

R.G. Colfer · J.A. Rosenheim

Predation on immature parasitoids and its impact on aphid suppression

Received: 8 February 2000 / Accepted: 19 July 2000 / Published online: 13 October 2000
© Springer-Verlag 2000

Abstract Many predatory arthropods eat both unparasitized herbivores and herbivores that are parasitized and contain the immature stages of endoparasitoids, a form of intraguild predation. Thus, the biological control of herbivorous arthropods can be either enhanced or disrupted by introducing a predator species to an existing host-parasitoid system. We evaluate the impact of introducing a predator, the convergent ladybird beetle, *Hippodamia convergens*, on the biological control of the cotton aphid, *Aphis gossypii*, by the parasitoid *Lysiphlebus testaceipes*, under field conditions. Predation on immature parasitoids by *H. convergens* was intense: 98–100% of aphid mummies were consumed by the end of the experiment, and *H. convergens* substantially reduced immature parasitoid populations. Despite the negative impact of *H. convergens* on aphid parasitoids, aphid population suppression was greatest in treatments containing both *H. convergens* and parasitoids. The parasitoid alone or in combination with *H. convergens* suppressed cotton aphids in a density-dependent manner and increased total plant leaf area and biomass, *H. convergens* did not substantially alter the percentage of aphids mummified by parasitoids and showed a partial feeding preference for unparasitized aphids over aphid mummies. We conclude that under conditions where a predator shows both a partial preference for unparasitized hosts and high levels of predation on unparasitized hosts, we may expect the predator to improve suppression of herbivores even if it produces high levels of intraguild predation. While intraguild predation is an important ecological interaction in the early-season cotton agroecosystem, it does not disrupt cotton aphid biological control.

Keywords Biological control · Density-dependent predation · Herbivore natural enemies · Intraguild predation · Trophic cascade

Introduction

Although the “top-down effects” of predation and parasitism are important regulating forces for some terrestrial herbivore species, for other herbivore species different regulatory factors may be more important. There are several potential reasons why predation and parasitism may fail to regulate herbivore populations. First, other ecological factors such as the “bottom-up effects” of host plant resource limitation and the “lateral effects” of competition may limit herbivore populations more than predation (Karban 1989; Hunter and Price 1992; Cappuccino and Price 1995; Denno et al. 1995). Second, complex interactions between the natural enemies of herbivores (i.e., higher-order predation, intraguild predation, and cannibalism) may prevent predators from exerting strong mortality on herbivore populations (Polis et al. 1989; Rosenheim et al. 1995; Polis and Strong 1996; Sunderland et al. 1997; Rosenheim 1998). Third, predators and parasitoids may not always display density-dependent predation and parasitism, a condition necessary for predators to regulate herbivores (Murdoch 1970; Harrison and Cappuccino 1995). Finally, some ecologists have argued that herbivore populations may not be regulated by biotic factors, but that instead their populations may fluctuate with changing abiotic conditions (Andrewartha and Birch 1954).

Agroecosystems have traditionally been viewed as three trophic level communities, consisting of a primary producer (the crop), primary consumers (pests), and secondary consumers (natural enemies of pests). Biological control theory has followed the Hairston et al. (1960) model for terrestrial communities, which posits that if predatory species are sufficiently abundant, they will limit herbivore population size and allow plants to grow until they are limited by competition. A major assump-

R.G. Colfer (✉) · J.A. Rosenheim
Department of Entomology and Center for Population Biology,
University of California, Davis, CA 95616, USA

Present address:

R.G. Colfer, Mission Organics, P.O. Box 2357, Salinas,
CA 93902, USA, e-mail: ramy@nsfoods.com

tion behind this model and some of its later extensions (Hairston and Hairston 1993, 1997) is that all predators and parasitoids of herbivores can be lumped into a single trophic level and that higher-order predation and intraguild predation are not sufficiently important to influence the fundamental structure of most terrestrial communities. If this theory of terrestrial communities also correctly describes agroecosystems, then increasing the diversity and abundance of predators and parasitoids should consistently improve the biological control of herbivores. This view, that enhancing consumer diversity improves biological control, has received some empirical support (Riechert and Bishop 1990; Croft and Slone 1997; Riechert and Lawrence 1997; Riechert et al. 1999). However, there is a growing consensus that the Hairston et al. (1960) model is not appropriate for many terrestrial ecosystems; instead, a more flexible model that includes more than three trophic levels, omnivory, intraguild predation, and cannibalism, may be more appropriate for both natural terrestrial ecosystems (Polis 1991, 1994; Wise 1993; Polis and Strong 1996) and agroecosystems (Rosenheim et al. 1995; Rosenheim 1998). The potential for higher-order predators to constrain top-down control of herbivores has been widely debated in the case of hyperparasitism, in which one parasitoid species uses another parasitoid as a host. Theoretical and empirical studies have, however, not resolved whether hyperparasitoids disrupt the biological control of herbivores (reviewed in Rosenheim 1998).

Intraguild predation (IGP hereafter), in which potential competitors also engage in predator-prey interactions (Polis et al. 1989; Polis and Holt 1992), occurs in many terrestrial arthropod communities (Polis et al. 1989; Spiller and Schoener 1990, 1994, 1996; Hurd and Eisenberg 1990; Diehl 1993; Rosenheim et al. 1993). IGP can have several important influences on herbivore regulation. If an intraguild predator preferentially preys on primary predators rather than herbivores (functioning predominantly as a secondary predator) or if the intraguild predator is inefficient at exploiting herbivores, primary predator populations may be suppressed and herbivore populations allowed to expand (i.e., a trophic cascade). IGP of this type can sometimes disrupt biological control of herbivores (Rees and Onsager 1982; Croft and MacRae 1992; Rosenheim et al. 1993, 1999; Rosenheim, in press). Alternatively, if an intraguild predator is efficient at exploiting the herbivore prey and/or preferentially feeds on herbivores over intermediate predators, then herbivore regulation could be either unchanged or enhanced by IGP (Diehl 1993; Spiller and Schoener 1996). Although theoretical analyses have suggested that this type of IGP may cause populations of intermediate predators to be excluded from the system (Polis et al. 1989; Holt and Polis 1997), many empirical studies have observed both reductions in herbivore (or shared resource) abundance and persistence of the intermediate predator (reviewed in Diehl 1993). Therefore, it appears that IGP is capable of producing diverse impacts on biological control of herbivorous pests.

We studied the effects of IGP in a beetle-parasitic wasp-aphid system. The cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is an important herbivore of cotton species worldwide (Leclant and Deguine 1994), and a common pest in commercially grown upland cotton, *Gossypium hirsutum* L., in the San Joaquin Valley of California (Head 1992). The cotton aphid is primarily associated with two groups of natural enemies during early-season cotton in the San Joaquin Valley: a parasitic wasp *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae) and a complex of coccinellid beetles (primarily *Hippodamia convergens* Guérin-Méneville; Coleoptera: Coccinellidae). Most insect herbivores are attacked by both predators and parasitoids, creating abundant opportunities for IGP when predators consume parasitized hosts (Kot 1971; Brodeur 1994). The larval and pupal stages of aphid parasitoids, such as *L. testaceipes*, develop within aphids, causing the aphid to swell up, change color, and die; the swollen exoskeleton of the dead aphid containing the parasitoid prepupa or pupa is called a "mummy." When a predator attacks an aphid mummy, the parasitic wasp inside is generally consumed. There are several examples in the literature of parasitized aphids being consumed by many different aphid predators even after mummification (Wheeler et al. 1968; Frazer and van den Bosch 1973; Frazer and Gilbert 1976; Wheeler 1977; Nowierski 1979; Brodeur and McNeil 1992; Ferguson and Stiling 1996; Rosenheim et al. 1997).

The primary question we address is: what are the ecological consequences of IGP on immature parasitoids by coccinellid beetles? We performed a manipulative field experiment with natural densities of predators and parasitoids to examine how IGP by coccinellids influences aphid and parasitoid population dynamics and plant performance. We further conducted a laboratory prey-preference experiment to examine the mechanism underlying IGP on immature parasitoids.

We examined several aspects of IGP by *H. convergens* on the parasitoid *L. testaceipes*. Specifically, we examined: (1) the number of aphid mummies in the absence and presence of *H. convergens*, (2) the percentage of aphid mummies consumed by *H. convergens*, (3) the influence of hyperparasitoids on the population dynamics of *L. testaceipes* wasps, (4) the degree of aphid suppression produced by the parasitoid *L. testaceipes* alone and in combination with *H. convergens*, to determine if IGP disrupts aphid suppression, (5) the proportion of aphids parasitized by *L. testaceipes* wasps in the absence and presence of *H. convergens*, (6) the influence of initial aphid density on predation and parasitism, (7) the indirect influence of aphid predators and parasitoids on plant biomass, and (8) the preference of coccinellid adults when given the choice between feeding on unparasitized aphids and aphid mummies.

Materials and methods

Field site, materials, and treatments

To evaluate the interaction between coccinellid beetles and parasitoids, we conducted an inclusion/exclusion experiment in the field. As described in detail below, we used cages with "windows" that allowed free movement of natural enemies into and out of the cages, thereby ensuring that densities of natural enemies inside the cages were similar to naturally occurring densities. This design differs from many manipulative experiments in which there is a fixed and sometimes higher than natural density of natural enemies confined within the enclosure. The experiment was conducted from 26 April to 17 June 1994 in a 1150-m² plot of *G. hirsutum* cv. "Maxxa" surrounded by zucchini, grapevines, and fallow fields at the University of California Student Experimental Farm, Davis, Yolo County, California.

On 26 April, cotton plants at the cotyledon stage were manually cleaned of all insects and inoculated with adult cotton aphids (4 aphids/seedling) from a laboratory colony that had been maintained under abiotic conditions similar to April field conditions (temperature: 18°C, 13 h light per day). Forty cone-shaped cages with stainless steel sheet-metal bases, steel wire frames, and fine polyester mesh netting (cage dimensions: diameter of bottom, 32 cm; diameter of top, 20 cm; height, 30 cm; "Fibe-Air Sleeve", Kleen Test Products, Milwaukee, Wis., USA) were placed over groups of aphid-inoculated plants (3–7 seedlings per cage). The cage mesh had an irregular fine weave, with pores small enough to prevent insect migration yet large enough to allow air flow. The aphid populations were then allowed to increase for 18 days free of natural enemies and other herbivores. All contaminant species of herbivores and natural enemies were manually removed every 4–5 days.

On 13 May, ten cages were randomly allocated to each of four treatments: (1) aphids-only, with fine mesh cages retained to prevent insect migration and to allow aphid population growth unregulated by natural enemies; (2) aphids plus *L. testaceipes* wasps, with fine mesh cages containing two "windows" (dimensions: 2 cm width, 15 cm length) covered with a medium-mesh screen (pores 1.5 mm×1.5 mm), which allowed *L. testaceipes* and hyperparasitic wasps to move in and out of cages, but which excluded *H. convergens*; (3) aphids plus *L. testaceipes* plus *H. convergens*, with fine mesh cages containing two windows (dimensions: 2 cm width, 15 cm length) covered with a coarse-mesh screen (pores 8 mm×8 mm), which allowed both *L. testaceipes* and *H. convergens* to move in and out of cages; and (4) no-cage control, to determine if the presence of the mesh cage influenced aphid population growth, natural enemy efficacy, or plant growth. Replicates were blocked by initial aphid density to control statistically for any influence of aphid abundance on treatment effects.

Sampling techniques

Non-destructive sampling techniques were used to estimate the number of nymphal and adult cotton aphids, the number of aphid mummies intact, the number of aphid mummies consumed (mummies that were severely damaged from coccinellid chewing but that were not dislodged from the leaf), and the total leaf area in each cage. In cages harboring moderate aphid populations (≤ 1500 aphids/cage), we did a complete count of all nymphal, adult, and mummified aphids on the upper and lower surfaces of all leaves. If aphid numbers were extremely high (>1500 aphids/cage), we subsampled each leaf by counting aphids located on either the left or the right half of the leaf (chosen randomly). Aphids were sampled every 3–5 days for 24 days.

Coccinellid beetles were collected from the field and identified throughout the experiment. Any natural enemies that were found within treatments from which they were supposed to be excluded were removed; thus, aphid mummies, parasitic wasps, and coccinellid beetles were removed from the aphids-only treatment, and coccinellid beetles were removed from the aphids plus wasps

treatment. Ants, including the pavement ant, *Tetramorium caespitum*, and the thief ant, *Solenopsis molesta*, were prevented from tending aphids by placing toxic ant bait into cages (Grants' Kills Ants, Grants Laboratories Inc., San Leandro, Calif., USA) in which ants were found.

The proportion of mummies hyperparasitized and the proportion of mummies that successfully yielded the primary parasitoid *L. testaceipes* were estimated by collecting mummies from cages in the aphids plus *L. testaceipes* treatment on days 11–36 (mummy numbers were too low in other treatments to obtain adequate samples). Mummies were placed singly in gelatin capsules and reared at room temperature in the laboratory. All emerging wasps were identified.

Leaf area was estimated by collecting a sample of leaves ($n=43$) from the cages, measuring their lengths and widths, and then measuring leaf areas using a LICOR LI-3000 area meter. Multiple linear regression was applied to obtain the relationship between leaf area and leaf length and width [total leaf area = $-9.67 + 3.88(\text{leaf width}) + 1.70(\text{leaf length})$; $R^2=0.938$]. Total leaf area per cage was then estimated by counting the number of leaves per cage and measuring the length and width of five randomly selected leaves.

After termination of the experiment (on day 36), the above-ground parts of all of the cotton plants within each cage were collected, dried to a constant weight, and weighed.

H. convergens preference study

The purpose of this investigation was to determine if *H. convergens* show a feeding preference when given equal densities of two prey items: unparasitized aphids and aphid mummies. We define prey preference as a tendency to eat more of a prey type than would be expected based on its abundance in the habitat (Chesson 1983). This experiment was conducted in the laboratory on 1–17 June 1994 after the termination of the field cage experiment. Feeding preference was measured by placing adult beetles on cotton leaves infested with equal numbers of unparasitized aphids and aphid mummies. Infested leaves were obtained with the following steps

1. Leaves infested with mummies were obtained from the aphid+*L. testaceipes* treatment.
2. All aphids not mummified on these leaves were removed.
3. Unparasitized adult aphids were obtained from aphid-infested leaves that came from the aphid alone treatment (to ensure that the aphids were not parasitized) and then were added to the mummy-infested leaves.
4. Mummies were removed and aphids added to obtain an equal number of mummies and aphids. Only adult aphids were used to minimize the size difference between unparasitized aphids and mummies, although mummies are generally larger than aphid adults. In 9 of the 24 replicates the initial number of aphids and mummies per leaf varied (44–165 of each prey type per leaf), and in the remainder of the replicates (15/24) leaves were initiated with 50 aphids and 50 mummies. Adult beetles were hand-collected from aphid-infested weeds at our field site and starved for 4 h before preference trials were initiated. Beetles were confined on a single leaf in fine polyester mesh cages (20 cm×20 cm). Leaf petioles were inserted into wetted florist's foam to keep the leaves turgid. After 24 h, final aphid abundance was quantified by counting living aphids on both sides of a given leaf plus the inside of the cage, and final mummy abundance was quantified by counting undamaged mummies still attached to the leaf surface.

Monitoring of an unmanipulated aphid population

To determine if the high levels of predation on mummified aphids observed in the field cage experiment might have been an artifact of our experimental procedures, we sampled an unmanipulated aphid population at the same field site (a 0.2-ha plot of *G. hirsu-*

tum cv. "Maxxa" at the University of California Student Experimental Farm, Davis, Yolo County, California) on 25 August and 3 September 1999. We censused the aphid population by sampling a single mainstem leaf located five nodes below the apex of the plant from 100 randomly chosen plants. Aphids and aphid mummies were counted and aphid mummies categorized as intact, emerged, or consumed.

Analysis

The abundance of aphids and mummies and the percentage of mummified aphids [(mummies intact)(100%)/(mummies intact+aphids)] for the last four sampling dates were analyzed using two-factor, repeated-measures ANOVA tests (JMP Statistical Software for the Macintosh; SAS Institute Inc., Cary, N.C., USA) with treatment and block as main effects. Average percentage of mummy predation [(mummies consumed)(100%)/(mummies consumed+mummies emerged+mummies intact)] for the last four sampling dates, and final plant biomass were analyzed using two-factor ANOVA with treatment and block as main effects. The Greenhouse-Geisser probabilities corrected for sphericity were also calculated. To meet the requirements necessary for the ANOVA models, abundance data were either log or square-root transformed and percentage data were arcsine transformed. Planned paired comparisons for the above response variables were performed using two-factor ANOVA and two-factor, repeated measures ANOVA tests. The experiment-wise alpha error rate was maintained at 0.05 by adjusting the critical P value for the number of paired comparisons being conducted using the sequential Bonferroni method. Coccinellid beetle prey preference was analyzed using a paired t test. Effects of initial aphid abundance and different treatments on aphid population growth rates were analyzed by: (1) regressing aphid densities against census dates (four final samples) and calculating the slope of the population growth (i.e., average aphid population growth rate), and then (2) regressing initial aphid densities against aphid population growth rates for each treatment. Regression models were chosen by maximizing the adjusted coefficient of multiple determination R^2_{adj} (Neter et al. 1990).

Results

Natural enemy species

The only species of adult coccinellid beetle collected was the convergent ladybird beetle, *Hippodamia convergens*. *L. testaceipes* was the only primary parasitoid that emerged from the mummies collected. Two species of hyperparasitoids emerged: the commoner *Pachyneuron siphonophorae*, and the rarer *Alloxysta bakeri*. Other predators that were observed at very low densities included green lacewing eggs (Chrysopidae) and hover fly larvae (Syrphidae).

Population dynamics of cotton aphids

The abundance and population growth rate of cotton aphids differed greatly between treatments (Figs. 1, 2, Table 1). Aphid abundance in the aphids-only treatment increased relatively rapidly throughout the duration of the experiment. Aphid densities in the wasps treatment also increased throughout the experiment, but at a consistently slower rate. There was a significant difference

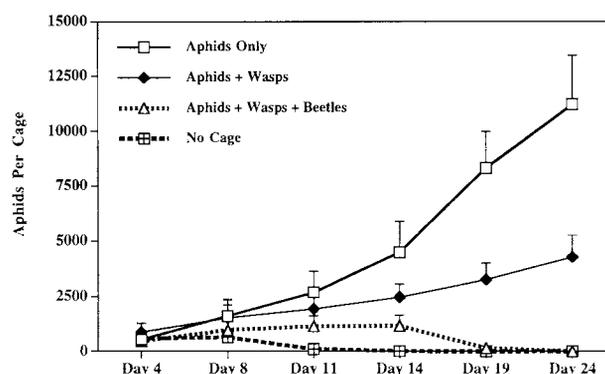


Fig. 1 Mean number (\pm SE) of cotton aphids (*Aphis gossypii*) in treatments with no natural enemies, with parasitic wasps (*Lysiphlebus testaceipes*) and hyperparasitoids, with wasps and coccinellid beetles (*Hippodamia convergens*), and with no cage. Natural-enemy treatments were manipulated by providing cages with "windows" of varying mesh size

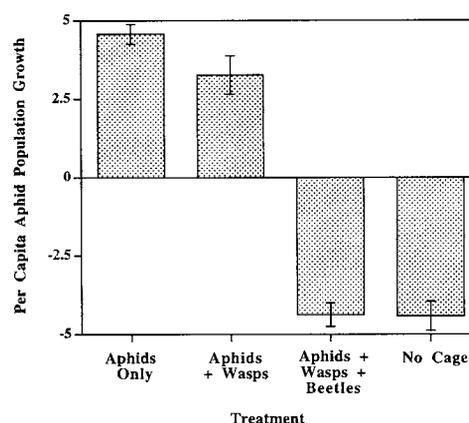


Fig. 2 Mean (\pm SE) per capita aphid population growth across the full duration of the 24-day field experiment. Paired comparisons: aphids-only vs. aphids+wasps, $F=6.5$, $P=0.032$; aphids-only vs. aphids + wasps + beetles, $F=765.1$, $P<0.0001$; aphids + wasps vs. aphids + wasps + beetles, $F=308.1$, $P<0.0001$; aphids + wasps + beetles vs. no cage, $F=0.02$, $P=0.89$

between the wasps treatment and aphids-only treatment for the entire time series ($F=5.6$, $P=0.042$). There were even greater differences in aphid abundance between the aphids-only treatment and the wasps+beetles treatment ($F=99.6$, $P<0.0001$). *H. convergens* reduced aphid numbers to near zero by the end of the experiment (day 24, mean aphids per cage in the wasps+beetles treatment, 1.1 ± 0.6 , mean \pm SE; no-cage treatment, 0.2 ± 0.2). Aphid suppression was significantly stronger in the treatment with both beetles and wasps compared to the treatment with just wasps ($F=100.8$, $P<0.0001$). Thus, in this system adding an intraguild predator to an existing host-parasitoid interaction led to enhanced top-down control of the target herbivore population.

The presence of the mesh cage caused the abundance of aphids to decline more gradually in the wasps+beetles treatment in comparison to the dramatic decline in aphid

Table 1. Repeated measures two-way analysis of variance for effects of treatment (predator community) and block (initial aphid density) on aphid populations and aphid mummy (pupating parasitic wasp) populations in the field experiment. The Greenhouse-Geisser (*G-G*) probabilities corrected for sphericity are also presented

Species	Source	<i>df</i>	<i>F</i>	<i>P</i>	<i>G-G</i>
Aphids	Treatment	3	67.37	<0.0001	
	Block	4	3.85	0.019	
	Treatment×Block	12	3.37	0.009	
	Error	38			
	Sampling date	3	10.19	<0.0001	0.0012
	Date×Treatment	9	25.34	<0.0001	<0.0001
	Date×Block	12	4.58	<0.0001	0.0024
	Date×Treatment×Block	36	1.56	0.066	0.142
	Error	155			
	Aphid mummies	Treatment	3	24.75	<0.0001
Block		4	3.07	0.0412	
Treatment×Block		12	1.36	0.2665	
Error		38			
Sampling Date		3	0.863	0.466	0.432
Date×Treatment		9	5.66	<0.0001	0.0002
Date×Block		12	4.92	<0.0001	0.0003
Date×Treatment×Block		36	2.02	0.0087	0.0247
Error		155			

abundance seen in the no-cage control, which led to overall lower aphid numbers in the no-cage control ($F=14.2$, $P=0.0037$). However, aphid abundance was similar in the wasps+beetles treatment and the no-cage control by the end of the experiment (day 24, $F=1.4$, $P=0.267$). The significant treatment×block interaction (Table 1) indicates that treatment effects were influenced by initial aphid density. This result is discussed further in the section on the effect of initial aphid abundance and predation on aphid population growth.

Aphid mummy predation and population dynamics

Predation on aphid mummies was intense in treatments containing *H. convergens* (Fig. 3), reaching 98–100% of the mummies consumed by the end of the experiment. Some mummy predation was observed in the wasps-alone treatment due to natural enemies gaining access into cages from which we were trying to exclude them. However, the wasps+beetles treatment had substantially higher average levels of mummy predation than the wasps treatment ($F=17.6$, $P=0.0023$). Mummy predation increased to very high levels approximately one week earlier in the no-cage control compared to the wasps + beetles treatment (Fig. 3). Attacked mummies sustained damage that indicated they had been attacked by predators with chewing mouthparts: mummies had large ragged-edged holes chewed into their dorsal or lateral surfaces. This observation suggests that coccinellid beetles, the only common predators in early-season cotton with chewing mouthparts, were responsible for the mummy predation we observed in this system.

The presence of *H. convergens* also had a large negative influence on aphid mummy abundance (Fig. 4, Table 1). The wasps-alone treatment had greater numbers of aphid mummies than the wasps+beetles treatment ($F=27.3$, $P=0.0005$). Also, aphid mummies remained abundant throughout most of the experiment in the wasps-alone treatment, while mummy abundance re-

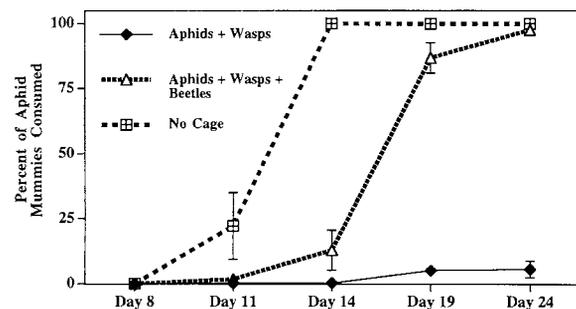


Fig. 3 Mean (\pm SE) percentage of aphid mummies consumed by *H. convergens* in the natural-enemy treatments. Percentage consumed=(number consumed)/(number consumed+number intact+number emerged) \times 100%

mained low in the wasps+beetles treatment. The presence of the mesh cage increased overall mummy abundance ($F=45.5$, $P<0.0001$), perhaps because mummy predation was delayed in the wasps+beetles treatment compared to the no-cage control (Fig. 3). The aphids-only treatment was largely successful in excluding wasps, as indicated by a significantly lower overall mummy abundance in the aphids-only treatment compared to the aphids+wasps treatment ($F=30.1$, $P=0.0004$). It is also important to note that when the percentage of mummies that had been attacked by coccinellid beetles increased rapidly (days 14–19), the total number of mummies on the leaves actually decreased, indicating that beetles dislodge many mummies while attacking them (Figs. 3, 4).

The negative effect of *H. convergens* on mummy abundance could be derived from either of two sources: predation of mummies (a direct effect), as shown above, or competition for aphids (an indirect effect). To determine if competition for aphids is also a means by which beetles affect wasps negatively, an additional analysis was performed comparing the three treatments in which parasitoids were present. We used two-factor repeated measures ANCOVA tests with treatment and block as main effects, average aphid number over the final five

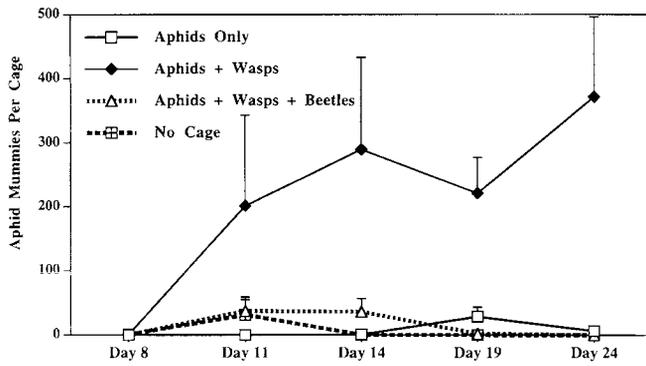


Fig. 4 Mean (+SE) number of intact aphid mummies

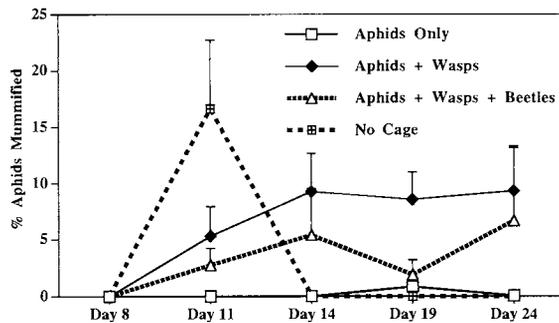


Fig. 5 Mean (+SE) percent of aphids that were mummified due to parasitism by wasps

sampling dates as the covariate, and square-root-transformed mummy abundances for the final four sampling dates as the response variables. The analysis showed that average mummy abundance did not covary with aphid abundance ($F=1.2$, $P=0.29$), suggesting that competition for aphids was not an important mechanism by which beetles suppressed mummy densities. The effect of *H. convergens* remained significant with the addition of the covariate ($F=28.8$, $P<0.0001$), indicating that mummy predation itself had an important effect on mummy abundance.

The highest rate of parasitism was observed in the wasps-alone treatment (Fig. 5); however, even in this treatment parasitism levels remained low, never exceeding 10%. Parasitism rates were consistently but not significantly lower in the wasps+beetles treatment compared to the wasps-alone treatment ($F=3.1$, $P=0.129$).

Effect of initial aphid abundance and predation on aphid population growth

Our primary analysis of aphid dynamics (Table 1) revealed a strong main effect of block (i.e., initial aphid abundance) and treatment \times block interactions on final aphid abundance. To understand these effects of initial aphid densities, we regressed average aphid population growth rates (calculated as the slope of the linear regression of aphid abundance against time over the final four

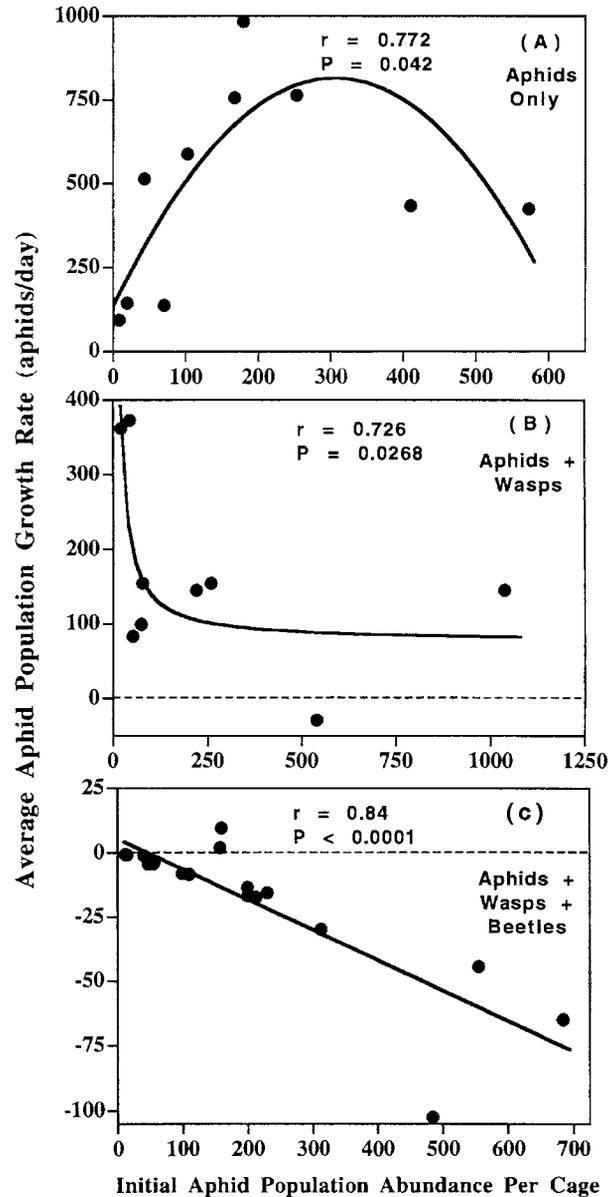


Fig. 6 Relationship between average aphid population growth rate (aphids day⁻¹) and initial aphid density, in **A** the aphids-only treatment ($y=135.8+4.44x-0.0073x^2$), **B** the aphids+wasps treatment [$y=76.6+6315.4(1/x)$] and **C** the two treatments where beetles were present (aphids+wasps+beetles treatment and the no-cage control replicates combined; $y=5.32-0.118x$). Dashed line shows the location of zero population growth

sampling dates) against initial aphid abundance for each of the treatments (note: no-cage control data were combined with the wasps+beetles treatment for this analysis). Initial aphid abundance influenced average aphid population growth rates differently in the three treatments (Fig. 6A–C). In treatments with *H. convergens*, aphid population growth rates declined linearly with increasing initial aphid abundance ($r=0.84$, $F=44.3$, $P<0.0001$) and most aphid growth rates were negative. In the treatment with wasps alone, aphid population growth rates declined as the reciprocal of the initial

aphid abundance ($r=0.73$, $F=7.8$, $P=0.027$). In the aphids alone treatment, the relationship between average aphid population growth and initial aphid density was best described using second order polynomial regression ($r=0.77$, $F=5.2$, $P=0.042$); aphid growth rates were highest at intermediate initial aphid densities. The observation that aphid population growth rates declined with increasing initial aphid densities in the natural enemies treatments indicates that predators and parasitoids had a greater impact at higher aphid densities (i.e., behaved in a density-dependent manner).

To determine if aphid populations experienced density-dependent mortality (the requisite for a factor to regulate a population), we examined the relationship between initial aphid abundance and the per capita rate of aphid population growth (aphids day⁻¹ initial aphid⁻¹). As we had observed with the absolute aphid population growth rate, initial aphid abundance influenced proportional aphid population growth differently in the three treatments (Fig. 7A–C). First, in treatments with *H. convergens*, proportional aphid population growth rates declined linearly with increasing initial aphid abundance ($r=0.469$, $F=5.1$, $P=0.037$) and most growth rates were negative. Thus, the per capita aphid mortality was greater for populations with higher initial abundance. Second, in the wasps-alone treatment, proportional aphid population growth rates declined as the reciprocal of the initial aphid abundance ($r=0.946$, $F=60.0$, $P<0.0001$) and growth rates were near or below zero for high initial aphid abundance. Consistent with this pattern, proportional aphid population growth rates declined with increases in the percentage of aphids mummified ($r=0.72$, $F=9.8$, $P=0.016$, Fig. 8A) and the percentage of aphids mummified increased with increases in initial aphid abundance ($r=0.67$, $F=6.0$, $P=0.049$, Fig. 8B) in the wasps only treatment. Finally, in the aphids-only treatment, proportional population growth rates declined with increases in initial aphid abundance ($r=0.912$, $F=39.8$, $P=0.0002$), but growth rates were all above zero (Fig. 7A). This relationship was most likely due to the population growth being limited by the plant resources. Indeed, in the aphids-only treatment, final plant biomass declined with increases in initial aphid abundance ($r=0.927$, $F=49.6$, $P<0.0001$, Fig. 8C).

Wasp emergence and hyperparasitism

The percentage of mummies from which adult *L. testaceipes* successfully emerged in the aphids+wasps treatment ranged from 73.3 to 90% on days 11–26 (Fig. 9). However, *L. testaceipes* emergence declined to 9.1–38.3% during days 29–36, and the decline in *L. testaceipes* emergence over the duration of the experiment was significant (Spearman's $r=-0.93$, $P=0.0025$). Hyperparasitism increased throughout the experiment (Spearman's $r=0.82$, $P=0.023$), reaching 40–65.2% during days 29–36.

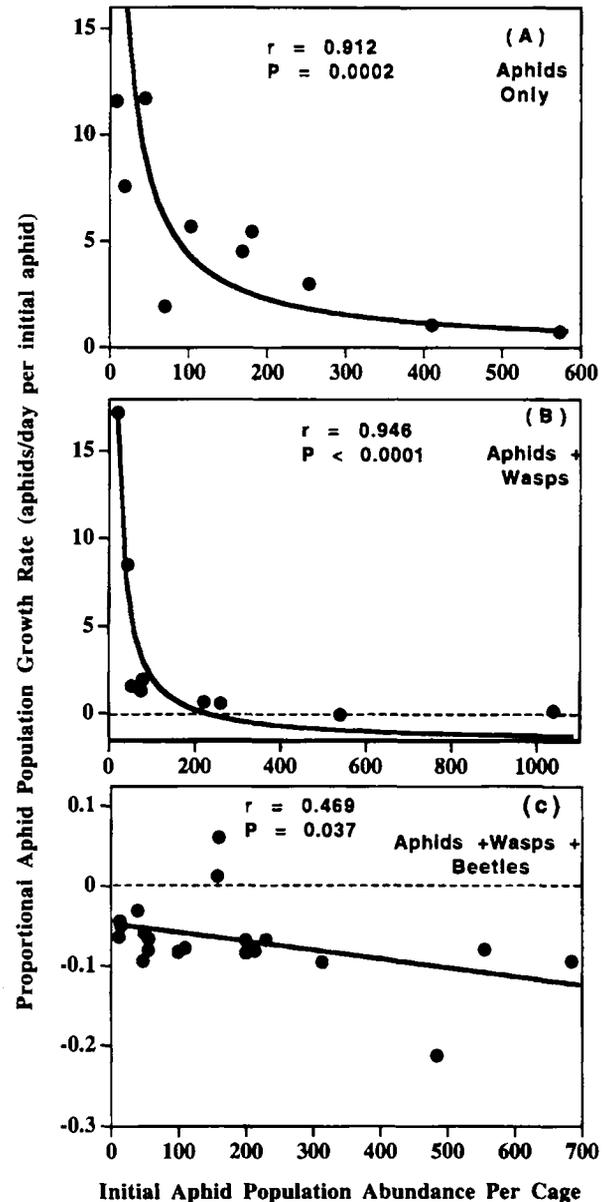


Fig. 7 Relationship between proportional aphid population growth rates (aphids day⁻¹ per initial aphid) and initial aphid density in **A** the aphids-only treatment [$(1/y)=0.019+0.0021x$], **B** the aphids+wasps treatment [$y=-1.63+368.8(1/x)$], **C** the two treatments with beetles ($y=-0.046-0.00012x$). Dashed line shows the location of zero population growth

Plant biomass and leaf area

Plant biomass and leaf area differed significantly across treatments (plant biomass, $F=7.5$, $P=0.0006$; leaf area, $F=7.9$, $P=0.0012$; Fig. 10). Plant biomass and total leaf area were significantly greater in the wasps treatment and the wasps+beetles treatment compared to the aphids-alone control (Fig. 10). Plant traits did not differ, however, between the wasps treatment and the wasps+beetles treatment. The presence of the cage also did not affect plant biomass or leaf area. No correction was made for differences in the number of plants per cage.

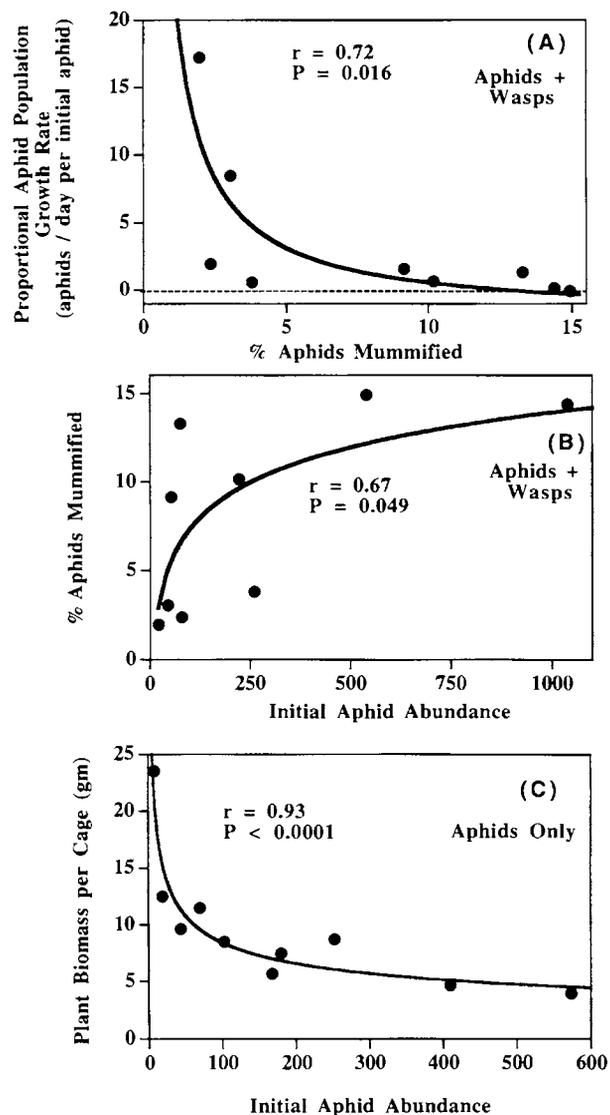


Fig. 8 Relationship between **A** proportional aphid population growth rates and the percentage of aphids mummified [$y = -2.03 + 0.26(1/x)$] in the aphids+wasps treatment, **B** percentage of aphids mummified and initial aphid abundance [$y = -0.056 + 0.03[\ln(x)]$] in the aphids+wasps treatment and **C** final plant biomass and initial aphid abundance (Box-Cox transformed $y = 87.2 - 0.024x$) in the aphids-only treatment. Dashed line shows the location of zero population growth

H. convergens prey preference

Prey preference trials showed that *H. convergens* preferentially fed on unparasitized aphids over mummified aphids ($t = -2.38$, $P = 0.013$, Fig. 11), although the preference was not particularly strong and beetles commonly fed on both prey items: during the 24-h trial period, *H. convergens* on average consumed 21.9 ± 3.6 mummies and 32.9 ± 4.6 unparasitized aphids.

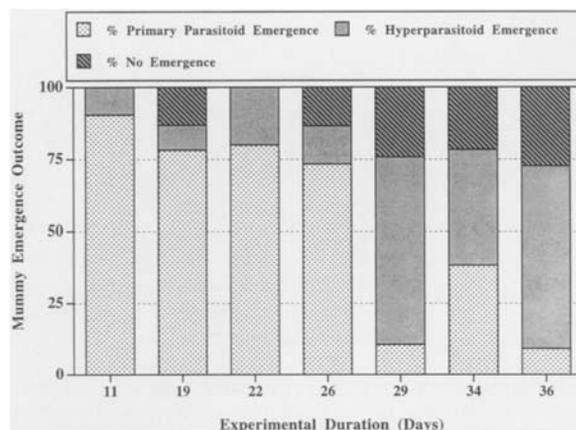


Fig. 9 Percentage of primary parasitoids (*L. testaceipes*) and hyperparasitoids (*Pachyneuron siphonophorae* and *Alloxysta bakeri*) emerging from aphid mummies collected in the aphids+wasps treatment. The day numbers indicated on the bar graphs indicate when the mummies were collected from the field

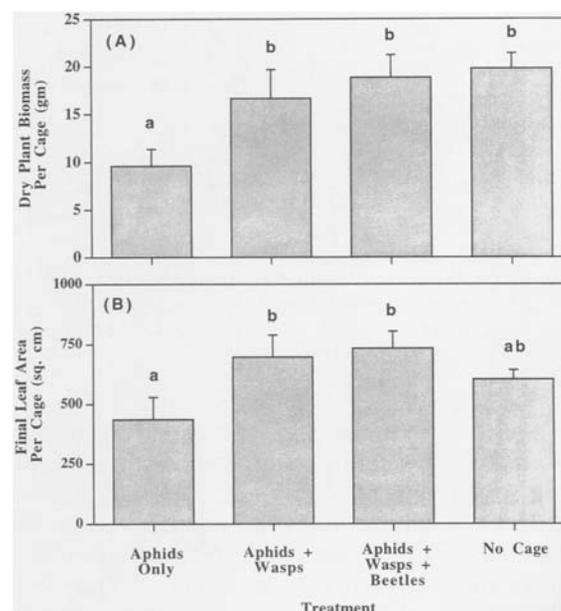


Fig. 10 Mean (+SE) of **A** dry plant biomass per cage (g) and **B** total leaf area (cm^2) at the termination of the experiment. Different letters above the bars indicate significant differences between treatments with experimentwise $\alpha = 0.05$

Monitoring of an unmanipulated aphid population

We sampled a natural field population of cotton aphids whose densities were collapsing under strong combined impacts of parasitoids and coccinellid beetles. Aphid densities declined from 12.2 to 1.3 per leaf, and mummy densities declined from 4.5 to 0.8 per leaf. At the same time, coccinellid populations increased from 2 juveniles (larvae and pupae) to 10 juveniles per 100 leaves. The percentage intact mummies decreased between sampling dates, whereas the percentage consumed mummies increased to high levels, similar to those observed in our

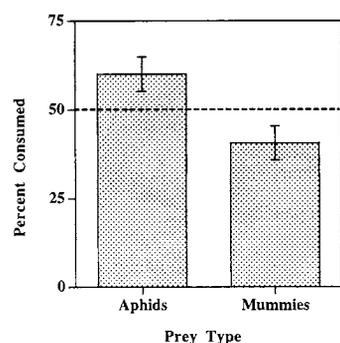


Fig. 11 Mean percentage (\pm SE) of unparasitized aphids and aphid mummies consumed in a laboratory preference experiment. Dashed line indicates the expected percentage of each prey type consumed if *H. convergens* displayed no preference

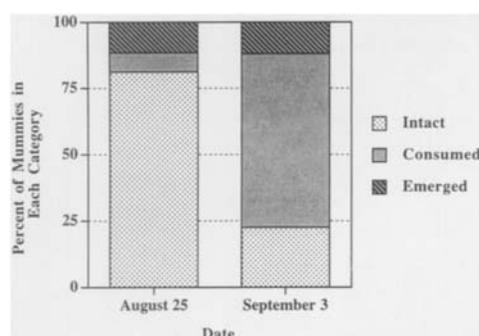


Fig. 12 Intraguild predation on aphid mummies in an unmanipulated field population being suppressed by coccinellid beetles. Percentage of aphid mummies intact, emerged, and consumed on 25 August and 3 September 1999

manipulative experiment (Fig. 12). Aphids in this population were very patchily distributed, with some plants harboring thousands of aphids and most plants harboring fewer than 100 aphids. Many of the aphid colonies were tended by Argentine ants (*Linepithema humile*) and pavement ants (*Tetramorium caespitum*), which were unusually abundant at the site. These results are noteworthy because they show that aphid and mummy population dynamics that are similar to those in our experiment can be observed under unmanipulated conditions and later in the season.

Discussion

Our field experiment used natural densities of aphid parasitoids and coccinellid beetles to determine the direct impact of IGP on aphid mummies and the indirect influence of IGP on aphid population suppression. We found that *H. convergens* consumed nearly all of the aphid mummies present on plants, thereby greatly reducing the aphid mummy population. However, despite this devastating effect of coccinellid beetles on aphid parasitoids, aphid population suppression improved with the addition of *H. convergens*. Natural enemies suppressed

aphid populations in a density-dependent manner across the full range of aphid densities studied. Aphid suppression by coccinellid beetles and parasitoids led to greater total leaf area and above-ground plant biomass compared to plants without natural enemies.

Aphid mummy predation and population dynamics

Predation by *H. convergens* on aphid mummies was intense at the end of the experiment as beetles suppressed aphid densities to very low levels. Beetles caused 98–100% mortality in the prepupal and pupal stage of *L. testaceipes*, which are found in mummified aphids. Thus, IGP by *H. convergens* can be a major factor limiting *L. testaceipes* population growth in the cotton agroecosystem. These estimates of *L. testaceipes* mortality caused by *H. convergens* are conservative for two reasons. First, some aphid mummies fall off leaves when coccinellid beetles feed on them. Our predation estimates include only mummies that remained on leaves after being attacked. Second, our analyses do not include *L. testaceipes* larvae that were killed when *H. convergens* fed on parasitized aphids that were not yet mummified. High levels of aphid mummy predation have been observed in unmanipulated early-season cotton fields throughout California's Central Valley (Rosenheim et al. 1997) as well as later in the cotton-growing season in the Sacramento Valley (Fig. 12); thus, the results observed in our manipulative experiment may be quite general for the cotton agroecosystem. IGP can occur on either parasitized hosts, in which both the host and the parasitoid are living, or on mummified hosts, in which the host has already been killed by the parasitoid. In either case, the result is that the immature parasitoid is killed. This type of IGP, where predators prey on parasitized hosts and mummified hosts, is common (Rosenheim et al. 1995; Sunderland et al. 1997; Rosenheim 1998). A diverse group of predators, including syrphid larvae, chrysopid larvae, coccinellid beetles, ants, reduviids and others, are known to consume parasitized and mummified aphids (Wheeler et al. 1968; Frazer and van den Bosch 1973; Frazer and Gilbert 1976; Wheeler 1977; Nowierski 1979; Brodeur and McNeil 1992; Ferguson and Stiling 1996; Rosenheim et al. 1997). The proportion of aphid mummies attacked by predators can be very high in other agroecosystems as well; Nowierski (1979), for example, observed that predation on mummies of the walnut aphid, *Chromaphis juglandicola*, harboring *Trioxys pallidus* increased continuously across the growing season and peaked at 81%.

Intraguild predators can negatively affect intraguild prey in two ways: by directly consuming them and by competing with them for a shared resource. In this system, coccinellid beetles have the potential to affect parasitic wasps negatively in both of these ways, because they readily feed on both unparasitized and parasitized aphids. We found that beetles greatly reduced aphid mummy abundance. Although the presence of beetles

strongly suppressed aphid populations, competition for aphids did not appear to be an important means by which beetles negatively influenced mummy abundance; direct predation on mummies appeared to be the more important mechanism. As a caveat, it is possible that our analysis was simply unable to detect competition between beetles and parasitoids. In systems with IGP, it is frequently difficult to tease apart statistically the effects of competition and predation, because the intensity of both of these forces may be mediated by the availability of the shared resource (Schoener 1983; Polis et al. 1989).

IGP and aphid population dynamics

The presence of beetles enhanced aphid population suppression compared to the treatment with only parasitoids. The strong decrease in absolute mummy density caused by beetles (Fig. 4) was not associated with an equally strong decrease in the percentage of aphids that were mummified (Fig. 5). Beetles may not have affected the per capita aphid mortality caused by parasitism. Coccinellid beetles and parasitoids together drove aphid populations to near local extinction. The effective control of the cotton aphid in early season cotton by a community of natural enemies dominated by coccinellid beetles and the parasitoid *L. testaceipes* is commonly observed in California's cotton ecosystems, despite the fact that beetles consume a high proportion of immature parasitoids (Rosenheim et al. 1997).

In other agroecosystems, IGP has been found to have variable effects on biological control. Heinz and Nelson (1996) studied a system of IGP with dynamics broadly similar to those we have observed in cotton. They studied a greenhouse system that includes the whitefly *Bemisia argentifolia*, two parasitoids, *Encarsia formosa* and *Encarsia pergandiella*, and the coccinellid beetle *Delphastus pusillus*. The addition of *D. pusillus* consistently improved whitefly control, even though *D. pusillus* did not discriminate between unparasitized whiteflies and those harboring parasitoid eggs or young larvae (Hoelmer et al. 1993; Heinz et al. 1994). However, there are two examples where the addition of an intraguild predator to a host – parasitoid system did disrupt biological control. First, Press et al. (1974) observed that the predator *Xylocoris flavipes* consumed both the moth *Plodia interpunctella* and the immature stages of the ectoparasitoid *Bracon hebetor*. When the predator *X. flavipes* was added to this host – parasitoid system, biological control was disrupted and moth densities nearly doubled. A less extreme example involves the study of the aphid *Dactynotus* sp., the parasitoid *Aphidius floridaensis*, and the coccinellid beetle *Cycloneda sanguinea* in a field cage experiment (Ferguson and Stiling 1996). In this case, the parasitoid was a superior biological control agent and aphid densities slightly increased when the beetle *C. sanguinea* was added to the aphid-parasitoid complex. However, the positive indirect effect that beetles had on aphids was only significant during part of the

experiment. It appears that the addition of predators to host-parasitoid systems will either enhance or disrupt biological control. Predator preference for unparasitized versus parasitized hosts may be one of the important factors shaping the net effect of predation in these systems.

H. convergens prey preference

The predatory coccinellid *H. convergens* preferred unparasitized aphids over aphid mummies when given the opportunity to feed on equal numbers of both prey types. The preference was, however, not particularly strong. Preference for aphid mummies versus unparasitized hosts can be quite variable for other predator species; predators may attack only unparasitized hosts, only parasitized hosts, or may show a partial preference (reviewed in Fritz 1982; Rosenheim et al. 1995; Sunderland et al. 1997). Generally, predators consume both unparasitized and newly parasitized hosts without preference, but discriminate increasingly against parasitized prey as the parasite develops (Quezada and DeBach 1973; Kindlmann and Ruzicka 1992; Hoelmer et al. 1993; Heinz et al. 1994). In the cotton aphid system, we expect that the partial preference for unparasitized hosts weakens the suppression of immature parasitoid populations and strengthens the suppression of aphid populations. Under conditions where a predator shows both a partial preference for unparasitized hosts and high levels of predation on unparasitized hosts, we may expect to observe improved suppression of herbivores even with high levels of IGP.

Influence of hyperparasitism on *L. testaceipes* emergence

L. testaceipes populations also experienced substantial immature mortality from hyperparasitism. Rates of hyperparasitism by *Pachyneuron siphonophorae* and *Alloxyta bakeri* averaged 31.5% and reached as high as 65.2%. The mortality caused by the combination of predation and hyperparasitism on immature *L. testaceipes* populations may help to explain why this parasitoid is often absent from the cotton agroecosystem during the middle and late seasons (mid-June through October), even when cotton aphid populations are at outbreak levels (J.A. Rosenheim and R.G. Colfer, unpublished work). A polyphenism in aphid populations, in which aphids shift from an early-season form that is large and dark, and which is highly susceptible to parasitism, to a later-season small and yellow form, which appears to be less susceptible to parasitism, may also help to explain this pattern (J.A. Rosenheim, unpublished work). We do not know if hyperparasitism reduced the impact of *L. testaceipes* on aphid populations, because our treatment manipulations did not affect hyperparasitoids. There is, however, both theoretical and empirical evidence that hyperparasitism can disrupt biological control (Burton

and Starks 1977; Shi 1986; Goergen and Neuenschwander 1992; Briggs 1993; Sunderland et al. 1997; Rosenheim 1998). A final point about hyperparasitoids is that they, like *L. testaceipes*, probably experienced high levels of immature mortality due to coccinellid attacks on aphid mummies. Thus, coccinellid beetles in this system probably commonly consume prey from three different trophic levels: the cotton aphid, the primary parasitoid *L. testaceipes*, and the hyperparasitoids *P. siphonophorae* and *A. bakeri*.

Ant tending and mummy predation

We did not experimentally evaluate how ant tending of aphids might influence the interactions between coccinellid beetles, primary parasitoids, hyperparasitoids, and aphids. Because cotton is an annual row crop with cultural practices that cause frequent disturbance, it is likely that ant tending has less of an impact compared to more permanent systems (Völkl 1992, 1997). Also, we observed a strong decline in aphid populations and an increase in the percentage of mummies consumed at an unmanipulated site (Fig. 12) at which many aphid colonies were being tended by ants. How ants mediate interactions between coccinellid beetles and aphid parasitoids requires further research.

Density-dependent predation by aphid natural enemies

For natural enemies to regulate herbivore populations, the mortality that they exert must increase with increasing herbivore densities ("density-dependent" mortality). In this study, we present evidence that predators and parasitoids reduced aphid population growth more in aphid populations with high initial densities than in those with low initial densities. It is important to distinguish between a predator that behaves in a density-dependent manner and a predator that causes density-dependent mortality to its prey. While it is necessary for predators to behave in a density-dependent manner to cause density-dependent mortality to their prey, it is not sufficient. Thus, not all predators that increase their rates of predation with increasing prey densities will cause top-down density-dependent regulation of their prey populations.

In this study, we present evidence that predators and parasitoids behave in a density-dependent manner and that these predators and parasitoids are capable of causing density-dependent mortality to cotton aphid populations. Suppression of aphid population growth was particularly pronounced in treatments that contained both *H. convergens* and *L. testaceipes* wasps, where aphid populations decreased at rates that were more than 25 times greater in populations with high initial densities compared to low initial aphid densities (Fig. 6C). These results show that *H. convergens* and *L. testaceipes* wasps behaved in a density-dependent manner. This pattern is

in contrast to that seen in the aphid populations free of natural enemies (Fig. 6A), where aphid population growth rates were greatest at intermediate initial densities, as predicted for population growth by the logistic growth model.

Treatments with *L. testaceipes* wasps alone and in combination with *H. convergens* reduced per capita aphid population growth more strongly with increases in initial abundance (Fig. 7B,C). Also, percentage of aphids mummified was positively correlated with increases in initial aphid abundance and negatively correlated with proportional aphid population growth rates (Fig. 8). These results demonstrate that *L. testaceipes* wasps and *H. convergens* produced density-dependent mortality in aphid populations. Thus, these predators may be important top-down regulating factors for cotton aphid populations. In the aphids-only treatment, our results suggest that aphid population growth was being limited by plant resource availability (i.e., bottom-up effects; Fig. 7A, Fig. 8C).

Density-manipulation experiments have shown that not all natural enemies of herbivores show direct density dependence (Harrison and Cappuccino 1995). Direct density dependence, inverse density dependence, and density independence have all been observed for natural enemies of herbivores (Cronin and Strong 1985; Cappuccino 1987; Gould et al. 1990). In our experiment, it is unclear whether density-dependent predation was observed because predators reproduced in response to abundant prey (numerical response), increased their foraging efficiency (functional response), or immigrated to areas of high prey density (spatial response). If spatial responses were responsible for the pattern we observed, it is unclear whether this would lead to temporal aphid population regulation (Harrison and Cappuccino 1995). However, spatial responses by natural enemies may be an important means by which they control herbivorous pests (Murdoch et al. 1985).

Terrestrial trophic cascade

Despite the occurrence of IGP by coccinellid beetles, trophic links between natural enemies and aphids and between aphids and the cotton plants were sufficiently strong to produce cascades from natural enemies to cotton plant biomass. Above-ground dried plant biomass and total leaf area were nearly doubled in communities with natural enemies compared to communities free of natural enemies. This study adds to a growing body of experimental literature reporting that terrestrial predators lead to improved plant performance and changes in the plant community (e.g., Gomez and Zamora 1994; Schmitz 1994, 1998; Carter and Rypstra 1995; Chase 1996, 1998; Moran et al. 1996; Agrawal and Karban 1997; Letourneau and Dyer 1998). Although some forms of early-season herbivory can lead to reductions in cotton plant yields (Wilson et al. 1987; Wilson 1993), cotton plants appear to compensate fully for early-season

cotton aphid herbivory (Rosenheim et al. 1997). However, the damage observed in the treatment without natural enemies could reduce yields if aphid populations persist into the period when cotton plants begin producing fruiting structures (Godfrey and Wood 1998).

In summary, we found that coccinellid beetle predation can be an important source of mortality for immature stages of the aphid parasitoid *L. testaceipes*. However, overall suppression of the cotton aphid was improved when coccinellid beetles were added to the aphid-parasitoid system. Furthermore, these natural enemies of aphids appear to act in a directly density-dependent manner, having the greatest impact on high-density aphid populations. Thus, the presence in arthropod communities of natural enemies that engage in IGP does not necessarily lead to the disruption of biological control.

Acknowledgements We would like to thank Jacques Brodeur, Brian Inouye, Erik Nelson, and Jennifer Thaler for constructive comments and discussion on the manuscript. Thanks also to Nicholas Ruiz for field assistance. We have greatly appreciated the logistic support from Mark Van Horn and the staff at the UC Student Experimental Farm. This work was funded by grants from the California State Support Board of Cotton Incorporated, UC Davis President's Undergraduate Fellowship (PUF) Program, the US EPA (STAR Fellowship Program), and the USDA NRICGP (grants 94-37302-0504 and 96-35302-3816).

References

- Agrawal AA, Karban R (1997) Domatia mediate plant-arthropod mutualism. *Nature* 387:562-563
- Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago
- Briggs CJ (1993) Competition among parasitoid species on a stage-structured host and its effect on host suppression. *Am Nat* 141:372-397
- Brodeur J (1994) Susceptibility of parasitized insect hosts to predators. *Norw J Agric Sci* 16:147-153
- Brodeur J, McNeil JN (1992) Host behaviour modification by the endoparasitoid *Aphidius nigripes*: a strategy to reduce hyperparasitism. *Ecol Entomol* 17:97-104
- Burton RL, Starks KJ (1977) Control of a primary parasite of the greenbug with a secondary parasite in greenhouse screening for plant resistance. *J Econ Entomol* 70:219-220
- Cappuccino N (1987) Comparative population dynamics of two goldenrod aphids: spatial patterns and temporal constancy. *Ecology* 68:1634-1646
- Cappuccino N, Price PW (eds) (1995). Population dynamics: new approaches and synthesis. Academic Press, San Diego
- Carter PE, Rypstra AL (1995) Top-down effects in soybean agroecosystems: spider density affects herbivore damage. *Oikos* 72:433-439
- Chase JM (1996) Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos* 77:495-506
- Chase JM (1998) Central-place forager effects on food web dynamics and spatial pattern in northern California meadows. *Ecology* 79:1236-1245
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297-1304
- Croft BA, MacRae IV (1992) Persistence of *Typhlodromus pyri* and *Metaseiulus occidentalis* (Acari: Phytoseiidae) on apple after inoculative release and competition with *Zetzellia mali* (Acari: Stigmaeidae). *Environ Entomol* 21:1168-1177
- Croft BA, Slone DH (1997). Equilibrium densities of European red mite (Acari: Tetranychidae) after exposure to three levels of predaceous mite diversity on apple. *Environ Entomol* 26:391-399
- Cronin JT, Strong DR (1990) Density-independent parasitism among host patches by *Anagrus delicatus* (Hymenoptera: Mymaridae): experimental manipulation of hosts. *J Anim Ecol* 59:1019-1026
- Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annu Rev Entomol* 40:297-331
- Diehl S (1993) Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* 68:151-157
- Ferguson KI, Stiling P (1996) Non-additive effects of multiple natural enemies on aphid populations. *Oecologia* 108:375-379
- Frazer BD, Bosch R van den (1973) Biological control of the walnut aphid in California: the interrelationship of the aphid and its parasite. *Environ Entomol* 2:561-568
- Frazer BD, Gilbert N (1976) Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) prey on field populations of pea aphids (Homoptera: Aphididae). *J Entomol Soc Br C* 73:33-56
- Fritz RS (1982) Selection for host modification by insect parasitoids. *Evolution* 36:283-88
- Godfrey LD, Wood JP (1998) Mid-season cotton aphid infestations in California: effects on cotton yield. In: Proceedings of the Beltwide Cotton Conference 1998. National Cotton Council of America, Washington, pp 1056-1058
- Goergen G, Neuenschwander P (1992) A cage experiment with four trophic levels: cassava plant growth as influenced by cassava mealy bug, *Phenacoccus manihoti*, its parasitoid *Epidinocarsis lopezi*, and the hyperparasitoids *Prochiloneurus insolitus* and *Chartocerus hyalipennis*. *Z Pflanzenkrankh Pflanzenschutz* 99:182-190
- Gomez JM, Zamora R (1994) Top-down effects in a tritrophic system: parasitoids enhance plant fitness. *Ecology* 75:1023-1030
- Gould JR, Elkinton JS, Wallner WE (1990) Density-dependent suppression of experimentally created gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae) populations by natural enemies. *J Anim Ecol* 59:213-233
- Hairston NG, Hairston NG (1993) Cause-effect relationships in energy flow, trophic structure and interspecific interactions. *Am Nat* 142:379-411
- Hairston NG, Hairston NG (1997) Does food web complexity eliminate trophic-level dynamics? *Am Nat* 149:1001-1007
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421-425
- Harrison S, Cappuccino N (1995) Using density-manipulation experiments to study population regulation. In: Cappuccino N, Price PW (eds) Population dynamics: new approaches and synthesis. Academic Press, San Diego, pp 131-147
- Head RB (1992) Cotton insect losses 1991. In: Proceedings of the Beltwide Cotton Conference 1992. National Cotton Council of America, Washington, pp 621-625
- Heinz KM, Nelson JM (1996) Interspecific interactions among natural enemies of *Bemisia* in an inundative biological control program. *Biol Control* 6:384-393
- Heinz KM, Brazzle JR, Pickett CH, Natwick ET, Nelson JM, Parrella MP (1994) *Delphastus pusillus* as a potential biological control agent for sweetpotato (silverleaf) whitefly. *Calif Agric* 48:35-40
- Hoelmer KA, Osborne LS, Yokomi RK (1993) Interactions of the whitefly predator *Delphastus pusillus* (Coleoptera: Coccinellidae) and parasitized sweetpotato whitefly (Homoptera: Aleyrodidae). *Environ Entomol* 23:136-139
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745-764
- Hunter MD, Price PW (1992) Playing chutes and ladders: bottom-up and top-down forces in natural communities. *Ecology* 73:724-732
- Hurd LE, Eisenberg RM (1990) Arthropod community response to manipulation of a bitrophic predator guild. *Ecology* 53:955-967

- Karban R (1989) Community organization of *Erigeron glaucus* folivores: effects of competition, predation, and host plant. *Ecology* 70:1028–1039
- Kindlmann P, Ruzicka Z (1992) Possible consequences of a specific interaction between predators and parasites of aphids. *Ecol Model* 61:253–265
- Kot J (1971) Factors affecting the efficiency of *Trichogramma* introduction. *Proc Int Congr Entomol* 13(2):155–158
- Leclant F, Deguine JP (1994) Aphids (Hemiptera: Aphididae). In: Mathews GA, Tunstall JP (eds) *Insect pests of cotton*. CAB International, Wallingford, pp 285–323
- Letourneau DK, Dyer LA (1998) Experimental test in lowland tropical forest shows top-down effects through four trophic levels. *Ecology* 79:1678–1687
- Moran MD, Rooney TP, Hurd LE (1996) Top-down cascade from a bitrophic predator in a old-field community. *Ecology* 77:2219–2227
- Murdoch WW (1970) Population regulation and population inertia. *Ecology* 51:497–502
- Murdoch WW, Chesson J, Chesson PL (1985) Biological control in theory and practice. *Am Nat* 125:344–366
- Neter J, Wasserman W, Kutner MH (1990) *Applied linear statistical models*. Irwin, Homewood
- Nowierski RM (1979) The field ecology of the walnut aphid, *Chromaphis juglandicola* (Homoptera: Aphididae) and its introduced parasite, *Trioxys pallidus* (Hymenoptera: Aphididae). A qualitative and quantitative assessment of population regulation. PhD dissertation, University of California, Berkeley
- Polis GA (1991) Complex trophic interactions in deserts: an empirical critique of food web theory. *Am Nat* 138:123–155
- Polis GA (1994) Food webs, trophic cascades and community structure. *Aust J Ecol* 19:121–136
- Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol Evol* 7:151–154
- Polis GA, Strong DR (1996) Food web complexity and community dynamics. *Am Nat* 147:813–846
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- Press JW, Flaherty BR, Arbogast RT (1974) Interactions among *Plodia interpunctella*, *Bracon hebetor*, and *Xylocoris flavipes*. *Environ Entomol* 3:183–184
- Quezada JR, DeBach P (1973) Bioecological and population studies of the cottony-cushion scale, *Icerya purchasi* Mask., and its natural enemies, *Rodolia cardinalis* Mul. and *Cryptochaetum iceryae* Will., in southern California. *Hilgardia* 41: 631–688
- Rees NE, Onsager JA (1982) Influence of predators on the efficiency of the *Blaesoxipha* spp parasites of the migratory grasshopper. *Environ Entomol* 11:426–428
- Riechert SE, Bishop L (1990) Prey control by an assemblage of generalist predators: spiders in the garden test system. *Ecology* 71:1441–1450
- Riechert SE, Lawrence K (1997). Test for predation effects of single versus multiple species of generalist predators: spiders and their insect prey. *Entomol Exp Appl* 84:147–155
- Riechert SE, Provencher K, Lawrence K (1999). The potential of spiders to exhibit stable equilibrium point control of prey: tests of two criteria. *Ecol Appl* 9:365–377
- Rosenheim JA (1998) Higher-order predators and the regulation of insect herbivore populations. *Annu Rev Entomol* 43:421–447
- Rosenheim JA (in press) Source-sink dynamics for a generalist insect predator in habitats with strong higher-order predation. *Ecol Monogr*
- Rosenheim JA, Wilhoit LR, Armer CA (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96:439–449
- Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological-control agents: theory and evidence. *Biol Control* 5:303–335
- Rosenheim JA, Wilhoit LR, Goodell PB, Grafton-Cardwell EE, Leigh TF (1997) Plant compensation, natural biological control, and herbivory by *Aphis gossypii* on pre-reproductive cotton: the anatomy of a non-pest. *Entomol Exp Appl* 85:45–63
- Rosenheim JA, Limburg DD, Colfer RG (1999) Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. *Ecol Appl* 9:409–417
- Schmitz OJ (1994) Resource edibility and trophic exploitation in an old-field food web. *Proc Natl Acad Sci USA* 91:5364–5367
- Schmitz OJ (1998) Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am Nat* 151: 327–342
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Shi DS (1986) Studies on the parasitoids of cotton aphid. III. Bionomics of *Aphidencyrus aphidivorus* (Mayr), a hyperparasite of cotton aphid. *Contrib Shanghai Inst Entomol* 6:35–41
- Spiller DA, Schoener TW (1990) A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. *Nature* 347:469–472
- Spiller DA, Schoener TW (1994) Effects of top and intermediate predators in a terrestrial food web. *Ecology* 75:182–196
- Spiller DA, Schoener TW (1996) Food web dynamics on some small subtropical islands: effects of top and intermediate predators. In: Polis GA, Winemiller C (eds) *Food webs, integration of patterns and dynamics*. Chapman and Hall, New York, pp 160–169
- Sunderland KD, Axelsen JA, Dromph K, Freier B, Hemptinne JL, Holst NH, Mols PJM, Petersen MK, Powell W, Ruggie P, Triltsch H, Winder L (1997) Pest control by a community of natural enemies. In: Powell W (eds) *Arthropod natural enemies in arable land. III. The individual, the population, and the community*. Acta Jutland 72:271–326
- Völkl W (1992) Aphids or their parasitoids: who actually benefits from ant-attendance? *J Anim Ecol* 61:273–281
- Völkl W (1997) Interactions between ants and aphid parasitoids: Patterns and consequences for resource utilization. In: Dettner K, Bauer G, W. Völkl (eds) *Vertical food web interactions*. Springer, Berlin, Heidelberg New York, pp 225–240
- Wheeler AG (1977) Studies on the arthropod fauna of alfalfa. VII. Predaceous insects. *Can Entomol* 109:423–427
- Wheeler AG, Hayes JT, Stephens JL (1968) Insect predators of mummified pea aphids. *Can Entomol* 100:221–222
- Wilson LJ (1993) Spider mites (Acari: Tetranychidae) affect yield and fiber quality of cotton. *J Econ Entomol* 86:566–585
- Wilson LT, Pickett CH, Leigh TF, Carey JR (1987) Spider mite (Acari: Tetranychidae) infestation foci: cotton yield reduction. *Environ Entomol* 16:614–617
- Wise DH (1993) *Spiders in ecological webs*. Cambridge University Press, Cambridge