Oecologia (1993) 96:439–449

Oecologia

Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population

Jay A. Rosenheim, Lawrence R. Wilhoit, Christine A. Armer

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

Received: 30 April 1993 / Accepted: 14 September 1993

Abstract. We evaluated the influence of intraguild predation among generalist insect predators on the suppression of an herbivore, the aphid *Aphis gossypii*, to test the appropriateness of the simple three trophic level model proposed by Hairston, Smith, and Slobodkin (1960). We manipulated components of the predator community, including three hemipteran predators and larvae of the predatory green lacewing *Chrysoperla carnea*, in field enclosure/exclosure experiments to address four questions: (1) Do generalist hemipteran predators feed on *C. carnea*? (2) Does intraguild predation (IGP) represent a substantial source of mortality for *C. carnea*? (3) Do predator species act in an independent, additive manner, or do significant interactions occur? (4) Can the experimental addition of some predators result in increased densities of aphids through a trophic cascade effect? Direct observations of predation in the field demonstrated that several generalist predators consume *C. carnea* and other carnivorous arthropods. Severely reduced survivorship of lacewing larvae in the presence of other predators showed that IGP was a major source of mortality. Decreased survival of lacewing larvae was primarily a result of predation rather than competition. IGP created significant interactions between the influences of lacewings and either *Zelus renardii* or *Nabis* predators on aphid population suppression. Despite the fact that the trophic web was too complex to delineate distinct trophic levels within the predatory arthropod community, some trophic links were sufficiently strong to produce cascades from higher-order carnivores to the level of herbivore population dynamics: experimental addition of either *Z. renardii* or *Nabis* predators generated sufficient lacewing larval mortality in one experiment to release aphid populations from regulation by lacewing predators. We conclude that intraguild predation in this system is widespread and has potentially important influences on the population dynamics of a key herbivore.

Key words: Intraguild predation – Trophic cascade – Biological control – Aphid

Ecologists continue to debate the manner in which predation influences community structure. Hairston et al. (1960) proposed for terrestrial communities comprising three trophic levels that predators regulate populations of herbivores below their carrying capacity, thereby allowing plant populations to expand until they experience strong competition. This is an example of a three-tiered trophic cascade, in which strong effects of predation propagate downwards through the food chain. The Hairston-Smith-Slobodkin model may be extended to four trophic levels by including a second level of predators (Fretwell 1977, 1987); in this case, secondary predators suppress populations of primary predators, allowing herbivore populations to expand and regulate plant populations. Experimental manipulations of primary or secondary carnivores have demonstrated trophic cascades through three or four trophic levels in many ecosystems (Carpenter et al. 1985; Carpenter and Kitchell 1988; Power 1990, 1992a; Brönmark et al. 1992; Spiller and Schoener in press).

The Hairston-Smith-Slobodkin model envisions predation operating across distinct trophic levels. However, many predators are "omnivorous", consuming whatever prey of an appropriate size they are able to subdue, without regard to whether the prey species is a carnivore or herbivore (Warren and Lawton 1987; Polis and McCormick 1987; Polis 1991; Wissinger 1992). (Note: we use omnivory to refer to species that feed on organisms occupying more than one trophic level in a food web.) Omnivory is compounded by predator ontogeny; as predators grow, the size range of utilized prey may change, and may include smaller individuals of other predatory species. Furthermore, some animals, including many holometabolous insects, shift between herbivorous, parasitic, and predatory feeding habits with developmental stage. The prevalence of omnivory introduces a new type of interaction to many food webs: intraguild predation ("IGP"), in which species that compete for the same resources also engage in predator-prey interactions (Polis and McCormick 1987; Polis et al. 1989; Polis and Holt 1992; Wise 1993). Studies that attempt to represent accurately the species diversity and

---

Correspondence to: J.A. Rosenheim

plethora of trophic links that exist in real communities produce trophic webs in which trophic levels are not readily defined (Polis 1991; Strong 1992). The prevalence of omnivory led Menge and Sutherland (1976, 1987) to propose an alternate model of community regulation, in which the importance of predation increases monotonically as one moves down through the trophic web, rather than being expressed only on alternate trophic levels as predicted by the Hairston-Smith-Slobodkin model. Empirical support for the Menge-Sutherland model is also widespread (Sih et al. 1985; Spiller and Schoener 1988; Diehl 1992), and indeed many studies perturbing carnivore populations reveal both cascading and non-cascading interactions within a single community, suggesting that both strong trophic links and more diffuse interactions may exist within a single interaction web (Pacala and Roughgarden 1984; Spiller 1986; Spiller and Schoener 1990; Hurd and Eisenberg 1984, 1990; Fagan and Hurd 1991; Power 1992b).

Many field studies that have demonstrated trophic cascades have involved organisms of very different sizes (e.g., large fish, small fish, insect predators, insect herbivores), in which the distinctness of trophic levels is maintained in large part by the diet of predators being restricted to prey in a certain size range. For interactions between insectivorous arthropods, however, the range of size variation in potential prey items is often greatly reduced. Thus, we might predict that trophic levels within arthropod communities will be indistinct, and that most predators will make at least some contribution to herbivore population suppression. On the other hand, arthropod communities in agroecosystems are simplified compared to natural ecosystems, thereby decreasing opportunities for diffuse predation and increasing the likelihood that a few strong trophic links will dominate the dynamics of herbivore populations. These strong trophic links may be created by predators preferring to consume certain prey species or by prey exhibiting defensive behavior that confers predator-specific vulnerabilities (McPeek 1990; Power et al. 1992). Thus, an alternate hypothesis is that predators occupying higher positions in the trophic web (either IGP predators or obligate secondary predators) may disrupt the control of herbivore populations.

Few experimental field studies of IGP and trophic cascades in arthropod communities have been conducted within agroecosystems. Studies by Croft and MacRae (1992a, b) with potted apple trees have, however, suggested that IGP can have significant influences on herbivorous arthropod population dynamics. Furthermore, the high level of disturbance that characterizes annual cropping systems may favor populations of generalist predators (Ehler 1977; Ehler and Miller 1978; Bisabri-Ershadi and Ehler 1981), which may be particularly likely to engage in extensive IGP.

In this paper, we address four aspects of IGP through experimental studies of the aphid *Aphis gossypii* Glover and its associated generalist predators, including three hemipteran predators and larvae of the predatory green lacewing *Chrysoperla carnea* (Stephens). First, do generalist hemipteran predators feed on *C. carnea*? Second, if lacewing larvae are subject to IGP, does IGP represent a substantial source of mortality? If IGP generates heavy mortality on lacewing prey, several influences on aphid population densities are possible. Thus, our third question: Do predator species act upon aphid populations in an independent, additive manner, or do significant interactions occur? And fourth: Can the experimental addition of predators result in increased densities of aphids through a trophic cascade effect?

Natural history of Aphis gossypii *and associated predators*

The aphid, *Aphis gossypii* (Homoptera: Aphididae), is one of the dominant herbivores of commercially grown upland cotton, *Gossypium hirsutum* L., in the San Joaquin Valley of California, USA (Head 1992). During the middle and later parts of the season, from June through October, aphid populations, which often become highly polymorphic (Wilhoit and Rosenheim 1993; see discussion), may undergo periods of rapid expansion despite the development of large populations of generalist predators, including predatory green lacewings. The predominant lacewing species is *C. carnea*, which co-occurs with lower densities of *Chrysopa nigricornis* Burmeister and other rarer species (Neuroptera: Chrysopidae) (van den Bosch and Hagen 1966). The larvae of these lacewings are known to be potentially important predators of aphids (Canard et al. 1984). As noted by Wilson and Gutierrez (1980) in California and Whitcomb and Bell (1964) in Arkansas, lacewing populations are often comprised of abundant eggs and rare larvae; these authors speculated that larval forms may be subject to heavy mortality, perhaps from intraguild predation. Despite the fact that lacewings are reared worldwide by commercial insectaries and are employed extensively in augmentative biological control efforts against aphids, we know of no studies quantifying the impact of generalist predators on lacewing larval survivorship (see review of lacewing natural enemies by Alrouechdi et al. 1984).

In addition to the lacewing species, the dominant generalist predators in cotton comprise species in four genera of predatory true bugs (Hemiptera): *Geocoris* spp. (*G. pallens* Stål, *G. punctipes* [Say], and *G. atricolor* Montandon; family Lygaeidae), *Nabis* spp. (*N. alternatus* Parshley and *N. americoferus* Carayon; family Nabidae), *Zelus* spp. (*Z. renardii* Kolenati and *Z. tetracanthus* Stål; family Reduviidae), and *Orius tristicolor* (White); family Anthocoridae. All of these predators, as well as lacewing larvae, have sucking mouthparts with which they consume the hemolymph and internal tissues of their prey, leaving the chitinous exoskeleton intact. The current consensus regarding the diet of these predators in cotton in the western United States is described in a University of California publication (1984): (i) *Geocoris* are described as feeding on lepidopteran caterpillars (several species in a variety of genera), *Lygus* bugs, whitefly (mostly *Trialeurodes vaporariorum* [Westwood] and *Bemisia tabaci* [Gennadius]), leafhoppers (mostly *Empoasca* spp.), spider mites (*Tetranychus* spp.), and aphids; (ii)

Nabis are described as feeding on aphids, leafhoppers, *Lygus* bugs, and lepidopteran caterpillars; (iii) *Zelus* are described as attacking "nearly any insect prey;" (iv) *Orius tristicolor* is described as attacking thrips (mostly *Frankliniella occidentalis* [Pergande]), spider mites, whitefly, aphids, *Lygus* nymphs, insect eggs, lepidopteran caterpillars, and other small arthropods. *Geocoris, Nabis,* and *O. tristicolor* also supplement their arthropod diet with direct feeding on plant material (Ehler 1977; Salas-Aguilar and Ehler 1977 and references therein). These descriptions not only summarize the recognized diet of these generalist predators, but also provide a description of the other arthropods commonly found in cotton, and which were present in our experimental plantings; most of these arthropod prey species are strict herbivores, although *Lygus* may feed opportunistically on moth eggs (Ehler 1977) and *F. occidentalis* can be an important predator of spider mite eggs (Trichilo and Leigh 1986).

Methods

Size of adult predators

We determined the relative size of the dominant generalist predators by collecting adults in the field, drying them to a constant weight at 60° C, and weighing them on a microbalance to the nearest 10 µg.

Population densities of lacewing eggs and larvae

We sampled five fields on 2 September 1992 to quantify the relative densities of lacewing egg and larval populations. The fields were located at the Kearney Agricultural Center (one field) and the University of California West Side Research and Extension Center (two fields), both in Fresno County, California, and the University of California Cotton Research Center, Shafter, Kern County, California (two fields). A transect of each field was made and five plants randomly selected for visual inspection of all foliage, stems, and fruiting structures. A sixth field at the Cotton Research Center was sampled on 26 August 1992 as above, except that twelve groups of four adjacent plants each were inspected.

Experiment 1

We conducted three enclosure/exclosure experiments in the field to investigate trophic relationships among generalist predators associated with *A. gossypii* on cotton. The first experiment was designed primarily to quantify predation on lacewing larvae by other generalist predators. The experiment was conducted 9–13 July, 1992 in a 0.4 ha experimental planting of *Gossypium hirsutum* cv. "GC-510" at the Kearney Agricultural Center. Plants were grown on rows separated by 76 cm following standard commercial practices. Plants were medium sized (approximately 12 mainstem nodes) and not yet setting fruit.

The experimental unit was the top 5–7 nodes of single plants bearing aphid populations. One plant on each side of the experimental plant was removed to limit predator movement onto the experimental plant during the set up of the experiment. Each leaf was inspected in the field to (i) count all nymphal and adult aphids, (ii) visually estimate the proportion of the lower leaf surface covered by active colonies of spider mites, an important alternate prey for several of the predators, (iii) record the presence or absence of other herbivorous arthropods, and (iv) remove the eggs, nymphs, and adults of all generalist insect predators; spiders; and parasitoid adults and immatures present in "mummified" aphids. Removal of predators was effective except for the egg stages of *Nabis* and *O. tristicolor*, which are imbedded in plant tissue and therefore not readily detectable in the field. The inspected portion of the plant was then enclosed in a tapered polyester mesh plant sleeve (height 58 cm, width at base 50 cm and at top 19 cm; "Fibe-Air Sleeve", Kleen Test Products), which had an irregular weave with pores fine enough to cage insects (largest pores ca. 0.3 mm) but coarse enough to permit substantial air flow. Bags were taped and clipped shut at the base around the plant's stem.

Plants were alternately assigned to one of three treatments, each replicated fifteen times: (1) aphids only; (2) aphids plus 8–11 *C. carnea* lacewing larvae; and (3) aphids plus 8–11 lacewing larvae plus two adult *Geocoris*, one adult *Nabis*, and two adult *Z. renardii*. (The rationale for selecting these predator densities is discussed below.) Lacewing larvae were obtained from a laboratory culture, fed on eggs of the moth *Anagasta kuehniella* (Zeller), and released as first instars or young second instars. Other predators were hand collected or netted the day of the experimental set-up in the same cotton field; no attempt was made to sex the predators. Sleeves were sealed at the top with tape after predators were added.

Plant stems were cut and the sleeve enclosures brought to the laboratory 3–4 days after set-up. Bags were opened, and aphids, mites, and other herbivores were sampled as before. In addition, all predators found in the bag were scored as dead or alive, counted, and identified to species.

Experiment 2

The second experiment, conducted 21–30 August 1992 in the same plot, was designed to isolate the influences of predation by each of the three hemipterans, *Geocoris*, *Nabis*, and *Z. renardii*, with and without the simultaneous presence of *C. carnea* lacewing larvae. The cotton plants had matured to the stage of fruit set (small bolls). Experimental protocols were identical to those described for experiment 1 with the following modifications. Because aphid populations had declined, a larger and more variable number of nodes (from the top 6 nodes to the entire plant) were enclosed to obtain a suitable initial aphid population per cage (mean of 138.7 ± 35.1 [SD]); cages were sealed with tape, clips, and staples. The number of treatments was expanded to eight, each with ten replicates: (1) aphids only; (2) aphids plus two *Geocoris* adults; (3) aphids plus two *Nabis* adults; (4) aphids plus two *Z. renardii* adults; (5) aphids plus five lacewing larvae; (6) aphids plus five lacewing larvae plus two *Geocoris* adults; (7) aphids plus five lacewing larvae plus two *Nabis* adults; (8) aphids plus five lacewing larvae plus two *Z. renardii* adults. This design allowed us to test for interactions between the influences of lacewings and each of the other predators by analyzing groups of treatments as 2 × 2 factorials (e.g., treatments 1, 4, 5, and 8 comprise a factorial test of lacewings and *Z. renardii*). Lacewings were obtained from a commercial insectary, fed on *A. kuehniella* larvae, and released as young second instars. The duration of the experiment was extended to 7–8 days. Eleven of the 80 replicates were lost due to predation by ants, *Solenopsis xyloni* McCook, which chewed holes in the cages, tended the aphids, and may have attacked other predators.

Experiment 3

The third experiment returned our focus to the impact of a combined predator guild on lacewing survivorship and aphid population dynamics. We evaluated predation by nymphal, rather than adult, generalist predators, and we used lacewing eggs collected in the field rather than lacewing larvae reared in the laboratory. The experiment was conducted 26 August to 30 September, 1992 at the University of California Cotton Research Center. *Gossypium hirsutum* cv. GC-510 was grown on rows separated by 102 cm following standard commercial practices. Plants were fully mature, with most bolls fully open. Irrigation was continued through the experimental period, and plants, which normally cease vegetative growth late during the season because of the cessation of irrigation, underwent strong regrowth.

To prevent ants from foraging on the plants, each plant stem was ringed at the base with Stickem Special, and any low branches touching the ground were removed. To remove the background predator population, including nymphs hatching from *O. tristicolor* and *Nabis* eggs imbedded in the plant tissue, groups of four plants were first caged in a large enclosure (2 × 4 × 2 m) consisting of a metal frame covered with Saran plastic 0.8 mm mesh; all other plants within the enclosure were removed. Plants were visually inspected to remove predators on four dates: 26–27 August, 3 September, 8 September, and 18–20 September. The experiment was initiated on 19–20 September, when the large field cages were removed, and the tops of plants were again enclosed in plant sleeves as in experiment 2. At least the top seven nodes were enclosed; regrowth produced many additional leaves, and by the end of the experiment an average of 23.9 ± 11.9 leaves was present in each sleeve. An average of 137.6 ± 38.1 (SD) aphids was initially present in cages.

On 19–20 September plants were alternately assigned to one of two treatments, each replicated twelve times: (1) aphids plus six *C. carnea* lacewing eggs and (2) aphids plus six lacewing eggs plus two nymphal *Geocoris*, one nymphal *Nabis*, and two nymphal *Z. renardii*. Lacewing eggs were collected in the same cotton field on the day of the experimental set-up by cutting parts of leaves or petioles bearing the eggs and pinning them onto the recipient plants with insect pins. Only eggs that had been deposited singly were collected to distinguish *C. carnea* eggs from the eggs of *C. nigricornis*, which are deposited in groups. Lacewing eggs hatch 3–5 days after oviposition under fall field conditions, and change color from green to tan just prior to hatching; we collected only tan eggs to minimize variation in lacewing age structure. Lacewing eggs were pinned only to leaves, or petioles of leaves, harboring aphids. Nymphs of the other predators were collected in the same cotton field on the day of the experiment; middle and late instar nymphs of all species were used. The final sampling of aphid and predator densities was made on 30 September.

Relationship of experimental treatments to natural predator densities

All the predators manipulated in experiments 1–3 are abundant in commercial cotton fields (van den Bosch and Hagen 1966; University of California 1984; Sterling et al. 1989). The highly disturbed nature of an annually cropped agroecosystem produces densities, however, that fluctuate dramatically both temporally and from field to field. Manual removal of predators from plants can be used to estimate natural densities of nymphal predators, but not of adults, which fly when disturbed. On average, 4.38 ± 2.30 (SD) nymphal *Geocoris*, 1.08 ± 1.00 nymphal *Nabis*, and 1.63 ± 0.61 nymphal *Zelus* were removed from each plant (N = 24) during the first two combined rounds of predator removal in experiment 3. Our observations of other fields suggest that these densities were not unusually high or low, and similar values have been reported previously (Ehler 1977; Byerly et al. 1978; Sterling et al. 1989). We tentatively suggest that all of our experimental treatments employed predator densities within the range of common field densities, with one exception: densities of two adult *Z. renardii* per plant are higher than normal. However, combined nymphal and adult *Z. renardii* densities are probably common in this range. Lacewing egg densities also vary in space and time (see below); manipulated lacewing densities were within the range of field densities.

Direct observations of trophic links

Because all of the predators under study have sucking mouthparts, prey consumption was a relatively slow process, increasing the likelihood that predation would be observed in the field. During the 1991 and 1992 field seasons, we recorded any incidental observations of predation, including the genus or species of the predator and prey. Many of these observations were made while removing predators from plants during experiments 1–3.

Statistical analyses

Lacewing survival and aphid population growth (expressed as per capita change in population size over the entire experiment: [final aphid count − initial aphid count]/[initial aphid count]) were analyzed with Kruskal-Wallis rank-sum tests and planned paired comparisons using two-tailed Wilcoxon rank-sum tests. For experiments 1 and 3 experiment-wide α error rate was maintained at 0.05 by adjusting the critical P value for the number of paired comparisons being conducted (Bonferroni's inequality). For experiment 2, we allocated α = 0.05 to each of two groups of treatment comparisons (those with single species of predators being compared with aphids alone, and those with predators grouped with lacewing larvae being compared to lacewings alone), for an experiment-wide α error rate of 0.10. To test for interactions between the action of different predators on aphids in experiment 2, changes in aphid densities, transformed as $\ln((\text{final number of aphids} + 1)/(\text{initial number of aphids}))$, were analyzed in a series of 2-way ANOVA's.

Results

Size of adult predators

Mean adult weights (± SD) for the dominant generalist predators were: *G. pallens*, 910 ± 300 μg (n = 13); *G. punctipes*, 1290 ± 210 μg (n = 3); *Nabis* spp., 3450 ± 960 μg (n = 12); *Z. renardii*, 12,710 ± 6190 μg (n = 12); *O. tristicolor*, 120 ± 30 μg (n = 12); and *C. carnea*, 3230 ± 1200 μg (n = 23). Adult aphid live weights are highly variable, ranging from 32–323 μg, and perhaps somewhat larger (Wilhoit and Rosenheim 1993).

Population densities of lacewing eggs and larvae

Observations made at six field sites revealed that while lacewing eggs were generally common, lacewing larvae were rare (Table 1). These observations suggest that under unmanipulated field conditions, significant mortality forces were acting on lacewing egg or larval populations.

Experiment 1

The mean number of aphids initially present in each of the three treatments was similar (aphids only,

Table 1. Mean densities (SE) of predatory green lacewing eggs and larvae per whole plant sample of *Gossypium hirsutum*

Field	Plants sampled	Eggs per plant	Larvae per plant
Kearney	5	4.6 (2.0)	0.0 (0.0)
West Side-1	5	2.8 (0.9)	0.0 (0.0)
West Side-2	5	7.8 (2.8)	0.4 (0.25)
Shafter-1	5	2.6 (0.9)	0.0 (0.0)
Shafter-2	5	8.0 (6.0)	0.0 (0.0)
Shafter-3	48	9.9 (2.2)	0.7 (0.2)

223.0 ± 25.0 [SE]; aphids + lacewings, 215.3 ± 20.4; aphids + lacewings + predators, 226.9 ± 20.4; Kruskal-Wallis Test, $\chi^2 = 0.08$, $P = 0.96$). The treatments were successful in creating environments with different densities of hemipteran predators, although *Nabis* densities were not substantially augmented due to high *Nabis* mortality (Fig. 1a). The species composition of the predators was: for *Geocoris* spp., 100% *G. pallens*; for *Nabis* spp., 80% *N. alternatus* and 20% *N. americoferus* (based on males, the only sex that we could reliably identify); and for *Zelus* spp., 100% *Z. renardii.*

Survival of lacewing larvae was greatly reduced in the aphids + lacewings + predators treatment compared to the aphids + lacewings treatment ($\chi^2 = 19.6$, $P < 0.0001$; Fig. 1b). This decreased survivorship was observed despite the greater availability of aphid prey in the aphids + lacewings + predators treatment (Fig. 1c). Lacewing larvae were also observed to be cannibalistic, which may have contributed to mortality in both treatments. Although aphid populations grew in all three treatments (i.e., per capita aphid population growth > 0), the increase was smaller in the aphids + lacewings treatment ($\chi^2 = 15.0$, $P < 0.0001$) and the aphids + lacewings + predators treatment ($\chi^2 = 12.0$, $P = 0.0005$) than in the aphids only treatment. These results are significant when the P value is compared with a critical value of 0.05 adjusted for three comparisons (0.05/3 = 0.017; Bonferroni's inequality). Despite the strong effect of predators on lacewing survival, the per capita aphid growth in the two treatments with lacewings did not differ significantly ($\chi^2 = 2.6$, $P = 0.11$).

Spider mite populations were low; active colonies of spider mites covered 1.4 ± 1.4 (SD)% of lower leaf surfaces at the beginning of the experiment, and grew to cover 2.6 ± 3.9%. Mite population growth was analyzed by calculating the relative change in the percentage of the lower leaf surface covered with active mite colonies: (final % − initial %)/(initial %). There were no significant differences between the three treatments in this index (aphids only, 1.5 ± 0.6 [SE]; aphids + lacewings, 2.0 ± 0.6; aphids + lacewings + predators, 0.9 ± 0.4; $\chi^2 = 1.77$, $P = 0.41$), suggesting that neither the lacewing larvae nor the adult hemipteran predators were especially effective at suppressing low densities of spider mites. None of the other potential prey species observed (thrips, leafhoppers, lepidopteran eggs and larvae, *Lygus* nymphs) were abundant.

Experiment 2

The mean number of aphids initially present in each of the eight treatments was similar, ranging from 120.0 ± 12.4 (SE) to 151.1 ± 9.6 (test for differences be-

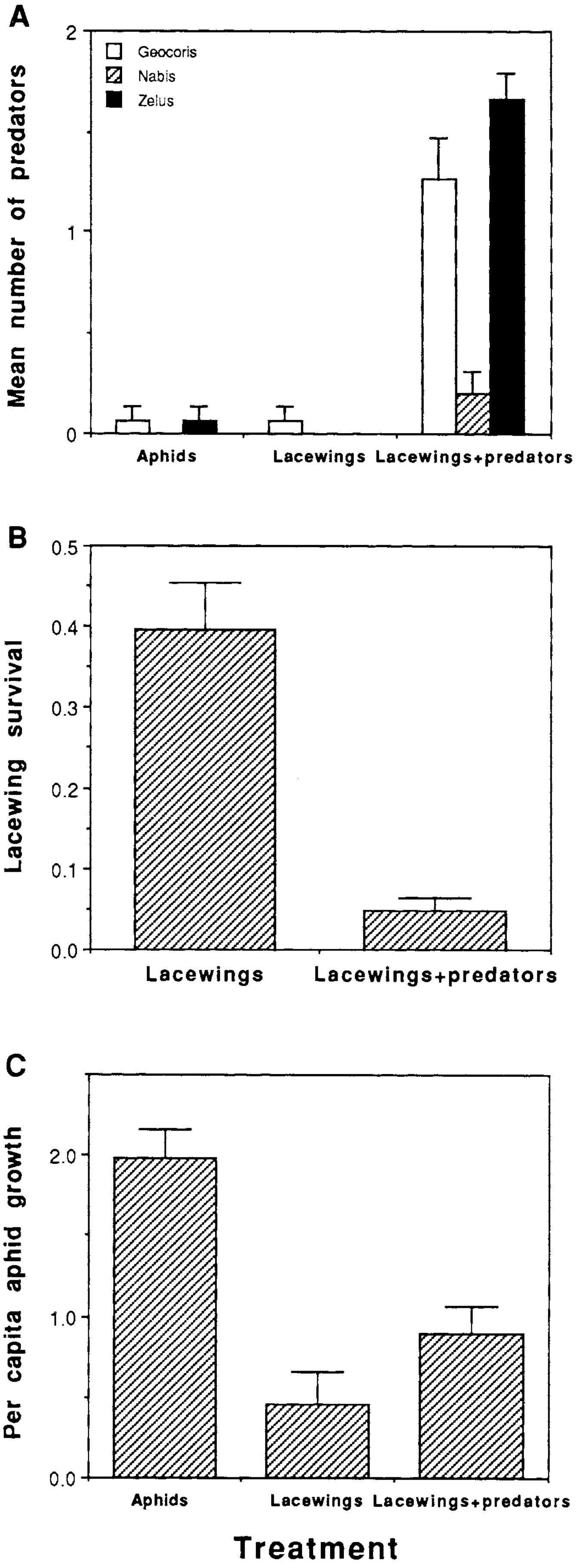

Fig. 1A–C. Experiment 1. **A** Mean (+1 SE) number of predators (adults plus nymphs combined) retrieved per field enclosure at the end of the experiment. **B** Mean (+1 SE) proportion of lacewing larvae surviving. **C** Mean (+1 SE) per capita aphid population growth

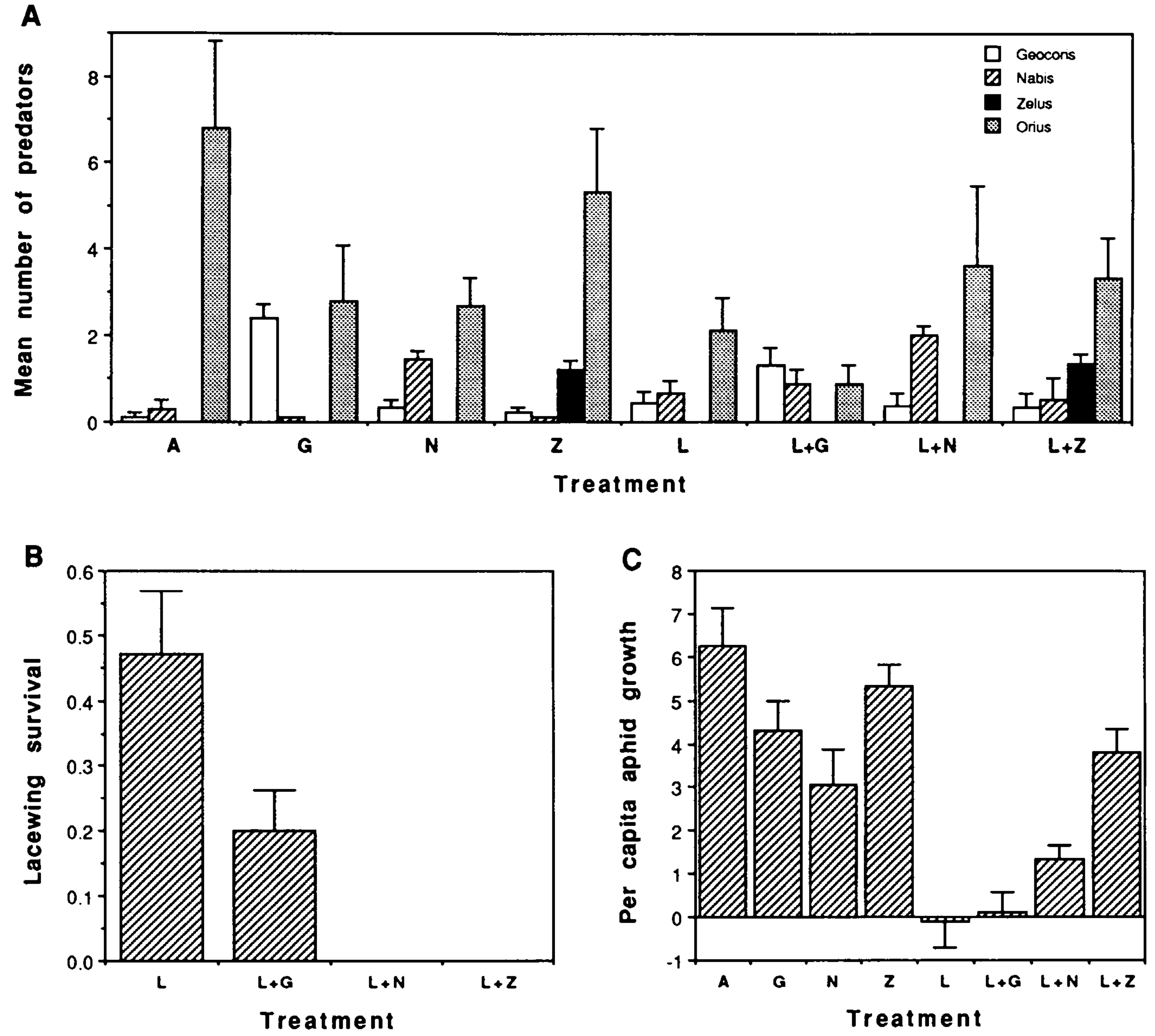

Fig. 2A–C. Experiment 2. **A** Mean (+1 SE) number of predators (adults plus nymphs combined) retrieved per field enclosure at the end of the experiment. **B** Mean (+1 SE) proportion of lacewing larvae surviving. **C** Mean (+1 SE) per capita aphid population growth. Treatments: A, aphids only (n = 10 replicates); G, *Geocoris* (n = 10); N, *Nabis* (n = 9); Z, *Z. renardii* (n = 10); L, lacewings (n = 9); L + G, lacewings + *Geocoris* (n = 7); L + N, lacewings + *Nabis* (n = 8); L + Z, lacewings + *Z. renardii* (n = 6)

tween treatments, $\chi^2 = 4.8$, $P = 0.68$). A wide variety of other arthropods also was present, including moderate densities of spider mites, leafhoppers and thrips (including the mite predator, *Scolothrips sexmaculatus* [Pergande]), and lower densities of whitefly, lepidopteran larvae, *Lygus* and other hemipteran herbivores, and foliar Collembola. The treatments were successful in creating environments with different densities of hemipteran predators, although predator densities were also augmented by nymphs hatching from *O. tristicolor* and *Nabis* eggs that were imbedded in plant tissue and to a lesser extent from *Geocoris* eggs laid on leaf surfaces (Fig. 2a). Each of the treatments with hemipteran predators added produced significantly enhanced numbers of the added predator compared to the associated control ($P < 0.01$) with one exception: the lacewings plus *Geocoris* treatment did not have more *Geocoris* than the lacewings treatment ($P = 0.10$). However, even in this case the predator environments were different; 9 of 10 *Geocoris* recovered from the lacewings plus *Geocoris* treatment were adults whereas 3 of 4 *Geocoris* recovered from the lacewings treatment were nymphs, which probably hatched from eggs present when the experiment began. The species composition of the predators was: for *Geocoris* spp., 80% *G. pallens* and 20% *G. punctipes*; for *Nabis* spp., 90% *N. alternatus* and 10% *N. americoferus* (based on males, the only sex that we could reliably identify); and for *Zelus* spp., 100% *Z. renardii*.

Survival of lacewings varied strongly across the four treatments to which lacewings were introduced (Fig. 2b; $\chi^2 = 19.7$, $P = 0.0002$). Survival decreased from 0.47 ± 0.10 (SE) in the lacewings only treatment to 0.20 ± 0.06 in the lacewings + *Geocoris* treatment ($\chi^2 = 3.6$, $P = 0.057$), 0.0 in the lacewings + *Nabis* treatment ($\chi^2 = 11.3$, $P = 0.0008$), and 0.0 in the lacewings + *Z. renardii* treatment ($\chi^2 = 9,1$, $P = 0.0026$); the last two comparisons are significant (the critical P value is $0.05/3 = 0.017$; Bonferroni's inequality). As in experiment 1, these declines in lacewing survival were observed despite the greater availability of aphid prey in the treatments with the hemipteran predators present (Fig. 2c). The substantial number of *O. tristicolor* nymphs that hatched from eggs during the experiment (mean $= 3.58 \pm 4.25$ [SD] per enclosure; range 0–20) did not have a measurable influence on lacewing survival (ANCOVA with treatment as the main factor and number of *O. tristicolor* as the covariate: effect for the covariate, $F = 0.02$, $P = 0.88$).

The treatments fall into two groups when considering the impact of predators on aphid population growth. The first group, involving the first five treatments (Fig. 2c), provides a test of whether each of the four predators considered alone has a substantial impact on aphid population dynamics compared to growth in the absence of predators. Of the four predators, only lacewings produced a large change in per capita aphid population growth; lacewings reversed the population expansion $\chi^2 = 11.2$, $P = 0.0008$; critical P value is $0.05/4 = 0.013$). The mean value of per capita aphid growth is deceptively high for the lacewings only treatment, because in the only replicate where, for unknown reasons, no lacewings survived, the aphid population grew rapidly; the median value of per capita aphid growth for the lacewings only treatment was -0.912 (i.e., a decrease of 91.2%). *Geocoris* and *Z. renardii* had little effect on aphid population growth ($\chi^2 = 2.1$, $P = 0.15$, and $\chi^2 = = 0.4$, $P = 0.55$, respectively), while the impact of *Nabis* predation was nearly significant ($\chi^2 = 4.9$, $P = 0.027$).

The second group of treatments addresses two aspects of the influence of predatory bugs on the effective suppression of aphid population growth generated by lacewings alone (Fig. 2c). First, we can ask if lacewings and predatory bugs have additive, independent effects on suppressing aphids, or rather if significant interactions occur. Two-way ANOVA revealed a marginally nonsignificant interaction between lacewings and *Geocoris* ($F_{1,32} = 3.9$, $P = 0.06$) and highly significant interactions between lacewings and *Nabis* ($F_{1,32} = 19.2$, $P = 0.0001$) and between lacewings and *Z. renardii* ($F_{1,31} = 22.4$, $P < 0.0001$). Predatory bugs and lacewings clearly did not exert independent effects on aphid population suppression. Second, we can ask if the interactions between predatory bugs and lacewings were strong enough to generate significant increases in aphid density, i.e., trophic cascades. Each of the three predatory bugs generated some disruption of the control generated by lacewings alone, and the effect was significant for *Nabis* and *Z. renardii* (for *Geocoris*, $\chi^2 = 2.0$, $P = 0.15$; *Nabis*, $\chi^2 = 6.3$, $P = 0.012$; for *Z. renardii*, $\chi^2 = 6.7$, $P = 0.001$; critical P value $= 0.05/3 = 0.017$). Thus, the influences of these predators on lacewing survival (Fig. 2b) produced trophic cascades with substantial indirect influences on the density of a dominant herbivore.

This experiment cannot easily be used to evaluate the impact of *O. tristicolor* predation on aphid population growth. Because *O. tristicolor* numbers were not manipulated experimentally, it is difficult to identify the direction of causation for correlations between *O. tristicolor* and aphid densities. *Orius tristicolor* nymphs do feed on aphids (see below), and *O. tristicolor* survival also appeared to be linked to the density of aphid prey (Spearman's rank correlation of *O. tristicolor* density on mean final aphid density per treatment: $r_s = 0.81$, df $= 6$, $P < 0.05$). With this caveat, we can say that *O. tristicolor* density was not significantly associated with per capita aphid growth after controlling for treatment effects (ANCOVA, $P > 0.05$; data not shown).

Spider mites were moderately abundant; active colonies of spider mites covered 6.6 ± 6.5 (SD) % of lower leaf surfaces at the beginning of the experiment, and grew to cover 12.0 ± 7.7% during the experiment. There was, however, no evidence that lacewing larvae or any of the adult hemipteran predators, alone or in combination, had any influence on spider mite population dynamics, as indicated by the final percent leaf surface area covered ($\chi^2 = 9.7$, $P = 0.20$) or by the proportional change in percent area covered ([final % – initial %]/[initial %]; $\chi^2 = 7.5$, $P = 0.38$). The proportional change in leaf area covered by mite colonies was 1.7 ± 0.7 in treatment 1 (the "aphids only" treatment), a figure very similar to the overall mean for the eight treatments (1.8 ± 0.3).

Experiment 3

Initial numbers of aphids in the lacewings-only treatment (149.9 ± 12.5 [SE] and the lacewings + predators treatment (125.3 ± 8.4) were not significantly different ($\chi^2 = 1.5$, $P = 0.23$). All other herbivorous arthropods were present at very low densities, including spider mites, whitefly, and hemipteran nymphs; the predatory thrips *S. sexmaculatus* was also present at very low densities. The repeated removal of predators from the lacewings only replicates was successful in creating distinct differences in predator densities in the two treatments (Fig. 3a). Many dead nymphal *Geocoris* and *Nabis* were recovered from the enclosures in the lacewings + predators treatment as intact exoskeletons from which nearly all internal tissues had been removed, diagnostic of attack by a predator with sucking mouthparts.

Across both treatments, only 2.8% (4/144) of lacewing eggs introduced to the experimental enclosures remained unhatched at the end of the experiment; one larva died during hatching. We observed no morphological signs of lacewing egg parasitism. Lacewing larvae surviving the experimental period had mostly entered the third and final larval instar (76.5%), with some larvae still present in earlier instars (second instar 17.6%; first instar 5.9%). Lacewing survival decreased dramatically in the lacewings + predators treatment compared to the lacewings only treatment (Fig. 3b; $\chi^2 = 18.2$, $P < 0.0001$). Thus, nymphal hemipteran predators depressed lacewing larval survivorship to approximately the same degree as observed during experiments 1–2 for adult predators. Survivorship decreased despite similar densities of aphid prey in the two treatments. Per capita aphid population growth was strong in both treatments, which did not differ significantly (Fig. 3c; $\chi^2 = 1.2$, $P = 0.27$). Aphid populations grew so rapidly in both treatments that predation pressure by the end of the experiment was negligible; the mean final aphid population across all 24 replicates was 1853 ± 1004 (SD) aphids, representing an 13.2-fold increase over initial numbers.

Direct observations of trophic links

Although some predator-prey interactions are readily observable in the field (e.g., lacewings, coccinellid spp., and syrphid spp. feeding on aphids), predation events involving *O. tristicolor*, *Geocoris*, *Nabis*, *Z. renardii*, and two other groups of predators, *Sinea* spp. (Reduviidae), and crab spiders (Thomisidae), were observed infrequently (N = 30 total recorded). For example, although *Nabis* nymphs and adults were common during the mid and late season, they were never observed feeding on prey. Nevertheless, the few observations that we made reveal complex trophic interactions among predatory arthropods (Table 2); the true trophic web is, we feel, likely to include many additional interactions. We made several observations of predatory bugs feeding on lacewing larvae (and adults), a result that is particularly relevant to the interpretation of experiments 1–3. Ten observations were made of *Zelus* and *Sinea* adults and nymphs feeding on arthropod prey; without exception, the prey were other predatory insects.

Discussion

To summarize and place in perspective our experimental results, we return to the four questions that we posed in the introduction.

First, do generalist hemipteran predators feed on *C. carnea*? Yes. Furthermore, some species like *Zelus* appear from limited observations to consume predominantly other predatory species, at least while in the adult and late nymphal stages.

Second, does intraguild predation represent a substantial source of mortality for *C. carnea*? Yes. Survivorship of lacewing larvae was severely reduced by nymphal or adult stages of other predators (mostly *Zelus* and *Nabis*, but also perhaps *Geocoris*). We can infer that the decreased survival of lacewing larvae was primarily a

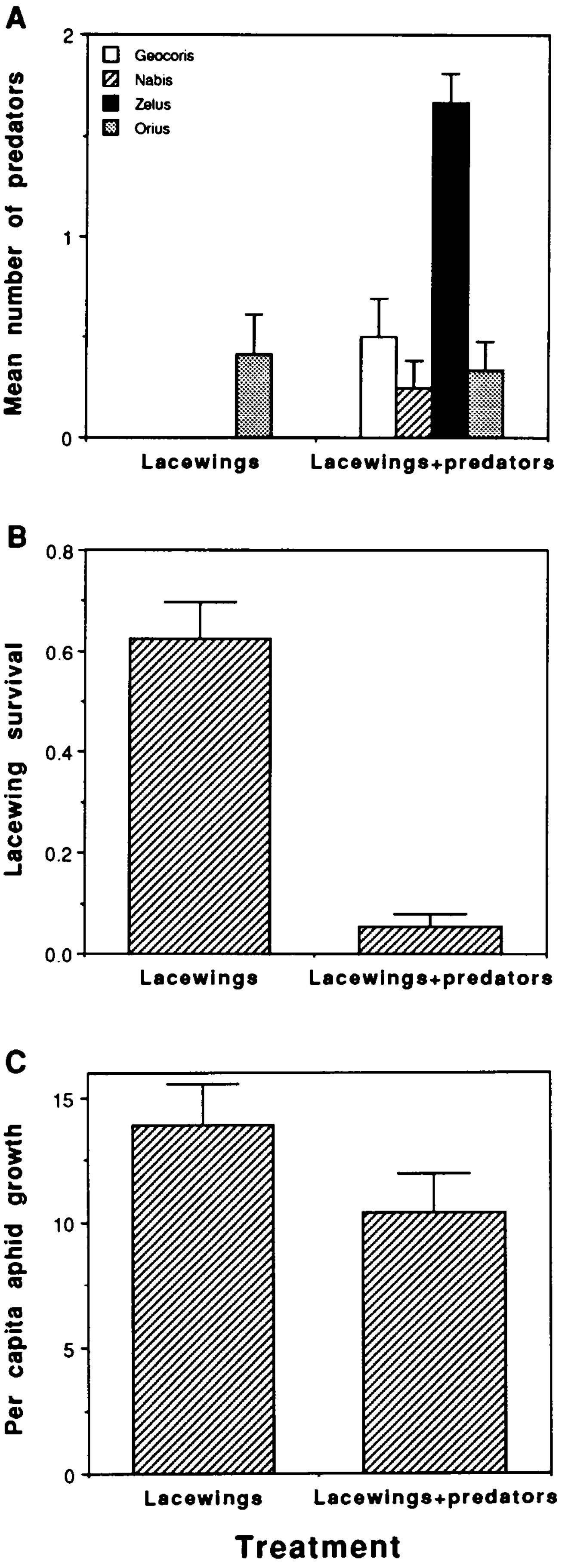

Fig. 3A–C. Experiment 3. **A** Mean (+1 SE) number of predators (adults plus nymphs combined) retrieved per field enclosure at the end of the experiment. **B** Mean (+1 SE) proportion of lacewing eggs surviving to larval stages. **C** Mean (+1 SE) per capita aphid population growth

Table 2. Number of predator-prey interactions observed in mid- and late-season cotton, *Gossypium hirsutum*, involving predatory arthropods associated with *Aphis gossypii*. Herbivores other than *A. gossypii* are omitted. +, interaction observed very frequently, not quantified. Chrys, Chrysopidae; *Orius*, *Orius tristicolor*; Geoc, *Geocoris* spp.; Syrph, Syrphidae; Cocc, Coccinellidae; *Nabis*, *Nabis* spp.; *Sinea*, *Sinea* spp.; *Zelus*, *Zelus* spp.; Thom, Thomisidae

Prey	Predator								
	Chrys	*Orius*	Geoc	Syrph	Cocc	*Nabis*	*Sinea*	*Zelus*	Thom
Aphis	+	11	3	+	+				
Chrys	1		1					5	
Orius			2					1	
Geoc								1	1
Syrph									
Cocc							2	1	
Nabis									
Sinea									
Zelus									2
Thom									

result of predation rather than competition; the availability of aphid prey was substantially higher in the treatments where lacewing survival was depressed (experiments 1 and 2) or was very high and not likely to be limiting in either treatment (experiment 3). The fact that lacewing survival was depressed despite the availability of aphid (and spider mite) prey also suggests that the small cages did not create this result artificially by simply caging the predators until they had nothing left to eat. Although we cannot completely rule out non-lethal forms of predator interference with lacewings, such interference was never observed in the field; furthermore, contact between two foraging lacewing larvae was frequently observed and, as long as cannibalism did not result, produced only a minor and transient interruption of normal foraging activity. These results suggest that the lacewing age structure that we observed in the field during 1991 and 1992 (high densities of eggs, low densities of larvae; Table 1) may be the result of heavy predation on lacewing larvae by natural populations of *Zelus*, *Nabis*, and *Geocoris*.

Third, do predator species act to suppress aphid populations in an independent, additive manner? No. We observed strong interactions between lacewings and *Nabis* and *Z. renardii*, and some evidence of a weaker interaction between lacewings and *Geocoris*. This is the first indication that the influence of IGP among predators of *Aphis gossypii* is ramifying beyond the predator guild to impact broader aspects of arthropod community structure.

Fourth and finally, can the experimental addition of some predators result in increased densities of aphids through a trophic cascade effect? Yes. Despite the fact that the (likely incomplete) trophic web is already too complex to delineate distinct trophic levels within the predatory arthropod community, some trophic links appear to be sufficiently strong to produce cascades from higher-order carnivores to the level of herbivore population dynamics (Fig. 4). These cascades were most evident in experiment 2, when experimental addition of either *Z. renardii* or *Nabis* generated sufficient lacewing larval mortality to release aphid populations from control by lacewing predators. Predatory bugs were unable to compensate fully for the loss of lacewing predation that they produced.

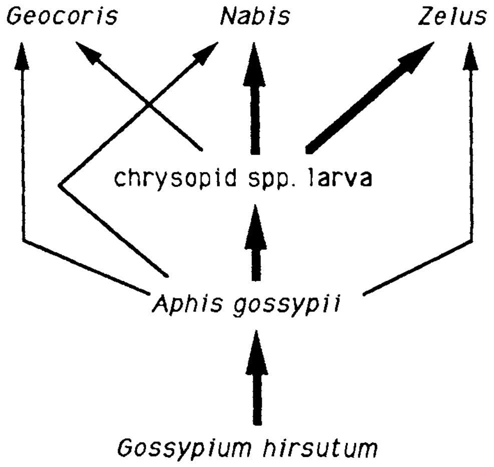

Fig. 4. Dominant interactions between arthropods associated with *Aphis gossypii* as revealed by experimental manipulations. Arrow thicknesses reflect the strength of the direct trophic effects; arrows point from prey to predator. (The absence of arrows indicates only that the interaction was not studied)

We have observed strong species-specific predator impacts on aphids and trophic cascades without the large differences in body sizes of top and intermediate predators that characterize many previously studied cascades (Pacala and Roughgarden 1984; Carpenter and Kitchell 1988; Power 1990; Spiller and Schoener 1990; Brönmark et al. 1992). Although all of the predators we studied were generalists, preferences for different prey types or differential vulnerabilities of prey apparently were important. Additional work is required to elucidate the mechanistic, behavioral basis for the population-level phenomena we have observed here.

In contrast to the results of experiment 2, trophic cascades were only hinted at in experiment 1 and not demonstrated at all in experiment 3, where aphid populations grew rapidly regardless of the associated predator community. What were the likely sources of this variation? We suggest that there may have been at least three. First, variation in the duration of the experiments may have been important. Experiment 1 lasted only 3–4 days, long enough for differences in lacewing survivorship to become established, but probably not long enough for the resulting difference in intensity of predation to have a measurable impact on aphid population growth; in contrast, experiment 2 lasted 7–8 days and experiment 3 lasted 10–11 days. Second, while experiments 1 and 2 were initiated with the introduction of lacewing larvae (first and second instars), which immediately begin feeding on aphids, experiment 3 was initiated with lacewing eggs. We suspect that during the approximately 4–5 days required for these eggs to hatch and the lacewing larvae to reach the second instar (when their consumption of prey increases substantially [Zheng et al. 1993]), the aphid populations had probably already surpassed densities at which they could be suppressed. Third, and perhaps most importantly, we discovered during the course of these experiments that aphid polymorphism that occurs during the mid and late season has profound implications for aphid population growth rates (Wilhoit and Rosenheim 1993). Aphids present during experiment 2 were small and yellow; these aphids develop slowly and have low levels of reproduction. Aphids present during experiment 1 were a mixture of yellow aphids and light green aphids, which are more reproductive. Aphids present during experiment 3 were large and primarily green or dark green morphs, which develop rapidly and are highly reproductive. The modest densities of lacewing predators (5–10 per enclosure) that we employed in our experiments may have been sufficient to regulate populations of aphids with limited reproductive capacities (yellow morphs), but apparently were not sufficient to regulate populations of aphids with high reproductive capacities (dark green morphs), regardless of the presence or absence of other, potentially disruptive, generalist predators.

We did not attempt to assess the importance of *Solenopsis* ants during our experimentation. These ants may be important generalist predators in some cases, and warrant additional investigation. The loss of 11 of 80 replicates during experiment 2 may, however, overestimate the general impact of ants for at least two reasons. First, the field had what appeared to be an unusually high density of ants. Second, our practice of removing plants adjacent to the experimental plant resulted in a focusing of ant foraging activity on the experimental plant. It was for this reason that we put a sticky ant barrier on plants during experiment 3, when a 2 × 4 m area was cleared of plants except for the central four experimental plants.

Our experiments provide only a crude estimate of the role of trophic cascades under natural field conditions. Our experiments were too short to measure reproductive recruitment of lacewings across generations. Were such recruitment not blocked in nature by the heavy mortality imposed on lacewing larvae by other generalist predators, we suspect that "natural" densities of lacewing eggs and larvae would increase rapidly during the growing season. Lacewing populations might then be capable of regulating populations of aphids regardless of polymorphism-related variation in reproductive rates. The experiments that we have reported here were artificial not only because of their short duration, but also because the plant cages constrained natural predator movement and may therefore have altered foraging behavior. Our plant for future work on this system include longer-term and larger-scale experimentation, which should quantify reproductive recruitment by lacewings and avoid the artificiality of small plant enclosures.

Acknowledgments. We thank T.F. Leigh for the use of large field cages, K.M. Daane for providing lacewing larvae, and P. Wynholds for assistance in the field. For helpful discussions or review of drafts of this manuscript we thank A. Corbett, K.M. Daane, L.E. Ehler, G.E. Heimpel, B. Jaffee, R. Karban, T.F. Leigh, B.C. Murphy, C.H. Pickett, G.A. Polis, M.E. Power, D.A. Spiller, D.R. Strong, C.A. Tauber, and M.J. Tauber. P.S. Ward kindly identified *Solenopsis xyloni*. We have greatly appreciated the logistic support of the staff and directorship of the Kearney Agricultural Center, the UC West Side Field Station, and the UC Cotton Research Station, Shafter. This work was supported by grants from Cotton Incorporated and the University of California Statewide IPM program.

References

Alrouechdi D, Séméria Y, New TR (1984) Ecology of natural enemies. In: Canard M, Séméria Y, New TR (eds) Biology of Chrysopidae. Dr W. Junk Publishers, The Hague, pp 187–204

Bisabri-Ershadi B, Ehler LE (1981) Natural biological control of western yellow-striped armyworm, *Spodoptera praefica* (Grote), in hay alfalfa in northern California. Hilgardia 49(5): 1–23

Brönmark C, Klosiewski SP, Stein RA (1992) Indirect effects of predation in a freshwater, benthic food chain. Ecology 73:1662–1674

Byerly KF, Gutierrez AP, Jones RE, Luck RF (1978) A comparison of sampling methods for some arthropod populations in cotton. Hilgardia 46(8):257–282

Canard M, Séméria Y, New TR (eds) (1984) Biology of Chrysopidae. Dr W. Junk Publishers, The Hague

Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. Bioscience 38:764–769

Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. Bioscience 35:634–639

Croft BA, MacRae IV (1992a) Biological control of apple mites by mixed populations of *Metaseiulus occidentalis* (Nesbitt) and *Typhlodromus pyri* Scheuten (Acari: Phytoseiidae). Environ Entomol 21:202–209

Croft BA, MacRae IV (1992b) 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

Diehl S (1992) Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646–1661

Ehler LE (1977) Natural enemies of cabbage looper on cotton in the San Joaquin Valley. Hilgardia 45(3):73–106

Ehler LE, Miller JC (1978) Biological control in temporary agroecosystems. Entomophaga 23:207–212

Fagan WF, Hurd LE (1991) Direct and indirect effects of generalist predators on a terrestrial arthropod community. Am Midl Nat 126:380–384

Fretwell SD (1977) The regulation of plant communities by the food chains exploiting them. Perspectives Biol Med 20:169–185

Fretwell SD (1987) Food chain dynamics: the central theory of ecology? Oikos 50:291–301

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Amer Nat 94:421–425

Head RB (1992) Cotton insect losses 1991. Proc Beltwide Cotton Conf 621–625

Hurd LE, Eisenberg RM (1984) Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. II. The influence of mantids on arthropod community structure. J Anim Ecol 53:955–967

Hurd LE, Eisenberg RM (1990) Arthropod community responses to manipulation of a bitrophic predator guild. Ecology 71:2107–2114

McPeek MA (1990) Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. Ecology 71:1714–1726

Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am Nat 110:351–369

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Amer Nat 130:730–757

Pacala S, Roughgarden J (1984) Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). Oecologia 64:160–162

Polis GA (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. Am Nat 138:123–155

Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol Evol 7:151–154

Polis GA, McCormick SJ (1987) Intraguild predation and competition among desert scorpions. Ecology 68:332–343

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

Power ME (1990) Effects of fish in river food webs. Science 250:811–814

Power ME (1992a) Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733–746

Power ME (1992b) Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73:1675–1688

Power ME, Marks JC, Parker MS (1992) Variation in the vulnerability of prey to different predators: community-level consequences. Ecology 73:2218–2223

Salas-Aguilar J, Ehler LE (1977) Feeding habits of *Orius tristicolor*. Ann Entomol Soc Am 70:60–62

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Annu Rev Ecol Syst 16:269–311

Spiller DA (1986) Interspecific competition between spiders and its relevance to biological control by general predators. Environ Entomol 15:177–181

Spiller DA, Schoener TW (1988) An experimental study of the effect of lizards on webspider communities. Ecol Monogr 58:57–77

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 (in press) Effects of top and intermediate predators in a terrestrial food web. Ecology

Sterling WL, El-Zik KM, Wilson LT (1989) Biological control of pest populations. In: Frisbie RE, El-Zik KM, Wilson LT (eds) Integrated Pest Management Systems and Cotton Production. John Wiley & Sons, New York, pp 155–189

Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754

Trichilo PJ, Leigh TF (1986) Predation on spider mite eggs by the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem. Environ Entomol 15:821–825

University of California (1984) Integrated Pest Management for Cotton in the Western Region of the United States. Univ Calif Div Agric Natural Resources Publ 3305

van den Bosch R, Hagen KS (1966) Predaceous and parasitic arthropods in California cotton fields. Calif Agric Expt Stat Bull 820

Warren PH, Lawton JH (1987) Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? Oecologia 74:231–235

Whitcomb WH, Bell K (1964) Predaceous insects, spiders, and mites of Arkansas cotton fields. Univ Arkansas Agric Expt Sta Bull 690

Wilhoit LR, Rosenheim, JA (1993) The yellow dwarf form of the cotton aphid, *Aphis gossypii*. Proc Beltwide Cotton Conf 969–972

Wilson LT, Gutierrez AP (1980) Within-plant distribution of predators on cotton: comments on sampling and predator efficiencies. Hilgardia 48(2):3–11

Wise DH (1993) Spiders in Ecological Webs. Cambridge University Press, Cambridge, U.K.

Wissinger SA (1992) Niche overlap and the potential for competition and intraguild predation between size-structured populations. Ecology 73:1431–1444

Zheng Y, Hagen KS, Daane KM, Mittler TE (1993) Influence of larval dietary supply on the food consumption, food utilization efficiency, growth and development of the lacewing *Chrysoperla carnea*. Entomol Exp Appl 67:1–7