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Herbivore population suppression by an intermediate predator, *Phytoseiulus macropilis*, is insensitive to the presence of an intraguild predator: an advantage of small body size?

Abstract Recent work in terrestrial communities has highlighted a new question: what makes a predator act as a consumer of herbivores versus acting as a consumer of other predators? Here we test three predictions from a model (Rosenheim and Corbett in Ecology 84:2538–2548) that links predator foraging behavior with predator ecology: (1) widely foraging predators have the potential to suppress populations of sedentary herbivores; (2) sit and wait predators are unlikely to suppress populations of sedentary herbivores; and (3) sit and wait predators may act as top predators, suppressing populations of widely foraging intermediate predators and thereby releasing sedentary herbivore populations from control. Manipulative field experiments conducted with the arthropod community found on papaya, *Carica papaya*, provided support for the first two predictions: (1) the widely foraging predatory mite *Phytoseiulus macropilis* strongly suppressed populations of a sedentary herbivore, the spider mite *Tetranychus cinnabarinus*, whereas (2) the tangle-web spider *Nesticodes rufipes*, a classic sit and wait predator, failed to suppress *Tetranychus* population growth rates. However, our experiments provided no support for the third hypothesis; the sit and wait predator *Nesticodes* did not disrupt the suppression of *Tetranychus* populations by *Phytoseiulus*. This contrasts with an earlier study that demonstrated that *Nesticodes* can disrupt control of *Tetranychus* generated by another widely foraging predator, *Stethorus siphonulus*. Behavioral observations suggested a simple explanation for the differing sensitivity of *Phytoseiulus* and *Stethorus* to *Nesticodes* predation. *Phytoseiulus* is a much smaller predator than *Stethorus*, has a lower rate of prey consumption, and thus has a much smaller requirement to forage across the leaf surface for prey, thereby reducing its probability of encountering *Nesticodes* webs. Small body size may be a general means by which widely foraging intermediate predators can ameliorate their risk of predation by sit and wait top predators. This effect may partially or fully offset the general expectation from size-structured trophic interactions that smaller predators are subject to more intense intraguild predation.

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Introduction

Recent empirically based models of the structure and function of terrestrial communities have suggested that different predator taxa may play different ecological roles: some predators ("intermediate predators") may operate primarily from the third trophic level, suppressing herbi-

vore populations, whereas other predators ("top predators") may operate primarily from the fourth trophic level, suppressing populations of intermediate predators and thereby releasing herbivore populations from control (Hurd and Eisenberg 1990; Polis 1991, 1994, 1999; Wise 1993; Polis and Strong 1996; Janssen et al. 1998; Rosenheim 1998; Halaj and Wise 2001). In nature, many predators have been shown experimentally to act as intraguild predators, straddling the third and fourth trophic levels by feeding both on herbivore prey and on other predators with whom they compete for access to those prey, and producing highly variable effects on herbivore population growth rates (Spiller 1986; Rosenheim et al. 1993, 1999; Rosenheim 2001; Snyder and Ives 2001; Snyder and Wise 2001; Finke and Denno 2002, 2003; Lang 2003; Chang and Eigenbrode 2004). These models and experiments have focused attention on a new and fundamental question: what traits predispose a predator to feed predominantly on herbivores versus on other predators?

Because there are many determinants of a predator's diet, the answer to this question is unlikely to be simple. However, for many predators, and especially those that are extreme generalists, a key determinant of diet composition is the frequency of encounter with different prey types. Rosenheim and Corbett (2003) used a spatially explicit model of predator and prey populations to explore the link between predator foraging behavior and predator function in a community where encounter frequency was the primary determinant of predator diet. Their model produced a number of testable predictions, three of which are the focus of this study: (1) widely foraging predators have the potential to suppress populations of sedentary herbivores; (2) sit and wait predators, in contrast, are unlikely to suppress populations of sedentary herbivores; and (3) sit and wait predators may, however, act as top predators, suppressing populations of widely foraging intermediate predators and thereby releasing sedentary herbivore populations from control. These predictions are straightforward extensions of the ideas first developed by Pianka (1966) (see also Gerritsen and Strickler 1977; Huey and Pianka 1981; Werner and Anholt 1993) relating the foraging behaviors of predators and prey to their likely positions in a trophic web.

Here we present field tests of these hypotheses, employing the community of arthropods found on papaya, *Carica papayae*, in Hawaii (Fig. 1). A dominant papaya herbivore is the carmine spider mite, *Tetranychus cinnabarinus* (Acari: Tetranychidae), a highly sedentary species that forms tight silk-lined colonies on papaya leaves. *Tetranychus* is associated with two specialist predators that forage widely. Early in the spring, the dominant spider mite predator is the beetle *Stethorus siphonulus* (Coleoptera: Coccinellidae). The larval stages of this beetle grow to a size that is large relative to the size of its prey [length of fourth instar *Stethorus* larvae=2.2 mm (Raros and Haramoto 1974); length of adult female *Tetranychus*=0.51 mm (Kono and Papp 1977)]. Later in the spring, the predatory mite *Phytoseiu-*
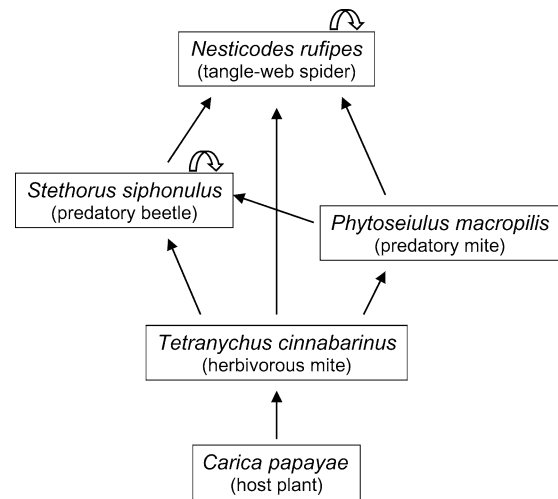

Fig. 1 Trophic web for the arthropod predators, *P. macropilis*, *S. siphonulus*, and *N. rufipes*, associated with the carmine spider mite, *T. cinnabarinus*, feeding on the foliage of papaya, *C. papayae* in Hawaii. *Looping arrows* indicate cannibalism

lus macropilis (Acari: Phytoseiidae) displaces *Stethorus* as the dominant predator of *Tetranychus*. *Phytoseiulus* is a smaller predator, similar in size to its prey [adult female body length=0.58 mm (Prasad 1966)]. Another spider mite specialist predator, *Oligota* sp. (Coleoptera: Staphylinidae) can also be present, generally at lower densities, but its impact on *Tetranychus* appears to be minor (Rosenheim et al., in press). Also present throughout the growing season is a generalist predator that is a classic sit and wait forager: the web-building spider *Nesticodes rufipes* (Araneae: Theridiidae). *Nesticodes* spins a sparse web consisting of a few strands of silk stretched across a portion of the leaf; attacks are triggered when arthropods walking on the leaf surface contact the web. *Nesticodes* consumes all motile stages of *Tetranychus* and *Phytoseiulus*, as well as all larval stages of *Stethorus*.

Previous experimentation conducted early in the spring, when *Stethorus* was the dominant predator of spider mites, provided support for each of the predictions described above: (1) *Stethorus*, a widely foraging predator, consistently suppressed *Tetranychus* populations when tested as the sole predator present; (2) *Nesticodes*, the sit and wait predator, did not suppress *Tetranychus* when tested singly; (3) instead, *Nesticodes* consistently accelerated *Tetranychus* population growth rates, apparently by preying upon larval *Stethorus* (Rosenheim et al., in press). Here we report two additional experiments conducted later in the spring, when *Phytoseiulus* had emerged as the dominant predator of spider mites. Our results reinforce the earlier support for predictions (1) and (2), but, in contrast to the earlier results, show that herbivore suppression by the intermediate predator *Phytoseiulus* is insensitive to the presence of the top predator, *Nesticodes*. We then describe field observations of *Stethorus* and *Phytoseiulus* foraging behavior to explore one possible basis for the observed difference in sensitivity to *Nesticodes*.

Materials and methods

Our experiments incorporated two key design features that we think contributed to the realism of our results. First, the architecture of the papaya tree provided an attractive opportunity to manipulate the predator community without using cages. Mature papaya leaves are large (midrib lengths ca. 30 cm), held on long petioles (length ca. 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 treatments by using manual removals of predators. Predators and prey were thus free to move naturally on and off leaves, except where we excluded predators. Second, except for selecting leaves with some minimum number of *Tetranychus*, we did not attempt to homogenize the starting densities of prey or predators across the experimental replicates; thus, our experiments reflect the natural variability in predator and prey densities.

Experiment 1. Manipulation of spiders

The goal of this experiment was to determine if spiders or their webs would disrupt the suppression of *Tetranychus* populations by a community of predators dominated by *Phytoseiulus*. The experiment was conducted 16–27 June 1997 in a pesticide-free mature papaya orchard of mixed genetic background grown at the Poamoho Experiment Station, University of Hawaii, Oahu, Hawaii. Single mature but not yet senescing (yellowing) leaves harboring ≥5 adult female *Tetranychus* were used as the experimental units. At the start of the experiment, each leaf was inspected in the field to count: (1) the number of adult female *Tetranychus*; and (2) the number of *Stethorus* (all stages), *Phytoseiulus* (all motile stages), and spiders (all motile stages). Leaves were then assigned sequentially to one of three treatments, each replicated 40 times: (1) control, with the full predator community present and unmanipulated; (2) −spiders, with all spiders removed but their webs left in place, and all other predators retained; (3) −spiders−webs, with all spiders and their webs removed, and all other predators retained. We included the second treatment, in which the spider was removed but the web retained, to examine the possibility that some prey might respond to the presence of the web itself (e.g., Gastreich 1999). Although the spider-removal treatments involved the removal of the complete spider community, because the spider community was heavily dominated by *Nesticodes* (see Results), the spider treatment effects can be attributed primarily to this single species. A probe was used to remove spiders without disrupting their webs, and a small brush was used to remove webs. Treatments were blocked by papaya tree, with one to three full sets of replicates per tree. Treatments were maintained as press perturbations; leaves were checked each morning to remove spiders and webs. Final counts were made after 9 days. Data were subjected to ANCOVA, with tree as a blocking factor, initial *Tetranychus* density as a covariate, main effects for spider and web removal, and the per capita rate of *Tetranychus* population growth, calculated as [ln((final count)/ (initial count))]/9 days, as the dependent variable. Here and throughout the paper, results are presented as the mean ±1 SE.

Experiment 2. Manipulation of spiders, *Stethorus*, and *Phytoseiulus*

The goal of this experiment was to evaluate the effects of spiders, *Stethorus*, and *Phytoseiulus* on the population growth rate of *Tetranychus*. Although this experiment was conducted early in the calendar year (23 March–8 April 1998), *Phytoseiulus* was already established, perhaps because the El Niño-associated drought and warmer temperatures of winter 1997–1998 accelerated the normal seasonal shift to a *Phytoseiulus*-dominated community. The experimental protocols were as described for experiment 1, with the following modifications.

At the start of the experiment, *Tetranychus*, spiders, *Stethorus*, and *Phytoseiulus* were counted and the less common predators (including lacewing larvae, thrips, and the beetle *Oligota* sp.) were removed. Leaves were assigned sequentially to one of eight treatments, each replicated 20 times, comprising a three-way factorial design, with each factor representing the retention (+) or removal (−) of one of the dominant predators (spiders, *Stethorus*, *Phytoseiulus*). Thus, the treatments included a control, from which all predators were removed; three treatments in which each predator was tested singly by retaining its natural population and removing all other predators; and treatments testing all two-species and three-species combinations. We used trees as blocks, but were unable to establish full sets of replicates on each tree.

To maintain the experimental treatments, leaves were checked each morning to remove spiders and 3 times a day to remove *Stethorus*. *Phytoseiulus*, which are smaller and more difficult to detect, were removed in separate detailed checks performed every other day; all motile stages were removed, and we also searched for and removed *Phytoseiulus* eggs from any spider mite colonies in which we found adult *Phytoseiulus*.

On day 10 of the experiment, any leaves showing signs of moderate senescence were inspected in the field to count *Tetranychus* and all predators; these 10-day counts were used in the final data analysis only for leaves (n=10) that senesced significantly before the end of the experiment (day 14). Final counts were conducted for all other leaves on day 14. We then collected leaves into 70% ethanol to recover the full mite community. Leaves were washed by swirling them for 2 min in 1 l of water to which five drops of household bleach (5.25% sodium hypochlorite) had been added. Leaves were then hand-washed over a fine metal mesh (pores 0.04 mm by 0.04 mm), and all recovered arthropods stored in 70% ethanol. *Tetranychus* (larvae, nymphs, and adults) were counted in the laboratory. All predatory mites were slide mounted, identified, and stage-classified (larvae, protonymphs, deutonymphs, and adult males and females).

We tested for interactions of spiders with *Phytoseiulus* using the multiplicative risk model (Soluk and Collins 1988, Sih et al. 1998).

Foraging behavior of *Nesticodes*, *Stethorus*, and *Phytoseiulus*

We conducted 1-h focal observations to quantify predator foraging behavior. We observed *Nesticodes* (immatures and adults), third- and fourth-instar *Stethorus* larvae and adults, and adult female *Phytoseiulus*. Observations were made during both daylight (0900–1900 hours) and nighttime hours (1900–0030 hours), 27 March–8 April 1998 in two insecticide-free, mature papaya orchards at Poamoho.

For observations of *Stethorus* and *Phytoseiulus* we worked in teams of two, one person making continuous observations while the second person entered data into a hand-held computer (Psion Organiser II) operating behavioral event recording software (The Observer 3.0). For *Nesticodes* we were able to watch up to four spiders simultaneously on a single leaf, and we took written notes rather than using the computer. A hand lens was used as needed to identify prey. Night observations were made with headlamps fitted with red filters. A few *Phytoseiulus* and *Nesticodes* were also observed at night using unfiltered white light; we never observed any reaction of the arthropods to either our red or white light illumination. We recorded the predator's behavior (rest, walk, feed), the identity of prey, its microhabitat use (upper or lower leaf surface, stem/petiole), and whether it was residing within or outside of an active *Tetranychus* colony.

At the end of each observation we collected the leaf and traced the outlines of all *Tetranychus* colonies with a permanent marker. Leaves were held in a cooler until they were washed, as described above, to recover all mites. After washing, the parts of the leaf that had harbored mite colonies were excised from the leaf, and the areas of the mite-colonized and non-colonized leaf blade measured using a LICOR LI-3000 leaf area meter. Motile stages of *Tetranychus* were counted in the laboratory.

Results

Experiment 1. Manipulation of spiders

Phytoseiulus was the most common specialist predator of spider mites when the experiment was initiated. Mean arthropod counts per leaf at the start of the experiment were: adult female *Tetranychus*, 29.9±2.9; *Oligota* (larvae and adults), 0.21±0.05; *Stethorus* (all life stages), 0.47 ±0.11; *Phytoseiulus* (all motile stages), 2.50±0.30; and spiders (all motile stages), 3.19±0.19. Over the course of the experiment, *Stethorus* densities increased to 1.36±0.23 per leaf, while *Phytoseiulus* densities reached 5.37±0.62. We successfully established large differences in spider densities through our manual removals: at the end of the experiment the mean density of spiders in the spider-removal treatments was 0.55±0.08, significantly less than 4.56±0.40 in the control treatment (Kruskal-Wallis rank sum test, χ^2=76.0, P<0.0001). Of 178 spiders present on experimental leaves at the end of the experiment, 166 (93.2%) were *Nesticodes*, and the remaining 12 were unidentified members of the families Salticidae (six), Araneidae (four), and Gnaphosidae (two).

Neither the spiders nor their webs had a significant effect on the population growth rate of *Tetranychus* (Table 1); spider mite populations declined slowly in all treatments (Fig. 2a). Spider mite densities declined more rapidly on leaves with higher initial spider mite densities (Table 1). Because we did not experimentally manipulate the presence of predators, we cannot identify definitively which predators contributed to the suppression of *Tetranychus* populations. Correlational analyses, however, suggest that *Phytoseiulus* was the predator primarily responsible: an ANCOVA including the initial densities of *Oligota*, *Stethorus*, *Phytoseiulus*, and spiders as covariates identified a significant role only for *Phytoseiulus* ($F_{1,96}$=7.0, P=0.0095; all other P>0.09). Spider mite densities increased on leaves that did not harbor *Phytoseiulus* at the start of the experiment, and declined strongly on leaves with many *Phytoseiulus* (Fig. 2b). This

Table 1 Experiment 1: manipulation of spiders. ANCOVA of factors influencing the per-capita population growth rate of *Tetranychus cinnabarinus*

Source	df	SS	F	P
Block	16	0.3193	2.85	0.0008
Initial *Tetranychus* density	1	0.0952	13.6	0.0004
Spiders	1	0.0067	0.95	0.33
Web	1	0.0120	1.72	0.19
Error	99	0.6940		
Total	118	1.0981		

pattern was not confounded with the effect of initial spider mite density (*Phytoseiulus* and *Tetranychus* densities were uncorrelated at the start of the experiment; R=−0.014, n=119, P=0.88). Finally, we conducted an ANCOVA to look specifically for any evidence that spiders or their webs were interfering with the ability of *Phytoseiulus* to suppress spider mite densities. This ANCOVA included main effects for block, spiders, and web; covariates of initial *Tetranychus* and *Phytoseiulus* densities; and terms for the interactions of initial *Phytoseiulus* density with spiders and with webs. The spider and web main effects and their interactions with initial *Phytoseiulus* density were all non-significant (all P>0.2). Furthermore, neither the presence of spiders nor their webs had a significant effect on the mean number of *Phytoseiulus* found at the end of the experiment on +*Phytoseiulus* leaves (−spiders, 5.85±0.81; +spiders, 4.28±0.88; Wilcoxon test, χ^2=2.0, P=0.16; −webs, 4.70±0.70; +webs, 5.66±0.86; χ^2=0.02, P=0.89). Thus, this experiment suggests that *Phytoseiulus* was capable of suppressing spider mite populations and was insensitive to the presence of spiders.
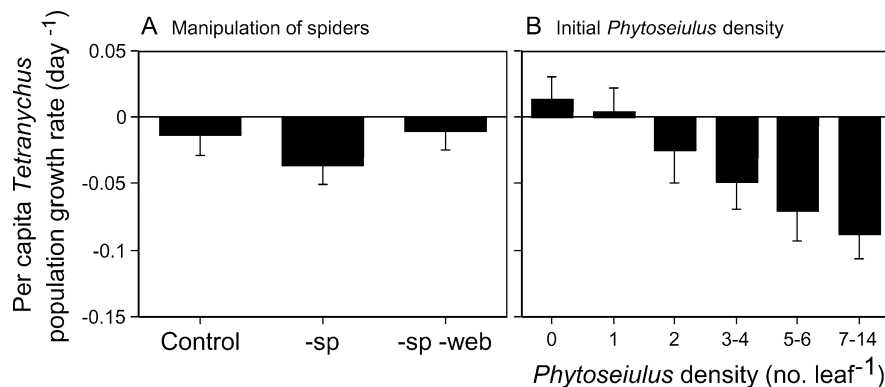

Fig. 2 Experiment 1: **a** Effect of spiders and spider webs on the per capita population growth rate of *Tetranychus cinnabarinus* in the presence of a predator community dominated by *Phytoseiulus*. Treatments and sample sizes: control, spiders and webs retained (*n*=39); spiders removed, but webs retained (−*sp*; *n*=40); both spiders and webs removed (−*sp* −*web*; *n*=40). **b** Influence of the initial number of *Phytoseiulus macropilis* (all motile stages) on the per capita population growth rate of *T. cinnabarinus*. Sample sizes are 42, 24, 11, 20, 8, and 14 for leaves with zero, one, two, three to four, five to six, and seven to 14 *Phytoseiulus*, respectively. Shown are means ±1 SE
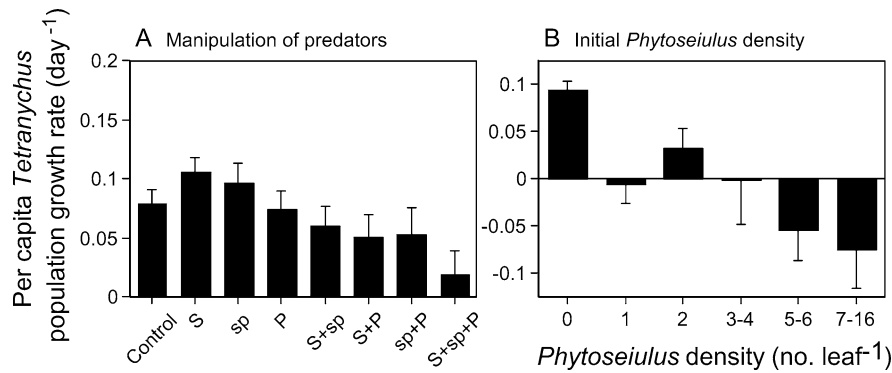
Fig. 3 Experiment 2: **a** Influence of spiders, *Stethorus*, and *Phytoseiulus*, alone and in combination, on the per capita population growth rate of *T. cinnabarinus*. Treatments and sample sizes: control (*n*=18); +*Stethorus* (*S*; *n*=16); +spiders (*sp; n*= 18); +*Phytoseiulus* (*P*; *n*=19); +*Stethorus* +spiders (*S*+*sp*; *n*=17); +*Stethorus* +*Phytoseiulus* (*S*+*P*; *n*=20); +spiders +*Phytoseiulus* (*sp*+*P*; *n*=19); *Stethorus*+spiders+*Phytoseiulus* (*S*+*sp*+*P*; *n*=18). Shown are means +1 SE. **b** Influence of the initial number of *P. macropilis* (all motile stages) on the per capita population growth rate of *T. cinnabarinus*. Sample sizes are 44, nine, eight, six, five, and four for leaves with zero, one, two, three to four, five to six, and seven to 16 *Phytoseiulus*, respectively. Note that the *y*-axis scales differ in panels (**a**) and (**b**). Shown are means±1 SE

Experiment 2. Manipulation of spiders, *Stethorus*, and *Phytoseiulus*

Phytoseiulus was again the most common specialist predator of spider mites when the experiment was initiated. Mean arthropod counts per leaf at the start of the experiment were: adult female *Tetranychus*, 19.5±1.7; *Stethorus* (all life stages), 0.44±0.08; *Phytoseiulus* (all motile stages), 1.55±0.24; and spiders (all motile stages), 1.51±0.10. We successfully generated large treatment differences in predator densities with our manual removals: (1) final *Stethorus* densities in the removal treatments were 0.11±0.05, significantly less than 0.89 ±0.33 in the treatments where they were retained (Kruskal-Wallis rank sum test, χ^2=7.3, *P*=0.0069); (2) final *Phytoseiulus* densities in the removal treatments were 1.15±0.27, significantly less than 7.26±2.29 in the treatments where they were retained (χ^2=7.5, *P*=0.0063); and (3) final spider densities in the removal treatments were 0.49±0.09, significantly less than 1.51±0.16 in the treatments where they were retained (χ^2=28.0, *P*<0.0001). The spider community was again strongly dominated by *Nesticodes*; 239 of 242 (98.8%) of the spiders present at the start of the experiment and 99 of 107 (92.5%) spiders present at the end of the experiment in the non-removal treatments were *Nesticodes*.

Although a casual inspection of *Tetranychus* population growth rates in the different treatments suggests that each of the predators might be contributing to population suppression (Fig. 3a), the statistical analysis identified a significant suppressive effect only for *Phytoseiulus*, with *Stethorus* and spiders exerting marginally non-significant effects (Table 2). The spiders×*Phytoseiulus* interaction term was not significant (Table 2), suggesting that spiders were not affecting the ability of *Phytoseiulus* to suppress spider mite populations. Spiders also had no significant effect on the mean number of *Phytoseiulus* present at the end of the experiment on +*Phytoseiulus* leaves (−spiders, 9.08±4.37; +spiders, 5.49±1.57; Wilcoxon test, χ^2=0.8,

P=0.38; the difference between the means was due to one strong outlier). A dominant and robust role for *Phytoseiulus* was further suggested by repeating the analysis using final counts of all motile stages of *Tetranychus*, rather than just the adult females that can be readily counted in the field; the suppressive effect of *Phytoseiulus* was highly significant ($F_{1,115}$=13.5, *P* =0.0004), whereas the effects of spiders and *Stethorus* were non-significant ($F_{1,115}$=0.7, *P*=0.39 and $F_{1,115}$=2.4, *P*=0.12, respectively); once again, the spiders×*Phytoseiulus* interaction term was non-significant ($F_{1,115}$=2.01, *P*=0.16).

As was observed in experiment 1, there was significant variation across experimental replicates in the initial density of *Phytoseiulus*, and this variation was associated with major differences in *Tetranychus* population growth rates; spider mite populations grew strongly on leaves that had not yet been colonized by *Phytoseiulus* at the start of the experiment, but generally declined on leaves harboring at least one predatory mite (Fig. 3b). To search for any evidence that spiders might be disrupting the suppressive effect of *Phytoseiulus*, we conducted an ANCOVA for

Table 2 Experiment 2. Manipulation of spiders, *Stethorus*, and *Phytoseiulus*. ANCOVA of factors influencing the per-capita population growth rate of *Tetranychus cinnabarinus*

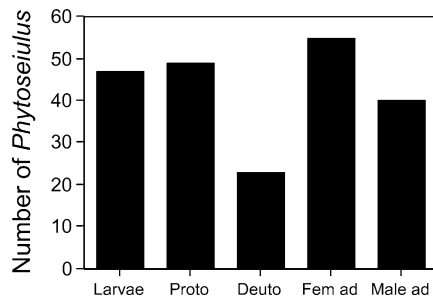| Source	df	SS	F	P
Block	19	0.2278	2.67	0.0007
Initial *Tetranychus* density	1	0.0149	3.31	0.071
Stethorus	1	0.0147	3.26	0.074
Spiders	1	0.0134	2.99	0.089
Phytoseiulus	1	0.0440	9.80	0.0022
Stethorus×spiders	1	0.0142	3.17	0.078
Stethorus×*Phytoseiulus*	1	0.0121	2.69	0.10
Spiders×*Phytoseiulus*	1	0.0021	0.46	0.50
Stethorus×spiders×*Phytoseiulus*	1	0.0021	0.46	0.50
Error	117	0.5258		
Total	144	0.8511		

Fig. 4 Experiment 2. Stage structure of the *P. macropilis* population at the end of the experiment on +spiders+*Phytoseiulus* treatment leaves. Shown are the total number of individuals found in each of the motile developmental stages. *Proto* Protonymphs, *Deuto* deutonymphs, *Fem ad* adult females, *Male ad* adult males

replicates in the +*Phytoseiulus* treatments with main effects for block and spiders, initial *Tetranychus* and *Phytoseiulus* densities as covariates, and an interaction term for spiders×initial *Phytoseiulus* density. This analysis revealed a highly significant effect for initial *Phytoseiulus* density ($F_{1,52}$=11.2, P=0.0015), but non-significant effects for spiders ($F_{1,52}$=2.5, P=0.12) and for the spiders×initial *Phytoseiulus* density interaction ($F_{1,52}$=0.4, P =0.84). Thus, we find no evidence that spiders were disrupting the ability of *Phytoseiulus* to suppress *Tetranychus* populations.

The stage structure of the *Phytoseiulus* population, measured at the end of the experiment on +spiders +*Phytoseiulus* treatment leaves, was consistent with expectations for a population that was enjoying substantial survival through the immature stages (Fig. 4). In the absence of any developmental mortality, and assuming approximately constant rates of natality in the population, we would expect to see ca. 70% more protonymphs and deutonymphs than larvae, simply because the larval stage lasts ca. 13 h, whereas the nymphal stages each last ca. 22 h (Prasad 1966). Although the numbers of protonymphs and deutonymphs observed were not as high as this zero-mortality expectation, there was no evidence for a severe deficit of late immature stages, as was previously observed for *Stethorus*, and apparently reflected a strong impact of *Nesticodes* predation (Rosenheim et al., in press).

Foraging behavior of *Nesticodes*, *Stethorus*, and *Phytoseiulus*

Our focal observations revealed large differences in predator foraging mode. *Nesticodes*, *Phytoseiulus*, and *Stethorus* larvae and adults differed strongly in their consumption of *Tetranychus* prey (Fig. 5a; χ^2=15.6, P=0.0013), percent time spent moving (Fig. 5b; Kruskal–Wallis rank sum test, χ^2=30.9, P<0.0001), and in net displacement per hour of observation (Fig. 5c; χ^2=36.4, P<0.0001). Observations were made under conditions of moderate prey availability [mean number of nymphal +adult *Tetranychus* per leaf=85.8±13.5, n=60; to compare this figure with the adult female *Tetranychus* density
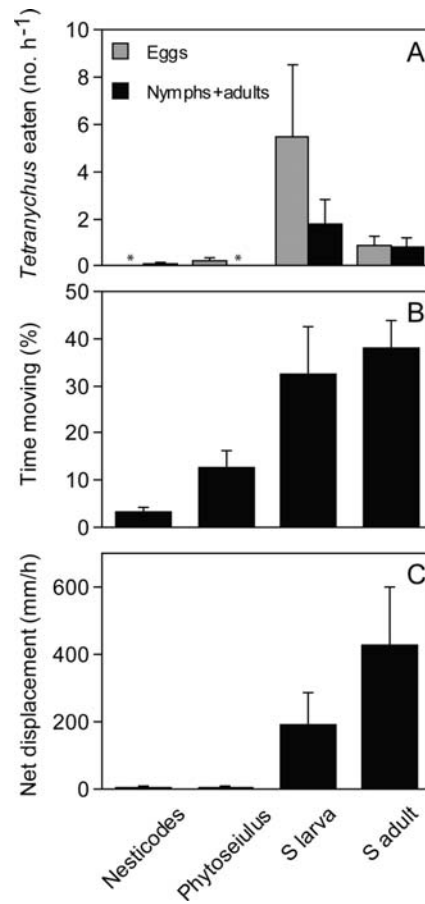

Fig. 5a–c Foraging behavior of *Nesticodes rufipes*, *P. macropilis*, and *S. siphonulus* (*S*), key predators of *T. cinnabarinus* spider mites in papaya, based upon 1-h focal observations. Shown are (**a**) the number of *Tetranychus* eggs and nymphs+adults consumed (* indicates none consumed); (**b**) the mean (+1 SE) percent of total observation time the predator spent moving; and (**c**) the net displacement over the total observation period. Data for *Nesticodes* (immatures and adults; n=26) and *Phytoseiulus* (adult females; n=17) include both day and night observations; data for *Stethorus* larvae (n=10) and adults (n=16) are for day observations only, as *Stethorus* are diurnal

estimates given in the remainder of the paper, note that adult females generally comprise about 15% of established nymph+adult populations (J. Rosenheim et al., unpublished data)]. *Tetranychus* density did not vary significantly across leaves on which different predator species were observed (χ^2=2.5, P=0.48).

Nesticodes employed a strict sit-and-wait foraging strategy: it spent almost all its time immobile on the web (Fig. 5b, c), waiting for mobile prey to contact the silken lines of the web stretched across the leaf surface. Spiders rested on the undersides of leaves (96.3±3.7% of observation time, n=26), generally in locations that offered some physical shelter, such as where the leaf ribs joined the leaf petiole, or in a curled leaf edge. Although spiders did emerge a few millimeters from these retreats early in the evening, spiders responded to prey during both day and night. Spiders appeared to be somewhat more active at night, but the differences in time spent moving (mean for

day =1.5±1.0% of observation time, *n*=15; night=5.4 ±2.5%, *n*=11; χ^2=1.2, *P*=0.27) and net displacement (mean for day=3.5±3.3 mm/h; night=7.3±7.3 mm/h; χ^2= 0.4, *P*=0.54) were not significant. We observed only three prey items being consumed during the focal observations; each was an adult female *Tetranychus*. Female spider mites do occasionally move outside of established spider mite colonies; we saw this primarily when *Stethorus* foraged in spider mite colonies, causing motile mites to flee the colony and run across the leaf surface. *Nesticodes* were not, however, strongly associated with *Tetranychus* colonies: spider ambush locations were located on or above spider mite colonies in four of 26 cases, which was not significantly more than would be expected by chance (6.3±1.4% of the leaf surface harbored mite colonies, on average; *G*-test for goodness of fit, *G*=2.6, *P*>0.10).

Phytoseiulus foraged actively to capture its immobile prey (four *Tetranychus* eggs were the only observed prey, Fig. 5a), but under the conditions of moderate prey availability *Phytoseiulus* did not need to move often (Fig. 5b) or far (Fig. 5c). We never observed *Phytoseiulus* on any plant substrate other than the bottom of leaves, and *Phytoseiulus* spent almost all of its time there within mite colonies (94.4±4.7%, *n*=17), which was significantly more than expected under a random model of leaf surface use (7.4±1.7% of the leaf surface harbored *Tetranychus* colonies; paired *t*-test, *t*=18.6, *P*<0.0001). *Phytoseiulus* did not show significant differences in activity between day and night (time spent moving: day=11.5±3.9%, *n*=11, night=15.2±6.6%, *n*=6, χ^2=0.4, *P*=0.55; net displacement: day= 1.4±0.5 mm/h, night=12.3±11.5, χ^2=0.3, *P*=0.57, the greater mean mobility at night was due to one strong outlier).

Like *Phytoseiulus*, late-instar larval and adult stages of *Stethorus* foraged actively to consume *Tetranychus* prey (Fig. 5a), but unlike *Phytoseiulus* their prey consumption rates were sufficiently high that they rapidly exploited prey within small spider mite colonies, and therefore had to move often (Fig. 5b) and far (Fig.5c) to find additional prey. This greater mobility also was manifested in *Stethorus* larvae and adults spending some time on the upper surfaces of leaves (larvae: 1.6±1.6%; adults, 11.4 ±5.2%) and on petioles or stems (larvae: 3.6±1.9%; adults, 2.0±1.6%) as they moved between leaves. Only *Tetranychus* were observed as prey. *Stethorus* were strictly diurnal; neither larvae nor adults showed any activity at night (*n*=4 observations for larvae, *n*=5 for adults; differences between day and night in proportion time spent moving and net displacement significant, *P*<0.05). Like *Phytoseiulus*, both larval and adult *Stethorus* were found in spider mite colonies more often than would be expected by chance (larvae: 86.6±7.6%, *n*=10, 11.0±2.3% of the leaf surfaces covered with spider mite colonies, *t*=8.5, *P*<0.0001; adults: 63.9±8.8%, *n*=16, 8.0±1.8% of the leaf surfaces covered with spider mite colonies, *t*=6.3, *P*<0.0001).

Discussion

Correlative and experimental evidence indicates that the only predator that produced statistically significant suppression of spider mites during our experimentation was *Phytoseiulus*. Thus, the predator community was different from that studied earlier in the spring by Rosenheim et al. (in press), in which the dominant predator of spider mites was the early colonizing *Stethorus*. The seasonally declining role for *Stethorus* was not surprising, given the lower density of this beetle during the two experiments reported here (experiment 1, mean density=0.92 per leaf; experiment 2, mean=0.67 per leaf) compared to the two experiments conducted earlier in the season (Rosenheim et al., in press; mean densities 1.81–2.00 across experiments). Of course, given that *Stethorus* did not produce measurable suppression of *Tetranychus* populations when tested singly in the experiments reported here, there was no opportunity for *Nesticodes* to accelerate *Tetranychus* population growth rates by interfering with *Stethorus*.

The trophic structure of the *Phytoseiulus*-dominated community exhibited both parallels and one key difference from the *Stethorus*-dominated community studied previously. In common with the earlier study, and supporting the first prediction of Rosenheim and Corbett (2003), a widely foraging predator, in this case *Phytoseiulus*, was capable of suppressing a sedentary herbivore population, *Tetranychus*. Also in common with earlier results, and supporting our second prediction, the sit and wait predator *Nesticodes* failed to suppress *Tetranychus* populations. However, in contrast to the earlier study, which showed that *Nesticodes* disrupted the suppression of spider mite populations produced by *Stethorus*, in the current study the suppression of spider mite populations produced by *Phytoseiulus* was entirely insensitive to the presence of *Nesticodes*. Thus, we have a widely foraging intermediate predator (*Phytoseiulus*) that appears to be an effective suppressor of a sedentary herbivore population (*Tetranychus*), even in the face of a sit and wait intraguild predator (*Nesticodes*), a result incompatible with our third prediction. How did this occur?

There are several possible explanations to consider. Perhaps the simplest is that *Phytoseiulus* has some effective defense against *Nesticodes* that *Stethorus* lacks, or that *Nesticodes* rejects *Phytoseiulus* as prey, while accepting *Stethorus*. Our informal observations, however, do not support these possibilities; during experimentation performed across four field seasons, we observed *Nesticodes* to consume *Phytoseiulus* fairly routinely. For example, one scan sample of *Nesticodes* taken 3–19 May, 2001 at Poamoho (*n*=777 spiders censused; 38 were eating) revealed that *Tetranychus* was the most common prey (*n*=13), and that each of the common spider mite predators was also preyed upon, including *Phytoseiulus* (*n*=3), *Oligota* (*n*=2), and *Stethorus* (*n*=1) (J. A. Rosenheim, J. Brodeur, and D. Goldvasser, unpublished data).

Our behavioral observations suggest another straightforward explanation: not all widely foraging predators are

equal in their overall mobility. *Phytoseiulus* are small relative to the size of their *Tetranychus* prey, and therefore have low rates of prey consumption (Fig. 5a) and low movement requirements when prey are moderately abundant, as was the case in this study (Fig. 5b, c). *Stethorus*, in contrast, are large relative to the size of their *Tetranychus* prey, and thus *Stethorus* larvae must consume many prey to develop successfully (Fig. 5a; Raros and Haramoto 1974), producing high movement requirements (Fig. 5b, c). Because it is movement across the leaf surface that generates encounters with *Nesticodes*, it follows that *Phytoseiulus* should experience a much lower risk of predation by *Nesticodes* than should *Stethorus*. This verbal argument has been explored with simulations of the papaya community, confirming that body size differences alone can explain nearly all of the observed insensitivity of *Phytoseiulus* to *Nesticodes* predation (Rosenheim and Corbett 2003).

Our study, then, suggests a very general means by which a widely foraging intermediate predator can ameliorate its risk of predation by a sit and wait top predator: be small. This suggestion is intriguing, because it is the reverse of the general prediction that smaller predators are subject to more intense intraguild predation, based on size-structured trophic interactions (Polis et al. 1989; Memmott et al. 2000; Woodward and Hildrew 2002). It is true in many animal communities, including communities of predatory arthropods, that body size is a primary determinant of who is capable of eating whom, due to size-based constraints on the ability to capture or ingest potential prey. In the papaya community, however, even the smallest *Nesticodes* spiderlings, only 0.7 mm long, were capable of subduing and consuming the largest *Stethorus* larvae, a reflection of the effectiveness of their combined use of webbing and venomous bites. More generally, it is likely that body size produces two opposing influences on predation risk experienced by intermediate predators: larger individuals: (1) may be more able to defend themselves against potential predators, but (2) their greater nutritional demands may also necessitate a greater foraging range, thus producing more encounters with predators, especially sit and wait predators.

Informal observations in papaya suggest that the mobility of *Phytoseiulus* may increase dramatically when prey populations are heavily exploited. [We were completely unable to maintain a *Phytoseiulus*-removal treatment during another experiment in which spider mite populations were suppressed to very low densities (see Rosenheim et al., in press, experiment 2), because leaves from which we removed all *Phytoseiulus* were recolonized within hours.] Thus, this community may be a good candidate for expressing the dynamics discussed by Anholt and Werner (1998), wherein adaptive increases in foraging intensity by a consumer as its resources are depleted result in an amplification of its risk of predation. The longer-term repercussions of these effects on the population dynamics of *Tetranychus*, *Phytoseiulus*, and *Nesticodes* are unexplored, but potentially quite interesting. Because *Nesticodes* predation might be expected to

become most intense when the ratio of *Phytoseiulus* to *Tetranychus* is highest, it might act as a stabilizing influence, reducing the likelihood of *Phytoseiulus* driving local *Tetranychus* populations to extinction.

In conclusion, the experimental results presented here, in combination with the results presented by Rosenheim et al. (in press), suggest that the trophic structure of the arthropod community associated with spider mites on papaya changes seasonally. Early in the season, when *Stethorus* is the dominant intermediate predator, the community exhibits four-trophic level dynamics, with *Nesticodes* disrupting control of spider mites by *Stethorus*. Later in the season, when *Phytoseiulus* emerges as the dominant intermediate predator, the community exhibits three-trophic level dynamics, with *Nesticodes* having no measurable impact on the short-term suppression of spider mites by *Phytoseiulus*. *Phytoseiulus* may achieve a high degree of insensitivity to its intraguild predator *Nesticodes* simply by being small, and thus having modest needs to forage across the leaf surface.

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