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

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## 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.
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## 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

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(e.g., Schoenig and Wilson, 1992), even in the absence of insecticide use spider mites can outbreak and defoliate cotton plants. The irruptive 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 *Galendromus 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–predator 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 americoferus* Carayon; Hemiptera: Nabidae), 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
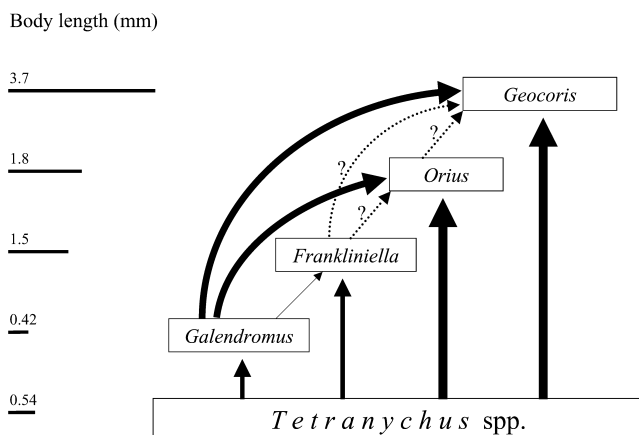


Fig. 1. A size-based ladder of intraguild predation among arthropods that prey on spider mites, *Tetranychus* spp. in California cotton. Arrows point from prey to predator, and the width of the arrow is approximately scaled to the strength of the effect of the predator on the prey population. Dashed arrows with question marks indicate interactions that have not been studied. Also shown are the body lengths of the adult female stages of each species.

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 inter-

action terms; all two-way interactions were, however, non-significant ($P \geqslant 0.40$), 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 ($P \geqslant 0.10$), 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 hand-held 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,
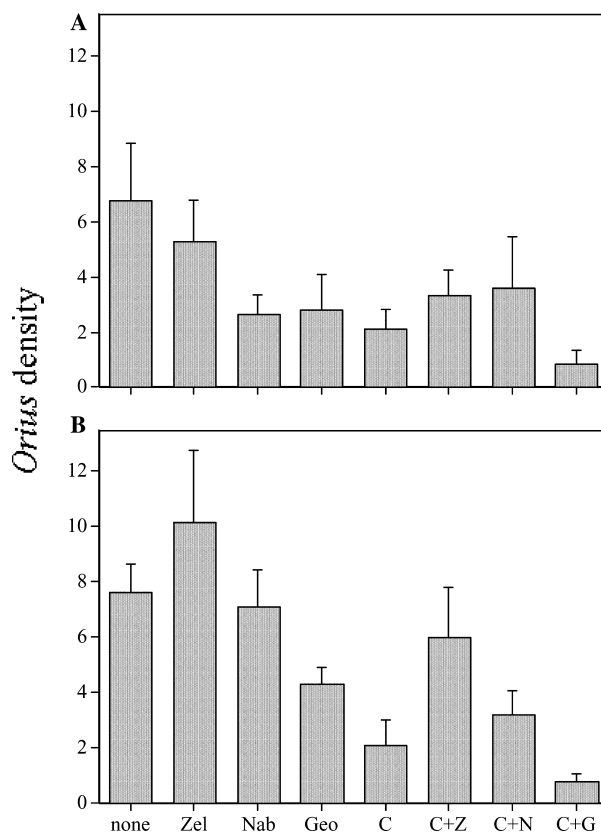


Fig. 2. (A) Enclosure/exclosure Experiment 1 and (B) Experiment 2. Shown are the mean ($\pm$1SE) number of motile *Orius* present per cage at the end of the experiment. Treatment labels below each bar indicate the predator(s) that were present in addition to the *Orius*. Abbreviations: Zel, *Zelus*; Nab, *Nabis*; Geo, *Geocoris*; and C, *Chrysoperla*.

had an average of $6.8 \pm 2.0$ (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* ($F_{1,62} = 5.0$, $P = 0.03$; main effects for *Zelus*, $F_{1,62} = 0.06$, $P = 0.81$, for *Nabis*, $F_{1,62} = 0.2$, $P = 0.66$; and for *Chrysoperla*, $F_{1,62} = 1.9$, $P = 0.17$). The spider mite and aphid prey availability covariates were not significant predictors of final *Orius* density per cage (spider mites: $F_{1,62} = 3.3$, $P = 0.07$; aphids: $F_{1,62} = 0.2$, $P = 0.62$), 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 ($F_{1,64} = 6.6$, $P = 0.009$) and the main effect for lacewings also became significant ($F_{1,64} = 5.0$, $P = 0.03$). 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

*Orius* alone treatment ($t = 2.28$, $df = 17$, $P = 0.036$), suggesting that either *Geocoris* 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 $7.6 \pm 1.0$ 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* ($F_{1,73} = 19.7$, $P \leqslant 0.0001$), 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 m$^2$, $127 \pm 63$) than during 1993 ($22 \pm 17$), probably in response to the much greater availability of the dominant herbivore prey (aphids: mean densities during 1993, $33 \pm 13$ per leaf; 1994, $118 \pm 48$; mites: 1993, $27 \pm 14$; 1994, $113 \pm 49$; thrips: 1993, $1.8 \pm 0.5$; 1994, $21 \pm 17$). However, the mean density of *Geocoris* were somewhat *lower* during 1994 ($9.9 \pm 2.0$) than during 1993 ($13.3 \pm 2.4$). 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
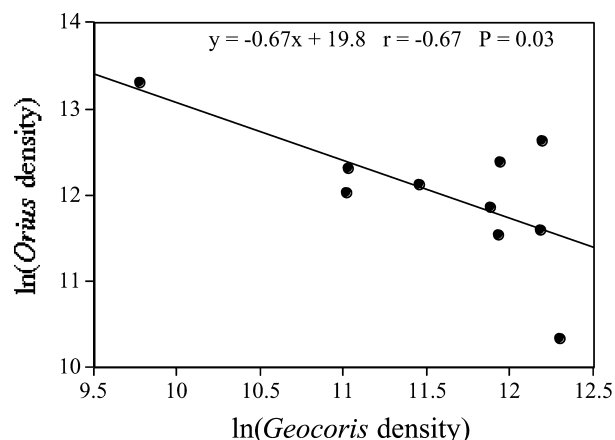


Fig. 3. 1993 population survey data for ten cotton fields, demonstrating the inverse relationship between mean mid- and late-season densities of *Orius tristicolor* (nymphs and adults; expressed as ln-transformed numbers per hectare) and its intraguild predators, *Geocoris* spp. (nymphs and adults).

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, $27 \pm 14$; 1994, $113 \pm 49$). 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
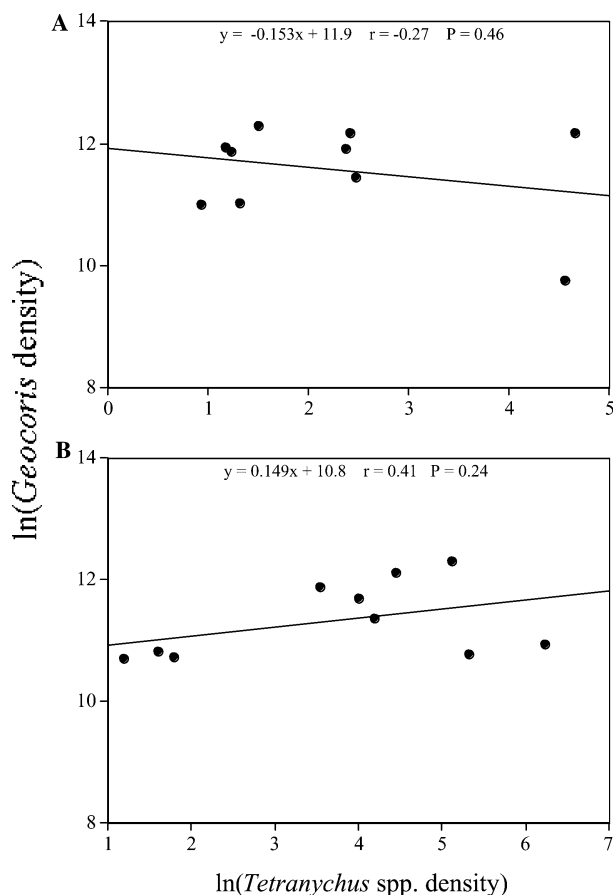


Fig. 4. Population survey data for (A) 1993 and (B) 1994. Shown are the mean mid- and late-season ln-transformed densities of *Geocoris* (nymphs and adults) per hectare versus the mean density of *Tetranychus* spp. per leaf.

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.

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