. Whether or not this is a result of intraguild predation is not known. Finally, van den Bosch et al. (1956) hypothesized that Geocoris might be important in suppressing populations of Orius. They derived this hypothesis from a study of pesticide effects on the cotton predator community; direct pesticide toxicity to Orius was minimal, but in treatments where Geocoris and other predators were suppressed, populations of Orius were 2.3–5.5-fold greater than in untreated plots. A similar suggestion that Geocoris spp. might suppress Orius populations was made by Loya-Ramírez et al. (2003), who based their hypothesis on an observed seasonal decline in Orius densities that roughly coincided with an increase in Geocoris densities.

In this paper, I examine evidence that Orius, which occupies the next rung in the size-based ladder (Fig. 1), is suppressed by intraguild predation. Field observations have revealed that each of the larger hemipteran predators, Geocoris spp., Nabis spp. (including Nabis alternatus Parshley and Nabis americofurcatus Carayon; Hemiptera: Nididae), and Zelus renardii Kolenati (Hemiptera: Reduviidae) as well as lacewing larvae (Neuroptera: Chrysopidae) can prey on O. tristicolor (Rosenheim, 2001); because each of these predators also consumes spider mites (Cisneros and Rosenheim, 1998; van den Bosch and Hagen, 1966), they can be considered “intraguild predators” of Orius. I employ three complementary approaches to explore intraguild predation imposed on Orius: (1) manipulative field experiments employing small enclosures; (2) an estimate of predation risk derived from direct focal observations of O. tristicolor foraging freely in cotton; and (3) correlative evidence derived from surveys of arthropod population dynamics in organic cotton fields.

2. Materials and methods

2.1. Enclosure/exclosure experiments

A field experiment, replicated twice across different years, was conducted to quantify the impact of predators on the survival of O. tristicolor in the cotton agroecosystem. Data on survival of another predator, Chrysoperla carnea, and effects on aphid population growth have been reported previously (Rosenheim, 2001; Rosenheim et al., 1993), where the methodology is described in detail.

The first experiment was conducted 21–30 July, 1992 in an insecticide-free experimental planting of Gossypium hirsutum at the University of California Kearney Agricultural Center. Part or all of a single cotton plant...
was enclosed in a polyester mesh plant sleeve cage after searching the plant to remove all predators, including all motile stages of *O. tristicolor*. The polyester cage material (“Fibe-Air Sleeve”, Kleen Test Products) had an irregular weave, but was generally fine enough to confine the arthropods addressed in our study. All herbivores were retained. Cotton aphids, *Aphis gossypii* Glover and spider mites were the dominant herbivores present, and their densities were estimated to provide measures of prey availability. All aphids present in the cage were counted at the start and end of the experiment and the counts averaged to estimate aphid prey availability. Spider mites are too small to count accurately in the field; we instead estimated the proportion of the undersurface of all leaves that were covered with active mite colonies at the start and end of the experiment, and then averaged these measures.

Because *O. tristicolor* inserts its eggs into the plant substrate, each experimental plant harbored a natural cohort of *Orius* eggs. These eggs are, however, very cryptic, and I did not attempt to count them at the start of the experiment. Thus, the experiment was performed against a backdrop of the natural variation in the per-plant density of *Orius* eggs; this should add to the realism of the experiment, albeit at the cost of some reduction in statistical power, due to the unexplained variation in starting egg densities. I established eight treatments, each replicated 10 times: (1) *Orius* only; i.e., the full herbivore community was present along with the natural cohort of *O. tristicolor* eggs; (2) *Orius* + two *Zelus* adults; (3) *Orius* + two *Nabis* spp. adults; (4) *Orius* + two *Geocoris* spp. adults; (5) *Orius* + five larval *Chrysoperla* (young second instar); (6) *Orius* + two *Zelus* + five *Chrysoperla*; (7) *Orius* + two *Nabis* + five *Chrysoperla*; and (8) *Orius* + two *Geocoris* + five *Chrysoperla*. Treatments 6–8, which tested combinations of *Chrysoperla* with the hemipteran predators, were included because previous work (see Rosenheim, 2001) had demonstrated important interactions between these two groups of predators. The experiment ran for 7–8 days, sufficient time for all eggs initially present to hatch (incubation time is approximately 3 days; Askari and Stern, 1972) and develop through a portion of their nymphal development (development time is approximately 8 days; Salas-Aguilar and Ehler, 1977), at which time the number of live motile *Orius* in each enclosure was counted. Ants invaded some of the cages, where they tended the aphids and killed predators; all invaded replicates were excluded, leaving 6–10 intact replicates of each treatment. Data were transformed as ln(final *Orius* count + 0.5) to satisfy the assumption of equal variances and analyzed with ANCOVA to test for main effects of the presence/absence of *Zelus*, *Nabis*, *Geocoris*, and *Chrysoperla*, and with mean spider mite and aphid density included as covariates. Because only one main effect proved to be significant, I report a model without interaction terms; all two-way interactions were, however, non-significant (*P > 0.40*), and their inclusion did not change the qualitative outcome of the analysis. When the ANCOVA identified a significant main effect of a predator on *Orius* densities, I performed a pairwise contrast comparing *Orius* densities in the ‘*Orius* only’ treatment versus the ‘*Orius* + the predator’ to see if the predator acting singly was able to suppress *Orius* numbers.

The second experiment was conducted 22 August–2 September, 1994, and employed the same methodology with the following modifications. The same treatments (replicated 8–14 times) were established, but we added only a single adult predator in the + *Nabis* and + *Zelus* treatments, and used six immatures in the + *Chrysoperla* treatments (three eggs, two first instars, and one second instar). The experiment was run for 10 days. Spider mites were present at only extremely low densities, and thus we used only mean aphid density as an index of prey availability. The analysis followed that described for the first experiment; again, all two-way interaction terms were non-significant (*P > 0.10*), and I report the analysis without interaction terms.

2.2. Focal observations

The enclosure experiments produced evidence that *Orius* is subject to strong predation from *Geocoris* and *Chrysoperla*. However, many ecologists view with suspicion the results of experiments conducted with confined animals. To address this concern, I conducted focal observations of *Orius* nymphs and adults foraging freely in cotton to evaluate the predation hypothesis under field conditions. Estimating predation rates through focal observation is labor-intensive, and it is generally impossible to produce a precise estimate without a large amount of observation time (e.g., Rosenheim et al., 1999). Nevertheless, my expectation was that any predation events observed during a shorter period of observation would argue that the experimental results were not an artifact of caging.

Third-instar nymphal and adult *Orius* (N=20 replicates for each stage) were observed for 2-h focal periods in unsprayed cotton fields from 21 July–10 September 1997 and 26 August–22 September 1998 in the southern San Joaquin Valley of California. *Orius* were found by searching the upper canopy of randomly selected cotton plants. Observers worked in teams of two, one or both watching the predator and one recording data in a handheld computer running behavioral event recording software. All contacts with potential predators, including instances of intraguild predation, were recorded.

2.3. Survey data

I employed a set of observational population survey data to examine whether predation imposed on *Orius* by
Geocoris or Chrysoperla would be evident at the population level. Although correlational data generally provide only weak inferences regarding predator–prey interactions, I felt that it was worth exploring in this case for two reasons. First, even if Geocoris or Chrysoperla have a strong impact on Orius, it is unlikely that Orius represents a significant prey resource for either of these two generalists, which are known to feed primarily on aphids, mites, and thrips. Thus, the direction of causation underlying any possible correlations would be more readily interpretable. Second, I was able to control for the possible influences of the density of shared prey populations (aphids, mites, and thrips) by including these variables as covariates in the data analyses.

Ten insecticide-free cotton fields, including plots at university experimental sites and commercial organically managed farms, were sampled weekly on 6–14 successive occasions during 21 June–29 September, 1993 and 5 July–27 September, 1994 in the southern San Joaquin Valley. The densities of cotton aphids, spider mites, and thrips were estimated by collecting 50 mainstem leaves at the fifth node from the growing tip and holding them in 70% ethanol until they could be processed to remove all arthropods, which were then counted under a stereomicroscope. Predator densities were estimated by randomly selecting plants in the field, cutting them at their base, and carrying them to the edge of the field where they were carefully searched for larval stages of Chrysoperla and nymphal and adult stages of Orius, Geocoris, Nabis, and Zelus. Geocoris eggs were also counted (they are deposited on leaf surfaces and are readily sampled). Because Geocoris females enter reproductive diapause near the end of August, we used egg counts through 20 August in analyses of Geocoris reproductive response to varying prey availability. Adult Nabis and Zelus often flew off handled plants, and thus our measures produce underestimates for these adults. Predator density per plant was corrected for varying planting densities to estimate predator densities per m². Mean herbivore and predator population densities were calculated for each site (we calculated the area under the plot of density versus time, and divided by the total duration of the sampling period) to produce a single independent observation for each field site. We used simple bivariate linear regression to explore the data; however, the small sample sizes (N=10 for each year) mandate that the results be viewed as exploratory.

3. Results

3.1. Enclosure/exclosure experiments

3.1.1. Experiment 1

Plants caged with the full herbivore community present, but with the motile stages of all predators removed, had an average of 6.8±2.0 (SE) motile Orius present by the close of the experiment (Fig. 2A), demonstrating that plants harbored a large natural cohort of Orius eggs at the start of the experiment. All treatments with other predators present supported fewer Orius, but there was a significant main effect only for Geocoris (F₁,₆₂=5.0, P=0.03; main effects for Zelus, F₁,₆₂=0.06, P=0.81, for Nabis, F₁,₆₂=0.2, P=0.66; and for Chrysoperla, F₁,₆₂=1.9, P=0.17). The spider mite and aphid prey availability covariates were not significant predictors of final Orius density per cage (spider mites: F₁,₆₂=3.3, P=0.07; aphids: F₁,₆₂=0.2, P=0.62), suggesting that the negative effect of Geocoris on Orius was not due to enhanced competition for shared prey resources. When the prey availability covariates were omitted from the model, the main effect for Geocoris was still significant (F₁,₆₄=6.6, P=0.009) and the main effect for lacewings also became significant (F₁,₆₄=5.0, P=0.03). This hints at the possibility that Chrysoperla may suppress Orius at least partially through competition for shared prey.

Finally, the pairwise contrast of the Orius+Geocoris treatment versus the Orius alone treatment was significant (t=2.14, df=18, P=0.046), as was the pairwise contrast of the Orius+Chrysoperla treatment versus the
Geocoris pallens acting alone or Chrysoperla acting alone was able to reduce Orius densities.

3.1.2. Experiment 2

Plants caged with the full herbivore community present, but with predators other than Orius eggs removed, supported 7.6 ± 1.0 motile Orius at the close of the experiment (Fig. 2B), again consistent with a large initial cohort of Orius eggs on the plants. Orius densities were significantly suppressed by both Geocoris ($F_{1,73} = 4.0$, $P = 0.05$) and Chrysoperla ($F_{1,74} = 30.0$, $P < 0.0001$), but not by Zelus ($F_{1,73} = 2.8$, $P = 0.10$) or Nabis ($F_{1,73} = 0.06$, $P = 0.81$). As in Experiment 1, the mean density of aphids, the dominant herbivore prey available, was not significant when included as a covariate ($F_{1,73} = 0.05$, $P = 0.82$), suggesting that competition for prey was not the mechanism by which Geocoris and Chrysoperla suppressed Orius. The significant main effects for Geocoris ($F_{1,74} = 4.0$, $P = 0.05$) and Chrysoperla ($F_{1,74} = 30.0$, $P < 0.0001$) were still observed when the aphid density covariate was omitted. Finally, the pairwise contrast of the Orius + Geocoris treatment versus the Orius alone treatment was significant ($t = 2.33$, $df = 22$, $P = 0.029$), as was the contrast of Orius + Chrysoperla versus Orius alone ($t = 4.59$, $df = 21$, $P = 0.0002$).

3.2. Focal observations

Third-instar Orius ($N = 20$) were observed continuously in the field over a total period of 36.5 h, during which there were two instances of the focal Orius being attacked and eaten by another predator: one adult male Geocoris pallens and one adult female G. pallens. There were no contacts with potential intraguild predators from which the focal Orius escaped. Adult Orius ($N = 20$) were observed for 32.9 h, during which there were also two contacts with potential intraguild predators, both adult Geocoris. However, in each case the adult Orius retreated from the contact, and within a minute flew off the leaf on which it had been foraging. Thus, we observed no predation acting on adults, but significant predation acting on third instars (calculated mortality rate = 0.055 predation events per hour, or a half-life for Orius nymphs of 12.7 h). Given that Orius require approximately 10 days to complete their nymphal development (Salas-Aguilar and Ehler, 1977), and thus are exposed to predation risk by Geocoris for >100 daylight hours, these data suggest that direct predation on Orius by Geocoris may be important.

3.3. Survey data

3.3.1. 1993 Survey

I used simple bivariate linear regression to explore whether the ln-transformed mean density of Orius within cotton fields ($N = 10$) during the mid-to-late portion of the growing season was correlated with either the ln-transformed densities of herbivore prey or intraguild predators. Orius densities were positively correlated with densities of thrips ($r = 0.89$, $P = 0.0005$), but not with mites ($r = 0.53$, $P = 0.12$) or aphids ($r = 0.28$, $P = 0.43$). Among the intraguild predators, only Geocoris emerged as a significant negative correlate of Orius population density ($r = -0.67$, $P = 0.03$; Fig. 3); the other predators showed no association ($Zelus$, $r = -0.22$, $P = 0.53$; Nabis, $r = -0.33$, $P = 0.36$; Chrysoperla, $r = 0.30$, $P = 0.40$).

3.3.2. 1994 Survey

Mean Orius densities were not tightly correlated with any of the herbivores considered singly (mites: $r = 0.013$, $P = 0.97$; thrips: $r = 0.57$, $P = 0.09$; aphids: $r = 0.52$, $P = 0.13$), but were significantly correlated with the summed density of all herbivores per leaf (mites + thrips + aphids; $r = 0.64$, $P = 0.05$). In contrast to 1993, a significant negative correlation with Geocoris was not observed ($r = 0.04$, $P = 0.92$). None of the other predators was significantly correlated with Orius densities ($P > 0.3$).

Why might the results from 1993 and 1994 have differed with respect to detecting a negative relationship between Geocoris and Orius densities? Orius densities during 1994 were much higher (mean Orius per m², 127 ± 63) than during 1993 (22 ± 17), probably in response to the much greater availability of the dominant herbivore prey (aphids: mean densities during 1993, 33 ± 13 per leaf; 1994, 118 ± 48; mites: 1993, 27 ± 14; 1994, 113 ± 49; thrips: 1993, 1.8 ± 0.5; 1994, 21 ± 17). However, the mean density of Geocoris were somewhat lower during 1994 (9.9 ± 2.0) than during 1993 (13.3 ± 2.4). Thus, predation effects on Orius may have been weakened during 1994 because of the much smaller ratio of Geocoris to Orius. I conclude, then, that the
survey data support a consistently positive influence of resource (prey) availability on Orius population density, and an intermittent negative effect of Geocoris on Orius densities.

3.3.3. Geocoris response to prey availability

If a size-based ladder of intraguild predation interferes with top-down control of spider mite populations, what prevents the largest major predator of mites, Geocoris, from emerging as the key spider mite predator? The survey data provide an insight into this question: population densities of the motile stages of Geocoris were not correlated with spider mite densities in either 1993 or 1994 (Fig. 4). Nor did Geocoris densities show any increase in 1994 compared to 1993, despite the much larger availability of spider mite prey (mean density of spider mites per leaf: 1993, 27 ± 14; 1994, 113 ± 49). Furthermore, at least in 1993 this failure of Geocoris populations to demonstrate a numerical response to spider mite prey availability was not due to a failure of Geocoris females to elevate their reproduction when spider mite prey were plentiful: a measure of per capita reproduction (density of Geocoris eggs per adult Geocoris) was strongly positively correlated with spider mite population size ($r = 0.90, N = 9, P = 0.0009$); in 1994 this relationship was not significant ($r = -0.38, N = 9, P = 0.32$). Thus, at least during 1993 some factor appeared to prevent the elevated fecundity of Geocoris from being translated into larger populations of nymphs and adults. Finally, Geocoris showed no numerical response to alternate herbivore prey (aphids and thrips) in either of the years surveyed (data not shown).

4. Discussion

The main goal of the work reported here was to evaluate the impact of intraguild predation on Orius by the other dominant predators in cotton, including Geocoris, Nabis, Zelus, and Chrysoperla. The small-scale field enclosure experiments demonstrated a consistent suppressive effect of Geocoris on Orius; these two predators occupy the top two “rungs” in a size-structured ladder of intraguild predation among the dominant predators of spider mites (Fig. 1). Focal observations of Orius foraging freely in cotton documented four attacks by Geocoris adults on Orius, two of which were successful. These observations, although not well enough replicated to produce a good quantitative estimate of the predation rate, do support the conclusion from the enclosure experiments that Geocoris imposes substantial predation on Orius. Finally, despite the limited statistical power afforded by our population survey data set (only 10 fields sampled each year), the impact of Geocoris on Orius was detectable at the population level in one of the two survey years: we observed a negative relationship between the average seasonal densities of Geocoris and Orius. These three forms of evidence suggest that intraguild predation by Geocoris on Orius is a significant influence on Orius survivorship and population density in cotton. Whether this effect interferes with the ability of Orius to regulate spider mite populations was not addressed in this work. However, given that Orius effectively suppress spider mites when tested singly in small enclosures, but often fail to prevent persistent spider mite outbreaks when imbedded in the full predator community, it is clear that some factor or combination of factors other than food limitation is limiting the impact of Orius. Intraguild predation appears to be a strong candidate explanation. Ecologically significant intraguild predation by Geocoris on Orius was also supported by studies reported by van den Bosch et al. (1956) working in California and by Whitcomb and Bell (1964), who summarized extensive natural history observations in Arkansas cotton by writing that Geocoris spp. attack Orius spp. “consistently”.

Geocoris is one member of what is likely to be a group of predators that imposes a strong risk of intraguild predation on Orius. The enclosure experiments demonstrated...
that *Chrysoperla* spp. lacewings also have the potential to suppress *Orius*; their ability to realize this potential appears to be limited primarily by their own suppression to low densities by intraguild predation imposed by the hemipteran predator community (Rosenheim, 2001; Rosenheim et al., 1993, 1999). We have observed *Orius* being preyed upon in the field by each of the numerically dominant predator taxa (*Geocoris*, *Nabis*, *Zelus*, *Chrysoperla*, and spiders; Rosenheim, 2001); as a small-bodied predator foraging actively on the leaf surface, *Orius* appears to be highly vulnerable to all of these larger-bodied species. Our focal observations suggest that of these predators, *Geocoris* may impose the strongest mortality in cotton fields, perhaps a simple reflection of its much higher density than that typically observed for *Nabis* or *Zelus*. The trials reported by van den Bosch et al. (1956) showed that broad-spectrum insecticides that suppress much of the predator community can actually boost *Orius* densities, apparently by releasing them from the suppressive effects of intraguild predation.

The suppression of *Orius* by *Geocoris* could, in theory, occur through either direct predation or through competition for shared prey resources. Because the densities of spider mite and aphid prey were consistently non-significant as covariates in Experiments 1 and 2, at least under these experimental conditions predation rather than competition appears to have been the dominant mode of interaction between *Geocoris* and *Orius*. As an omnivore, *Orius* is probably unlikely to actually starve over a short-duration experiment like the ones I report; however, over the longer term, competition could certainly also play a complementary role in the antagonistic interactions between *Geocoris* and *Orius*.

*Geocoris* is the largest of the predators that are known to suppress spider mite populations, and its larger body size makes it unlikely that *Geocoris* is heavily influenced by reciprocal intraguild predation from the smaller predators (Fig. 1). Nevertheless, *Geocoris* populations did not build up in fields harboring larger spider mite populations. Several non-mutually exclusive hypotheses can be advanced to explain the failure of *Geocoris* populations to respond numerically to spider mite prey. First, *Geocoris* may also be subject to intraguild predation; *Geocoris* is consumed by *Chrysoperla* spp. lacewings, by *Zelus*, and by thomisid spiders (Rosenheim, 2001), but whether these effects are ecologically significant is unknown. Second, *Geocoris* eggs are heavily parasitized by a scelionid wasp (unpublished data), but whether this parasitoid regulates populations of *Geocoris* is unknown. Third, *Geocoris* is cannibalistic, and natural history observations suggest that *Geocoris* may defend patches of prey (R. L. Bugg, pers. comm.). Finally, *Geocoris* populations reside partly on the plant and partly in the soil and leaf litter, and it may be that their population dynamics are more heavily influenced by the availability of prey in the detritivore-based food web, such as Collembola (Bugg et al., 1987). Further work is required to assess these hypotheses. What is clear, however, is that if *Geocoris*, which occupies the top rung in the intraguild predation ladder, is for whatever reason unable to mount a numerical response to spider mite populations, and if smaller-bodied mite predators are heavily suppressed by intraguild predation, then the failure of the predator community to produce top-down control of mite populations may be an expected outcome.

**Acknowledgments**

I thank Jason Harmon for constructive comments on an earlier draft of the manuscript. This work was supported by grants from the California State Support Board of Cotton Incorporated, the University of California Statewide IPM program, the California Crop Improvement Association, and the USDA NRICGP (Grants 94-37302-0504, 96-35302-3816, and 01-35302-10955).

**References**


University of California., 1996. Integrated pest management for cotton in the western region of the United States. Publication 3305, Division of Agriculture and Natural Resources, University of California, Oakland, CA.