LINKING A PREDATOR'S FORAGING BEHAVIOR WITH ITS EFFECTS ON HERBIVORE POPULATION SUPPRESSION

JAY A. ROSENHEIM,[1] TOBIAS E. GLIK, RACHEL E. GOERIZ,[2] AND BIRGITTA RÄMERT[3]

Department of Entomology, University of California, Davis, California 95616 USA

Abstract. The view of terrestrial arthropod communities as potentially exhibiting a mixture of three- and four-trophic-level dynamics creates a new challenge for researchers: the indeterminacy of predator function. Here we evaluate two predictions linking a predator's foraging behavior with its likely ecological role: (1) widely foraging predators may act as effective regulators of sedentary herbivore populations, and (2) sit-and-wait predators are unlikely to regulate sedentary herbivore populations but may act as top predators, consuming widely foraging intermediate predators and allowing herbivore populations to escape from control. We tested these predictions by manipulating the predator community associated with a sedentary herbivore, the spider mite *Tetranychus cinnabarinus*, feeding on papaya, *Carica papayae*. The predators included a widely foraging specialist consumer of spider mites, the ladybird beetle *Stethorus siphonulus*, and a sit-and-wait generalist predator, the tangle-web spider *Nesticodes rufipes*. The experiments provided support for both predictions. The widely foraging predator *Stethorus* when tested alone was capable of effective suppression of spider mite populations. In contrast, the sit-and-wait predator, *Nesticodes*, never suppressed spider mites. Instead, *Nesticodes* consistently increased the population growth rates of spider mites. This effect was most likely due to *Nesticodes* suppressing populations of the intermediate predator *Stethorus*. Our results underscore the presence of both three- and four-trophic-level dynamics within this arthropod community and begin to address the challenging problem of the indeterminacy of predator function.

Key words: biological control; food webs; foraging behavior; generalist predator; higher order predation; indirect effects; intraguild predation; trophic cascades.

INTRODUCTION

Community ecologists are engaged in an active debate concerning whether or not predators suppress populations of herbivores and generate cascading indirect positive effects on plant populations (Hairston and Hairston 1993, 1997, Polis and Strong 1996, Polis 1999, Chase 2000, Polis et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Schmitz et al. 2004), as originally proposed by Hairston et al. (1960, the HSS model). Although the HSS hypothesis has been controversial, one sphere in which the HSS model of three functional trophic levels has been embraced is the theory of biological control by predatory arthropods (DeBach 1974, Huffaker et al. 1976, van den Bosch et al. 1982). Although researchers have long recognized that parasitoids cannot be placed neatly in a single trophic level (Brodeur 2000), biological control theory has long viewed predators as a single functional trophic level, acting to suppress herbivores (Hagen et al. 1976).

Recently, however, empirical studies of terrestrial arthropod communities have revealed widespread traits of predators that are inconsistent with the model of three discrete trophic levels. First, omnivorous feeding habits are increasingly being recognized, including species that feed on both plants and arthropod prey (Coll and Guershon 2002) and species that prey on both herbivorous and predatory arthropods (''intraguild predation''; Polis et al. 1989, Polis 1991, Rosenheim et al. 1995). Second, experimental studies have now demonstrated that there may be more than three functional trophic levels in terrestrial ecosystems. Higher order predators, which occupy positions in the food web above the third trophic level, have been demonstrated to suppress populations of intermediate predators, thereby allowing herbivore densities to increase (Spiller 1986, Rosenheim et al. 1993, 1999, Letourneau and Dyer 1998, Dyer and Letourneau 1999, Gastreich 1999, Rosenheim 2001, Snyder and Ives 2001, Snyder and Wise 2001, Finke and Denno 2002, 2003, Lang 2003, Chang and Eigenbrode 2004), with concomitant negative effects on plant performance (Letourneau and Dyer 1998, Dyer and Letourneau 1999, Snyder and Wise 2001).

This is not to say that terrestrial arthropod communities never conform to the HSS model of trophic dynamics. Many communities are well described by a model of three functional trophic levels (Schmitz et al.

2000, Halaj and Wise 2001). Combinations of predators may outperform single predator species in suppressing herbivore populations (Riechert et al. 1999, Snyder and Ives 2003), and some predators produce additive or synergistic combined effects on herbivore suppression (Soluk and Collins 1988, Losey and Denno 1998, Sih et al. 1998, Sokol-Hessner and Schmitz 2002, Cardinale et al. 2003, Schmidt et al. 2003). Nevertheless, what is clear is that the HSS model is not sufficiently general to accommodate the full diversity of terrestrial trophic dynamics. Community ecologists have, therefore, proposed alternative models in which trophic levels are poorly defined, omnivory is common, and predator–predator interactions are dynamically important (Hurd and Eisenberg 1990, Polis 1991, Wise 1993, Polis and Strong 1996, Janssen et al. 1998, Rosenheim 1998, Polis 1999, Halaj and Wise 2001).

These new models pose a significant new challenge for community ecologists: the indeterminacy of predator function. Under the HSS model, predators had just one role: to suppress herbivore populations. Under the newer models, predators may continue to function in this manner if they operate primarily as consumers of herbivores, or they may have the opposite effect if they operate primarily as consumers of other predators.

A Hypothesis Linking Predator Foraging Behavior with Community Structure

Rosenheim and Corbett (2003) developed a simple model that used the foraging behaviors of herbivorous and predatory arthropods to predict a predator's trophic role. The model makes two basic predictions about short-term suppression of prey populations by their predators that we seek to test in this study. The first prediction is that a widely foraging predator has the potential to suppress a sedentary herbivore population. Many herbivorous arthropods live on their food resource, and can therefore feed with minimal movement. Thus, many herbivores are relatively sedentary. A widely foraging predator can, by moving through the environment, achieve a high encounter rate with sedentary herbivore prey (Pianka 1966, Gerritsen and Strickler 1977, Huey and Pianka 1981), and thus can potentially suppress the prey population. The second prediction concerns the function of sit-and-wait predators. Sit-and-wait predators cannot have a high encounter rate with sedentary prey, simply because two relatively immobile organisms will be unlikely to meet. Such predators may, however, intercept mobile widely foraging predators. Thus, the second prediction is that sit-and-wait predators are unlikely to suppress sedentary herbivore populations, but may act as top predators, consuming widely foraging intermediate predators and thereby disrupting the control of herbivores.

The Study System

We studied the community of arthropods associated with the carmine spider mite, *Tetranychus cinnabari-*
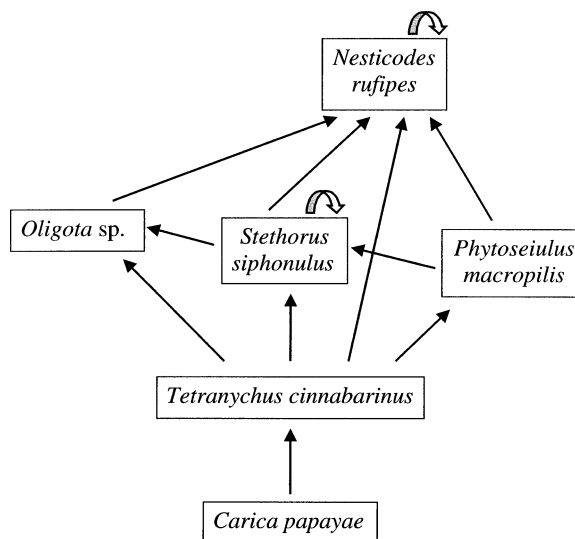

Fig. 1. Trophic web for the arthropods associated with the carmine spider mite, *Tetranychus cinnabarinus*, feeding on the foliage of papaya, *Carica papayae*, in Hawaii. Trophic linkages were established through direct observations (1997–2001). *Nesticodes* eat the larval stages of *Stethorus* and *Oligota* and all motile stages of *Phytoseiulus*. *Stethorus* eat the eggs and young motile stages of *Phytoseiulus*, and *Oligota* can eat the eggs of *Stethorus*. Looping arrows indicate cannibalism.

nus (Tetranychidae), feeding on papaya, *Carica papayae*, in Hawaii (Fig. 1). *Tetranychus* is a highly sedentary species that forms silk-lined colonies on the undersurface of papaya leaves; it can complete a generation in 7–10 days. The predatory beetles *Stethorus siphonulus* (Coccinellidae) and *Oligota* sp. (Staphylinidae) are specialist consumers of spider mites; both are widely foraging. *Stethorus* and *Oligota* are generally the first predators found in association with spider mite colonies early in the spring. All life stages of *Stethorus* (eggs, larvae, pupae, and adults) are found on papaya foliage, and the four larval instars are completed in approximately eight days under spring field conditions (Raros and Haramoto 1974). Little is known of the biology of *Oligota* sp. Although their eggs are laid on leaves, the eggs are highly cryptic, and they pupate in the soil. Thus, only the larval and adult stages are readily quantified with foliage samples. The widely foraging predatory mite *Phytoseiulus macropilis* (Phytoseiidae) is another specialist consumer of spider mites, and generally colonizes later in the spring.

In addition to these specialist mite predators, the papaya community harbored a generalist predator, the tangle-web spider *Nesticodes rufipes* (Theridiidae). *Nesticodes* is a classic sit-and-wait predator: it spins a sparse web that extends across a small portion of the leaf surface, and initiates attacks when arthropods walking across the leaf contact a silk line. *Nesticodes* are broad generalists, and include spider mites and each of the spider mite predators in their catholic diet. None

of the predators of spider mites possesses effective defenses against *Nesticodes*, except for the adult stages of the beetles, which the spiders almost always failed to subdue.

A pilot experiment conducted 9–18 April 1997 suggested that leaves harboring larger numbers of the spider *Nesticodes* were associated with more rapid spider mite population growth rates (regression of the daily ln-transformed per capita spider mite population growth rate on average *Nesticodes* densities per leaf: $r = 0.44$, $F_{1,20} = 4.7$, $P = 0.042$). The only predator observed consuming large numbers of spider mites during this pilot experiment was *Stethorus*. Thus, these preliminary data provided the first hint that *Nesticodes* might act as a top predator, disrupting the ability of *Stethorus* to suppress spider mites. Although the model reported by Rosenheim and Corbett (2003) was eventually parameterized to reflect the papaya arthropod community, the essential structure of the model and the two qualitative predictions that we test in this study were established before we began work on the papaya arthropod community. Thus, we are reporting an honest test of the model's predictions in this paper.

METHODS

We used the natural contrast between the hunting behaviors of the widely foraging predators, *Stethorus* and *Oligota*, and the sit-and-wait predator, *Nesticodes*, to test the link between predator foraging mode and predator function. Our experiments incorporated two key design features. First, the architecture of the papaya tree allowed us to study interactions in the papaya arthropod community without confining the animals in any way. Mature papaya leaves are large (typical midrib lengths are ~30 cm), are held on very long petioles (length ~30–60 cm), and generally do not touch one another. Thus, each leaf represents a naturally semi-isolated subpopulation of mites and their predators, and we were able to maintain predator-reduction treatments using manual removals. As a result, unmanipulated predators were able to move freely, for example in response to changing resource availability, and were therefore not "forced" to eat prey that they would not normally consume (Sih et al. 1985). Our cage-free design also allowed predators to influence potential prey and competitors through either direct consumption or through behaviorally mediated effects.

Second, beyond choosing papaya leaves that harbored a spider mite population of some minimum size, in Experiments 1 and 2 we did not attempt to homogenize the starting densities of prey or predators across the experimental replicates. Thus, the experimental units reflect both the mean and variance in natural arthropod densities, making the study a "field experiment" rather than a synthetic "microcosm experiment" conducted in the field (see discussion by Schmitz et al. 2000). Both of these design features

added to the realism of the experiments, albeit at the cost of reduced statistical power.

We emphasize that our cage-free design produces one significant interpretational limitation. Intermediate predators could exit experimental units either through predation by a top predator or through simple emigration. If, in the absence of a top predator, the intermediate predator effectively suppresses the local population of prey, it is likely to emigrate from the experimental arena. Thus, our experiments cannot be used to quantify the impact of top predators on intermediate predator survival. Furthermore, there is little reason to expect any clear difference between the final densities of intermediate predators in treatments with the top predator retained vs. excluded.

Experiment 1

The goal of this experiment was to evaluate the individual and combined effects of the dominant early-colonizing predators (*Stethorus*, *Oligota*, and spiders) on the spider mite population growth rate. The experiment was conducted 30 May–12 June 1997 in a papaya orchard that had not yet been fully colonized by the predatory mite *Phytoseiulus*.

The experiment was conducted in a pesticide-free mature papaya orchard of mixed genetic background grown at the University of Hawaii, Poamoho Experiment Station. Single mature leaves harboring ≥5 adult female spider mites were used as the experimental units. Each leaf was initially inspected in the field to (1) count the number of spider mites (adult females only), *Oligota*, spiders, and *Stethorus*, recording the developmental stage of the beetles, and (2) remove any of the infrequently observed species of generalist predators (e.g., lacewing larvae, predatory thrips) and any *Phytoseiulus* that had colonized the field. Leaves were then assigned sequentially to one of eight treatments, each replicated 10 times, comprising a three-way factorial design, with each factor representing the retention or exclusion of one of the dominant predators (*Oligota*, spiders, and *Stethorus*). The spider removal treatments involved the removal of the complete spider community; however, because the spider community was heavily dominated by *Nesticodes* (see Appendix A), the spider treatment effects can be attributed primarily to this single species. Treatments were blocked by papaya tree, with one or two full sets of replicates established per tree.

Treatments were maintained as press perturbations by manually removing predators. Spider removals were performed once a day, in the early morning. All leaves in the experiment were checked for adult *Oligota* and *Stethorus* approximately every two hours from 07:00 to 19:00. Leaves from which adult *Stethorus* were removed were inspected carefully to remove any *Stethorus* eggs that had been deposited. On nonremoval leaves, we recorded the number of adult beetles present. From these data we estimated the number and duration

of visits by *Stethorus* adults; visit durations included daylight hours only (07:00–19:00), because these beetles are inactive at night. Eggs laid by *Stethorus* on nonremoval leaves were checked twice daily to record their fate (successful hatch, missing from leaf, predation). Finally, all leaves were inspected to remove any colonizing *Phytoseiulus* on days 4 and 7.

The experiment ran for 10 d, at which time final counts of predators and adult female spider mites were taken. Leaves that had senesced during the experiment were excluded from the analyses. The experiment was analyzed as a three-way fully crossed ANCOVA, with main factors for *Oligota*, spiders, and *Stethorus*; trees as a blocking factor; initial spider mite density as a covariate; and the ln-transformed per capita rate of spider mite population growth, calculated as [ln((final count)/(initial count))]/10 d, as the dependent variable. The ANCOVA was followed by a series of planned pairwise contrasts, using the sequential Bonferroni technique (Rice 1989). We allocated $\alpha = 0.05$ to tests of single predator species (or a guild in the case of spiders) vs. the no-predator control. We allocated an additional $\alpha = 0.05$ to tests of *Stethorus* in combination with other predators vs. *Stethorus* alone. Based upon the results of our pilot experiment, we used one-tailed tests to examine the main effects of *Stethorus* and spiders; all other tests were two-tailed. We also tested for predator interactions using the multiplicative risk model (Soluk and Collins 1988, Sih et al. 1998). Throughout the text, summary statistics are presented as the mean $\pm$ 1 SE.

Experiment 2

This experiment was run when the guild of spider mite predators was in transition from one dominated by the early colonizers (*Oligota*, *Stethorus*, and *Nesticodes*) to one incorporating *Phytoseiulus* as well. The experiment was conducted 3–20 May 1999 in a mature papaya orchard of mixed genetic background grown at Poamoho. We followed the protocols of Experiment 1, with the following modifications.

Initial leaf surveys included counts of all motile stages of *Phytoseiulus*. Leaves were assigned sequentially to one of 16 treatments, each replicated 10 times, comprising a four-way factorial design, with each factor representing the retention or exclusion of one of the dominant predators (*Oligota*, spiders, *Stethorus*, and *Phytoseiulus*). We used trees as blocks, but were unable to establish full sets of replicates on each tree. We checked leaves three times a day to maintain the *Oligota* and *Stethorus* treatments. Motile stages of *Phytoseiulus* were removed on days 3, 9, and 12. The experiment ran for 14 d.

Experiment 3

This experiment had two goals. First, we wanted to test the impact of spiders on spider mite population growth on leaves where we imposed a fixed starting density of *Stethorus*. Second, we wanted to evaluate the plausibility of the hypothesis that *Nesticodes* accelerated spider mite population growth by preying on the key intermediate predator, *Stethorus*. Because *Stethorus* are large prey for *Nesticodes* spiderlings, we anticipated that *Nesticodes* might require a significant amount of time to ingest *Stethorus* prey, and therefore that daily checks of developing *Stethorus* larvae might reveal instances of spider predation on *Stethorus*.

This experiment was performed 9–19 May 1999 at Poamoho in a young papaya planting (cv. Sunset). At the start of the trial we removed *Oligota*, *Stethorus*, and *Phytoseiulus* from the experimental leaves (chosen on the basis that they harbor ≥ 5 adult female spider mites), and counted the adult female spider mites and spiders. We then established two treatments: (1) +spiders, in which we retained all spiders ($n = 26$ replicates) and (2) −spiders, in which spiders were removed ($n = 25$ replicates). We then released a single field-collected first-instar larval *Stethorus* in a randomly selected mite colony on the leaf, and recorded its position. Leaves were checked daily to record the status of the released *Stethorus* larva; if the larva was not found, all spiders on the leaf were observed to see if any were in the act of consuming it. The experiment ran for 7 d, at which time final counts of *Nesticodes* and adult female spider mites were made.

RESULTS

Experiment 1

The experimental treatments were established successfully (see Appendix A). The *Stethorus* population at the start of the experiment was made up of a moderate number of eggs and larvae, some adults, but no pupae (Fig. 2A). Given the abundance of spider mite prey (Appendix A), this stage distribution suggests that some strong mortality force other than food limitation was acting on *Stethorus* larvae or pupae.

Spider mite population growth rates were strongly influenced by the predator treatments (Fig. 2B). Whereas the main effect of *Stethorus* was significant because *Stethorus* suppressed spider mite populations ($F_{1,51} = 10.2$, $P = 0.0013$), the main effect of spiders was significant because spiders increased spider mite populations ($F_{1,51} = 7.82$, $P = 0.0037$; see Appendix B). The main effect of *Oligota* was not significant ($F_{1,51} = 1.51$, $P = 0.22$). Pairwise contrasts of predators tested individually compared to the no-predator control revealed a significant effect for only *Stethorus* ($F_{1,51} = 5.69$, $P = 0.021$), with a nonsignificant result for *Oligota* ($F_{1,51} = 1.65$, $P = 0.20$) and a marginally nonsignificant result for spiders ($F_{1,51} = 5.05$, $P = 0.029$, critical α-level for the sequential Bonferroni = 0.025). The spiders × *Stethorus* interaction term was nonsignificant ($F_{1,51} = 0.52$, $P = 0.47$); this means that we cannot definitively attribute the positive effect of spiders on spider mite population growth to their possible
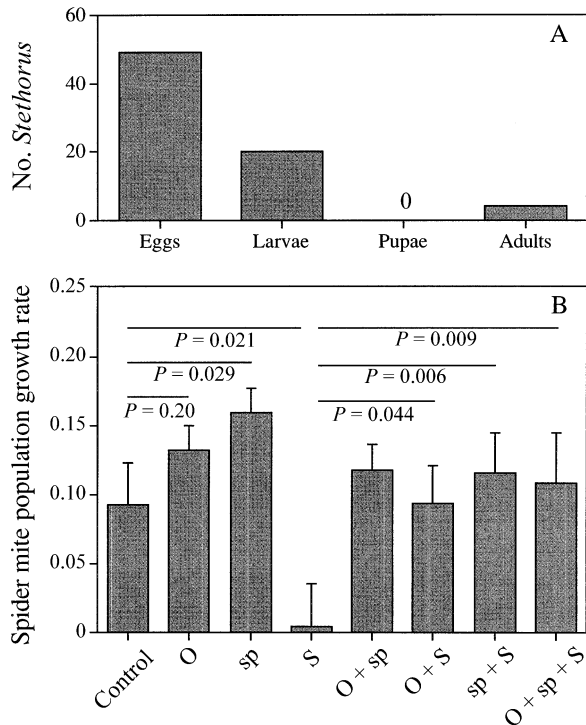
FIG. 2. Experiment 1: (A) stage structure of the *Stethorus siphonulus* population before treatments were initiated; (B) influence of different predators tested singly and in combination on the per capita population growth rate of the spider mite *Tetranychus cinnabarinus*. Treatments and sample sizes: Control ($n = 9$); O, +*Oligota* ($n = 7$); sp, +spiders ($n = 10$); S, +*Stethorus siphonulus* ($n = 8$); O + sp, +*Oligota* +spiders ($n = 6$); O + S, +*Oligota* +*Stethorus* ($n = 9$); sp + S, +spiders +*Stethorus* ($n = 9$); O + sp + S, +*Oligota* +spiders +*Stethorus* ($n = 9$). The figure shows means + 1 SE.

disruption of *Stethorus* (see *Discussion*). Our planned contrasts did show, however, that the positive effect of spiders on spider mite population growth was expressed in the presence of *Stethorus* (adding other predators to the system significantly weakened the sup-

pression of spider mite populations by *Stethorus*: for +*Oligota*, $F_{1,51} = 4.26$, $P = 0.044$; for +spiders, $F_{1,51} = 8.18$, $P = 0.006$; for +*Oligota* +spiders, $F_{1,51} = 7.36$, $P = 0.009$).

What mechanisms might underlie putative disruptive effects of *Oligota* and spiders on spider mite suppression by *Stethorus*? As discussed previously, our cage-free design prevents us from using a comparison of larval *Stethorus* densities at the close of the experiment in the presence vs. absence of spiders as a measure of spider predation on *Stethorus*, because *Stethorus* larvae were free to emigrate from leaves where they suppressed their local prey resources. There was no evidence that *Stethorus* oviposition or leaf visitation was changed by the presence of *Oligota* or spiders (Table 1). We also found no evidence for predation of *Stethorus* eggs by *Oligota* or spiders (Table 1).

Experiment 2

We had only mixed success in establishing our experimental treatments, generating significant density differences for *Stethorus* and spiders, but not for *Oligota* or *Phytoseiulus* (Appendix A). Thus, we collapsed our original four-way factorial design into a simpler two-way design, with *Stethorus* and spiders treatments. The blocking term was nonsignificant, and was therefore also dropped from the final model.

As we observed during Experiment 1, the stage distribution of *Stethorus* bore the distinctive signature of heavy mortality during the larval or pupal stages: significant numbers of eggs and larvae, but very few pupae, were observed (Fig. 3A), despite the presence of abundant prey (Appendix A).

Two opposing influences on spider mite dynamics were identified: *Stethorus* acted to decrease spider mite populations ($F_{1,136} = 13.2$, $P = 0.0002$; see Appendix C), whereas spiders acted to increase spider mite populations ($F_{1,136} = 4.25$, $P = 0.021$; Fig. 3B). *Stethorus* tested alone produced strong suppression of spider mite populations compared to the control ($F_{1,136} = 10.2$,

TABLE 1. Experiment 1: potential mechanisms underlying the disruptive effects of *Oligota* and spiders on the ability of *Stethorus* to suppress spider mite populations.

Effect on *Stethorus*	*Stethorus* alone	*Oligota* + *Stethorus*	Spiders + *Stethorus*	*Oligota* + spiders + *Stethorus*	χ^2	P
Visit number†	2.4 ± 0.8	1.0 ± 0.2	1.0 ± 0.3	1.6 ± 0.6	1.9	0.59
Visit duration‡ (h)	3.0 ± 0.3	5.4 ± 1.0	7.4 ± 2.3	5.1 ± 1.1	4.8	0.18
Oviposition§	3.9 ± 1.8	3.2 ± 0.8	2.7 ± 1.0	1.6 ± 1.0	4.2	0.24
Successful egg hatch‖	80 ± 9	95 ± 5	100 ± 0	94 ± 6	3.5	0.33
Larval densities¶	2.8 ± 1.5	1.0 ± 0.4	0.4 ± 0.2	2.0 ± 0.9	3.2	0.36

Notes: Values shown are means ± 1 SE for each of the four treatments that included *Stethorus*. Sample sizes for treatments are given in the legend to Fig. 2. *P* values are for Kruskal-Wallis rank-sums tests.

† Mean number of visits by adult *Stethorus* per leaf over the entire experiment.

‡ Mean duration of a visit by an adult *Stethorus* to an experimental leaf.

§ Mean number of eggs deposited per leaf over the full course of the experiment.

‖ Percentage eggs hatching successfully. The unit of replication here was taken as a leaf, rather than each egg; thus all eggs laid on a given leaf contributed a single, independent observation of proportion egg hatch. Sample sizes were 7, 4, 3, and 3 collections of eggs found on a given leaf for the four treatments, respectively; 75 eggs in all were scored.

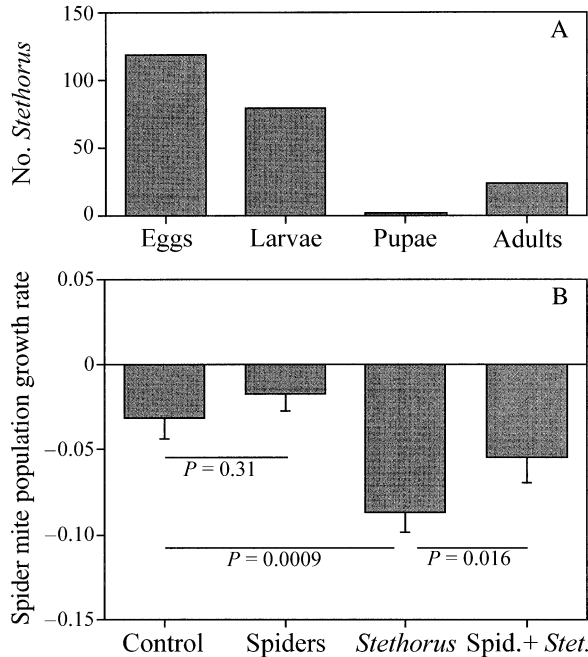¶ Mean density of *Stethorus* larvae per leaf at the end of the experiment.

FIG. 3. Experiment 2: (A) stage structure of the *Stethorus siphonulus* population before treatments were initiated; (B) influence of spiders and *Stethorus siphonulus* on the per capita population growth rate of the spider mite *Tetranychus cinnabarinus*. Treatments and sample sizes: Control ($n = 35$); +Spiders ($n = 35$); +*Stethorus* ($n = 36$); +Spiders +*Stethorus* ($n = 35$). The figure shows means − 1 SE.
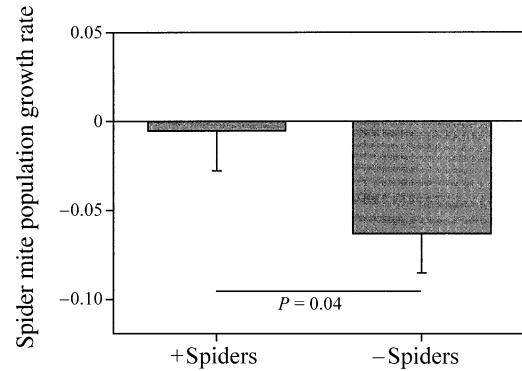

FIG. 4. Experiment 3: influence of spiders on the per capita population growth rate of the spider mite *Tetranychus cinnabarinus* on leaves on which a single neonate *Stethorus* larva was released. Treatments and sample sizes: +Spiders ($n = 26$); −Spiders ($n = 25$). The figure shows means − 1 SE.

$P = 0.0009$), whereas spiders tested alone had a nonsignificant effect on spider mites ($F_{1,136} = 1.0$, $P = 0.31$). Spiders did, however, increase spider mite population growth rates when *Stethorus* was present (comparison of +*Stethorus* +spiders vs. +*Stethorus* alone: $F_{1,136} = 4.6$, $P = 0.016$). Nevertheless, the *Stethorus* × spiders interaction term was nonsignificant ($F_{1,136} = 0.43$, $P = 0.51$). These results exactly mirror those obtained in Experiment 1.

We again found no evidence that spiders exerted behaviorally mediated effects on adult *Stethorus*. *Stethorus* oviposition and leaf visitation did not vary between the +spiders and −spiders treatments (Table 2). Rates of successful egg hatch also did not differ significantly between treatments (Table 2).

Experiment 3

We established the spider treatments successfully (see Appendix A). As was observed in Experiments 1 and 2, spider mite populations were suppressed more strongly by *Stethorus* acting alone than by *Stethorus* in the presence of spiders ($F_{1,48} = 3.03$, $P = 0.04$; Fig. 4). Daily checks of the *Stethorus* larvae revealed that *Nesticodes* were indeed acting as top predators: 3 of 26 *Stethorus* were observed being consumed by *Nesticodes* in the +spiders treatment, and 4 of 25 *Stethorus* were observed being consumed in the −spiders treatment. Thus, even where we attempted to remove spiders, a significant risk of *Nesticodes* predation re-

TABLE 2. Experiment 2: potential mechanisms underlying the disruptive effects of spiders on the ability of *Stethorus siphonulus* to suppress populations of spider mites.

Effect on *Stethorus*	*Stethorus* alone	Spiders + *Stethorus*	χ^2	P
Visit number†	2.1 ± 0.3	2.2 ± 0.4	0.2	0.62
Visit duration‡ (h)	7.7 ± 0.7	8.8 ± 0.9	1.0	0.31
Oviposition§	1.8 ± 0.5	3.3 ± 1.1	0.5	0.48
Successful egg hatch‖	80 ± 9	63 ± 9	2.5	0.11
Larval densities¶	1.1 ± 0.7	0.9 ± 0.3	0.4	0.55

Notes: Values shown are means ± 1 SE. Sample sizes are given in the legend to Fig. 3. P values are for Wilcoxon rank-sums tests.

† Mean number of visits by adult *Stethorus* to leaves over the entire experiment.
‡ Mean duration of a visit by an adult *Stethorus* to an experimental leaf.
§ Mean number of eggs deposited per leaf over the full course of the experiment.
‖ Percentage eggs hatching successfully. The unit of replication here was taken as a leaf, rather than each egg; thus all eggs laid on a given leaf contributed a single, independent observation of proportion egg hatch. Sample sizes were 12 collections of eggs found on a given leaf for each of the two treatments; 135 eggs in all were scored.
¶ Mean density of *Stethorus* larvae per leaf on day 10 of the experiment. Sample sizes are 14 and 21 larvae/leaf for the *Stethorus* alone and Spiders + *Stethorus* treatments, respectively.

mained. The only other observed sources of mortality were drowning following a heavy rain ($n = 1$ larva) and apparent starvation on the leaf ($n = 2$ larvae). *Stethorus* that we observed being consumed by *Nesticodes* were never still present on the following day's check; thus, we presumably observed only a subset of all predation events that occurred. By the end of the trial, only 4 of the 47 *Stethorus* remained on their original leaves, the rest having either died or emigrated.

Discussion

We have attempted to test a model that links the foraging behavior of a predator with its likely ecological function within a community of arthropods. The model made two predictions: first, that widely foraging predators have the potential to suppress populations of sedentary herbivores; and second, that sit-and-wait predators are unlikely to be effective regulators of sedentary herbivores, but may instead act as top predators, consuming widely foraging intermediate predators and thereby releasing herbivore populations from control. Our field experiments provided support for both predictions. First, an actively foraging predator, *Stethorus*, when tested alone, generated significant suppression of a sedentary herbivore, a spider mite, compared to a no-predator control. Second, a classic sit-and-wait predator, the tangle-web spider *Nesticodes*, did not produce any measurable suppression of spider mite populations when tested singly. Instead, spider mite population growth rates were consistently accelerated in the presence of *Nesticodes*. Thus, these two predators appear to be playing fundamentally different ecological roles, as predicted by theory linking predator foraging behavior with predator ecology (Pianka 1966, Huey and Pianka 1981, Rosenheim and Corbett 2003).

Mechanism of Nesticodes effect

How did *Nesticodes* consistently enhance spider mite population growth rates? We hypothesize that the most likely scenario is that *Nesticodes* predation on *Stethorus* disrupted *Stethorus*' control of spider mites, but we recognize that our experimentation did not establish this. The definitive evidence for *Nesticodes* disruption of spider mite control by *Stethorus* is a statistically significant spiders × *Stethorus* interaction term in our ANOVAs; we did not, however, observe these significant interactions. Furthermore, our cage-free experimental design prevented us from quantifying *Nesticodes* predation on *Stethorus*, because *Stethorus* that survived long enough to suppress their local prey population were free to disperse.

Why then do we continue to feel that intraguild predation by *Nesticodes* on *Stethorus* remains the most plausible explanation for the positive effect of spiders on spider mites? There are several contributing factors: (1) Our predator exclusions were never complete. *Stethorus* were still present on leaves where we attempted to remove them (densities in the −*Stethorus* treatments

were 17–50% of the densities in the +*Stethorus* treatments; see Appendix A). Thus, we expected to see residual positive effects of *Nesticodes* on spider mites in the −*Stethorus* treatments, and these indeed were observed, making it difficult to detect a significant spiders × *Stethorus* interaction. (2) Although the spiders × *Stethorus* interaction terms were nonsignificant, the trends in our data were consistent with the hypothesis that spiders were disrupting mite control by *Stethorus*; spiders had their strongest positive effects on spider mite population growth in the +*Stethorus* treatments (Figs. 2B, 3B). (3) The characteristic age structure of the *Stethorus* populations (many eggs and larvae, but few pupae) is consistent with mortality occurring during the larval or pupal stage. Once *Stethorus* reach the prepupal and pupal stages, which are immobile and therefore not at risk from *Nesticodes*, their survival to the adult stage is high (8 of 8 prepupae survived to pupate; 12 of 14 pupae successfully emerged as adults; J. A. Rosenheim, *unpublished data*). Because *Stethorus* in Hawaii have multiple overlapping generations (Raros and Haramoto 1974), we expected to see an approximately stable age distribution. Because we have not observed any other significant predators of *Stethorus*, and because our experiments were conducted in fields with substantial spider mite prey availability, we suggest that *Nesticodes* predation is the most likely cause of the observed deficit of *Stethorus* pupae. (4) Two additional experiments conducted later in the spring, when *Phytoseiulus* had replaced *Stethorus* as the dominant predator of spider mites, demonstrated that spiders no longer accelerate spider mite population growth rates (Rosenheim et al. 2004). Thus, spiders appear to accelerate spider mite growth only when the dominant spider mite predator is *Stethorus*. Although *Phytoseiulus* is also a widely foraging intermediate predator, and therefore might also be predicted to be vulnerable to a sit-and-wait top predator like *Nesticodes*, *Phytoseiulus* is much smaller and substantially less mobile than *Stethorus*, and simulations have shown that the mobility difference can account for nearly all of the observed insensitivity of *Phytoseiulus* to *Nesticodes* predation (Rosenheim et al. 2004). (5) Finally, we are not able to develop alternative hypotheses that we find plausible. Despite conducting extensive day and night observations, we have not discovered other important spider mite predators that might be impacted by *Nesticodes*. In sum, then, we suggest that the mechanism underlying the accelerating effect of *Nesticodes* on spider mite population growth rates is most likely to be that *Nesticodes* acts as a top predator, suppressing populations of a key intermediate predator, *Stethorus*. Further work is, however, required to establish this result.

We note also that the mechanisms underlying the disruptive effect of *Oligota* on *Stethorus*, observed in Experiment 1, remain enigmatic, as we did not docu-

TABLE 3. Field studies of four-trophic-level dynamics in terrestrial arthropod communities in which crossovers of foraging mode occur.

System	Plant	Sedentary herbivore	Actively foraging intermediate predator	Sit-and-wait top predator	Source
Coastal shrubland	bush lupine, *Lupinus arboreus*	root-boring caterpillar, *Hepialus californicus*	entomopathogenic nematode, *Heterorhabditis hepialus*	a complex of nematode-trapping fungi	Strong et al. (1996, 1999), Jaffee et al. (1996), Koppenhöfer et al. (1996), Preisser (2003)
Agroecosystem	upland cotton, *Gossypium hirsutum*	cotton aphid, *Aphis gossypii*	lacewing larvae, *Chrysoperla* spp.	assassin bug, *Zelus renardii*† and other predatory bugs‡	Rosenheim et al. (1993, 1999), Cisneros and Rosenheim (1997, 1998), Rosenheim (2001)
Agroecosystem	upland cotton, *Gossypium hirsutum*	silverleaf whitefly, *Bemisia argentifolii*	ladybird beetle, *Delphastus catalinae*	predator complex, dominated by hemipterans§	Heinz et al. (1999)
Tropical wet forest understory	ant-plant, *Piper obliquum*	egg stages of folivorous arthropods	ant, *Pheidole bicornis*	web-building spider, *Dipoena banksii*‖	Gastreich (1999)
Agroecosystem	squash, *Cucumis pepo*	squash bug nymphs, *Anasa tristis*	*Nabis* spp.	a complex of wolf spiders, dominated by *Pardosa* spp. and *Hogna* spp.¶	Snyder and Wise (2001)
Salt marsh	perennial cordgrass, *Spartina alterniflora*	planthopper, *Prokelisia dolus*	mirid bug, *Tytthus vagus*	wolf spider, *Pardosa littoralis*¶	Finke and Denno (2002, 2003)
Agroecosystem	papaya, *Carica papaya*	spider mite, *Tetranychus cinnabarinus*	ladybird beetle, *Stethorus siphonulus*	web-building spider, *Nesticodes rufipes*	this study

Note: Sedentary herbivores are consumed by mobile intermediate predators, which are in turn consumed by top predators that employ a sit-and-wait tactic or that use cues associated with arthropod movement to detect potential prey.

† Like many predatory bugs in the family Reduviidae, *Zelus renardii* uses visual cues associated with arthropod movement to detect potential prey, and can either ambush or stalk its victims (Parker 1972, Cisneros and Rosenheim 1998). *Zelus* produced the strongest evidence of four-trophic-level dynamics.

‡ Although some of the other predatory bugs use visual cues associated with arthropod movement to detect potential prey (e.g., *Geocoris* spp. [Eubanks and Denno 2000]), others, such as *Nabis* spp. may also use chemical cues (Freund and Olmstead 2000*a, b*).

§ The predator complex was diverse but was dominated by species that use sit-and-wait foraging or that use visual cues associated with arthropod movement to recognize prey.

‖ Because *D. banksii* is a specialist consumer of *P. bicornis*, its ecological role in the community could be inferred without reference to its sit-and-wait foraging mode.

¶ Wolf spiders are visually orienting predators that detect prey by movement and vibrations (Foelix 1982, Finke and Denno 2002).

ment strong consumptive or behaviorally mediated effects of *Oligota* on *Stethorus*.

Generality of the hypothesis linking predator behavior and ecology

A trade-off between foraging behavior and predation risk appears to be a nearly universal feature of animal ecology (Anholt and Werner 1995, Lima 1998). This trade-off has been shown to shape trophic cascades in a number of systems where consumers have a distinct spatial refuge from predators (Power 1984, Chase 1998, Bernot and Turner 2001). In this study, we have highlighted a different trade-off, one hinging on basic foraging mobility (e.g., Skelly 1994, Eubanks and Denno 2000).

Our confidence in the explanatory power of a general theory in ecology grows as multiple studies confirm its primary predictions. The two predictions developed in Rosenheim and Corbett (2003) and tested here should be broadly applicable, because systems with sedentary herbivores, mobile intermediate predators, and relatively sedentary top predators appear to be common (Table 3). Whereas some of the top predators studied to date exemplify the sit-and-wait foraging strategy in its purest form (e.g., web-building spiders and the nematode-trapping fungi), others, such as some hemipteran predators, exhibit foraging strategies that are intermediate between sit-and-wait and active foraging. The tendency of these top predators to consume actively foraging intermediate predators may be reinforced by the use of visual cues associated with arthropod movement as a primary means of detecting prey (e.g., Skelly 1994, Cisneros and Rosenheim 1998, Eubanks and Denno 2000). Likewise, some cursorial spiders (Foelix

1982) and parasitoids (Meyhöfer and Casas 1999) may use vibrational cues produced by arthropod movement to detect potential prey. Thus, sedentary herbivores are less likely to be detected and attacked than are mobile intermediate predators, and the resulting dynamics are similar to those for a strict sit-and-wait top predator.

The indeterminacy of predator function represents a significant challenge for community ecologists. What is needed is theory that allows us to predict predator function without having to conduct exhaustive experimentation to quantify interaction strengths within the focal community. Here we have tested model predictions that translate mobility traits into encounter frequencies and likely interaction strengths between predators and prey. Although encounters are the sine qua non of consumptive predator–prey interactions, they are not the sole determinant of a predator's diet. Predator–predator interactions can be shaped by habitat structure (Norton et al. 2001, Finke and Denno 2002, 2003), predator preferences (Colfer and Rosenheim 2001), prey defensive behaviors (Snyder and Ives 2001), the relative body sizes of predators and prey (Woodward and Hildrew 2002), and aspects of predator and prey life histories (Snyder and Ives 2003). A fuller theory of predator function in complex arthropod communities will emerge from an integration of these diverse influences on realized predator diet.

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APPENDIX A

Mean arthropod densities at the initiation of Experiments 1, 2, and 3, mean predator densities following the imposition of experimental manipulations, and species composition of the spider community are available in ESA's Electronic Data Archive: *Ecological Archives* E085-118-A1.

APPENDIX B

ANCOVA results for factors influencing the per capita population growth rate of the spider mite *Tetranychus cinnabarinus* during Experiment 1 are available in ESA's Electronic Data Archive: *Ecological Archives* E085-118-A2.

APPENDIX C

ANCOVA results for factors influencing the per capita growth rate of the spider mite *Tetranychus cinnabarinus* during Experiment 2 are available in ESA's Electronic Data Archive: *Ecological Archives* E085-118-A3.