Ecological Monographs, 71(1), 2001, pp. 93–116

SOURCE–SINK DYNAMICS FOR A GENERALIST INSECT PREDATOR IN HABITATS WITH STRONG HIGHER-ORDER PREDATION

JAY A. ROSENHEIM

Department of Entomology, University of California, One Shields Avenue, Davis, California 95616 USA

Abstract. The functional importance of higher-order predators in terrestrial ecosystems is currently an area of active inquiry. In particular, an understanding of the relative influences of prey availability and higher-order predation on predator populations is of immediate relevance to the theory of biological control of herbivorous arthropods. Biological control workers have repeatedly speculated that one cause of failure to establish predators and parasitoids in novel environments is the strong mortality imposed on released agents by higher-order predators. Nevertheless, the ability of higher-order predators to create a habitat where mortality exceeds natality (a ''sink'' habitat) has never been tested experimentally with a biological control agent in nature.

Although in isolation the predatory lacewing *Chrysoperla carnea* can consistently produce strong suppression of populations of the aphid *Aphis gossypii,* the full community of predators when tested together exerts minimal aphid control. The age structure of *Chrysoperla* spp. populations in cotton fields harboring low to intermediate densities of aphid prey is characterized by a sharp drop in densities from the egg to the first larval instar; this observation is consistent with heavy mortality during either the egg or first larval stage. Egg cohorts followed under unmanipulated field conditions showed relatively high rates of successful hatch, suggesting that the vulnerable developmental stage is the young larva. Larval survival is relatively high in the absence of hemipteran predators, suggesting that prey availability is not the primary limiting factor. Depressed survival is observed in the presence of *Geocoris* spp., *Nabis* spp., and *Zelus renardii,* all common hemipteran predators in cotton. Predation on lacewing larvae appears to disrupt the strong top-down control of aphid populations in cotton.

Chrysoperla spp. densities declined in fields harboring intermediate aphid densities when lacewing subpopulations were experimentally caged to block immigration and emigration. In one year (1993) *Chrysoperla* spp. densities fell to very low levels, suggesting that the field was either a true sink habitat or a pseudosink with a very low equilibrium density. In a second year (1994), densities declined to what appeared to be a lower but stable density, suggesting that the habitat was a pseudosink. Thus, in both years, declines in *Chrysoperla* spp. densities were observed following caging, suggesting that *Chrysoperla* spp. populations are spatially subsidized. Aphid prey availability and higher-order predation interacted strongly in their influence on *C. carnea* survival: larval survival in the presence of higher-order predators was 5.6% when prey availability was intermediate and 40.5% when prey were superabundant. Spatial heterogeneity in aphid prey densities modulates the intensity of higher-order predation and thereby appears to produce source–sink dynamics of *Chrysoperla* spp. in cotton fields.

Key words: *biological control;* Chrysoperla carnea; Chrysoperla comanche; *community structure; generalist predator; higher-order predator; immigration; intraguild predation; omnivory; pseudosink habitat; source–sink dynamics; spatial subsidy.*

INTRODUCTION

A long-standing debate on the structure and function of terrestrial communities has recently been renewed in the wake of new empirical developments in the study of food webs (Polis and Winemiller 1996). Hairston and Hairston (1993, 1997), in seeking to explain differences between freshwater and terrestrial ecosystems in the efficiency of energy transfer up the food chain, have extended the influential model first proposed by Hairston et al. (1960; see also Slobodkin et al. 1967). They argued that trophic levels are discernable and functionally distinct, and that, although secondary carnivores are important in freshwater communities, ''. . . in terrestrial communities, secondary carnivores are quantitatively an unimportant part of the mortality of primary carnivores'' (Hairston and Hairston 1997: 1002). In reply, Polis and Strong (1996) have argued that omnivory is sufficiently widespread in terrestrial ecosystems to preclude the recognition of discrete, homogeneous trophic levels. They, along with a group of ecologists working primarily with predatory arthropods, have described an alternate view of terrestrial

Manuscript received 12 April 1999; revised 9 December 1999; accepted 15 December 1999; final version received 18 January 2000.

community structure in which omnivory is widespread and higher-order predators (predators that consume other predators) may be dynamically significant (Polis 1991, 1994, Wise 1993, Moran et al. 1996, Polis and Strong 1996, Schoener and Spiller 1996, Fagan 1997, Janssen et al. 1998, Letourneau and Dyer 1998, Moran and Hurd 1998, Polis et al. 1998, Rosenheim 1998, Sih et al. 1998, Spiller and Schoener 1998, Palomares and Caro 1999, Schellhorn and Andow 1999, Schoener and Spiller 1999, Wise and Chen 1999).

Resolution of this debate is of direct significance to our understanding of forces regulating the population densities of generalist predators. The traditional view, supported by the model of Hairston et al. (1960) and reinforced by a large body of theory depicting predator–prey dynamics within the context of simple, two-species interactions (e.g., Hassell 1978), has emphasized the role of prey availability. More recently, this view has been elaborated following experiments demonstrating that plant-based resources, and especially pollen and nectar, may also be important for predatory arthropods (Alomar and Wiedenmann 1996, Coll 1998, Polis et al. 1998, Agrawal et al. 1999). Still, the focus has been on the availability of food resources (bottom-up effects). The potential role of higher-order predators (top-down effects) has received little attention.

The relative importance of bottom-up vs. top-down influences on populations of terrestrial predatory arthropods is germane to the practice of biological pest control. While some biological control programs have been spectacularly successful, the overall success rate of programs in which exotic natural enemies (predators and parasitoids) have been introduced to new habitats to control invasive herbivorous arthropods is quite low (10.8%, Greathead and Greathead 1992). Informal observations made during the course of introductions have led repeatedly to the suggestion that higher-order predators may preclude the establishment of new biological control agents by decimating the small, released populations (Stiling 1993). Local extinctions are predicted to be a common outcome of higher-order predation (Holt and Polis 1997), and higher-order predation has been observed to exclude predators from local habitats (Barkai and McQuaid 1988, Schoener and Spiller 1995, 1996, Wissinger et al. 1996, Spiller and Schoener 1998, Fincke 1999, Losos and Spiller 1999). To my knowledge, however, there have been no experimental studies addressing the possibility that higher-order predators may produce extinctions of local populations of predatory biological control agents, or that spatial subsidy through immigration is responsible for maintaining observed predator densities in habitats where higher-order predation is strong. The possibility that variation in the intensity of higher-order predation could generate source–sink dynamics in a biological control agent population, in which habitats where predation is intense act as sinks whereas habitats where predation is weak acts as sources, is important to our overall understanding of top-down forces in arthropod communities as well as to our ability to deploy biological control agents effectively.

Here I explore the possibility that variation in the intensity of higher-order predation produces source–sink dynamics in populations of common predatory insects, the green lacewings in the genus *Chrysoperla.* The investigation begins with experiments demonstrating strong predation on *Chrysoperla* spp. larvae. These experiments motivated a test of the hypothesis that some agroecosystems are sinks for *Chrysoperla* spp. populations, and further explorations of the mechanisms producing source–sink dynamics in *Chrysoperla* spp. populations in habitats with variable prey resources.

Green lacewings in the cotton agroecosystem

Green lacewings (family Chrysopidae) are common members of the predatory arthropod community in many agroecosystems, including upland cotton, *Gossypium hirsutum.* Because different lacewing species are discussed in this paper, a note on terminology will be helpful: I use species names (e.g., *Chrysoperla carnea* [= *Chrysoperla plorabunda* sensu latu], *Chrysoperla comanche*) when data pertain to only a single species. I use ''*Chrysoperla* spp.'' when data apply to some combination of *C. carnea* and *C. comanche* (these two species, which are the dominant members of the lacewing community in cotton, deposit their eggs singly, whereas *Chrysopa nigricornis*, a less abundant species observed in cotton, deposits eggs in large clusters; thus, a singly-laid egg can be inferred reliably to be a species of *Chrysoperla*). I use ''lacewings'' when the data apply to an unresolved combination of species within the family Chrysopidae (i.e., including potentially *Chrysoperla* spp. and *Chrysopa* spp.; the larval and pupal stages of these lacewings are difficult to distinguish in the field without destructive sampling). The larval stages of lacewings are generalist predators of soft-bodied arthropods; in California cotton the primary prey is the cotton aphid, *Aphis gossypii*, but additional prey include spider mites, *Tetranychus* spp.; thrips, primarily *Frankliniella occidentalis*; whiteflies, primarily *Bemisia argentifolia* and *Trialeurodes vaporariorum*; and others. The adult stages of some lacewings, including *C. carnea* and *C. comanche* are not predatory, but rather feed on homopteran honeydew, floral and extrafloral nectar, and pollen (Rousset 1984). Eggs are laid on long stalks, which are thought to be defensive in function (Duelli 1984, Eisner et al. 1996). At 25°C in the laboratory, the development times of *Chrysoperla* spp. eggs (oviposition until hatch) and each of the three larval instars are similar (4–5 d), whereas the prepupal and pupal stages together require ~12 d (Canard and Principi 1984). Thus, in the absence of developmental mortality and assuming an approximately steady rate of lacewing oviposition in the field, we expect to observe similar densities of *Chrysoperla*

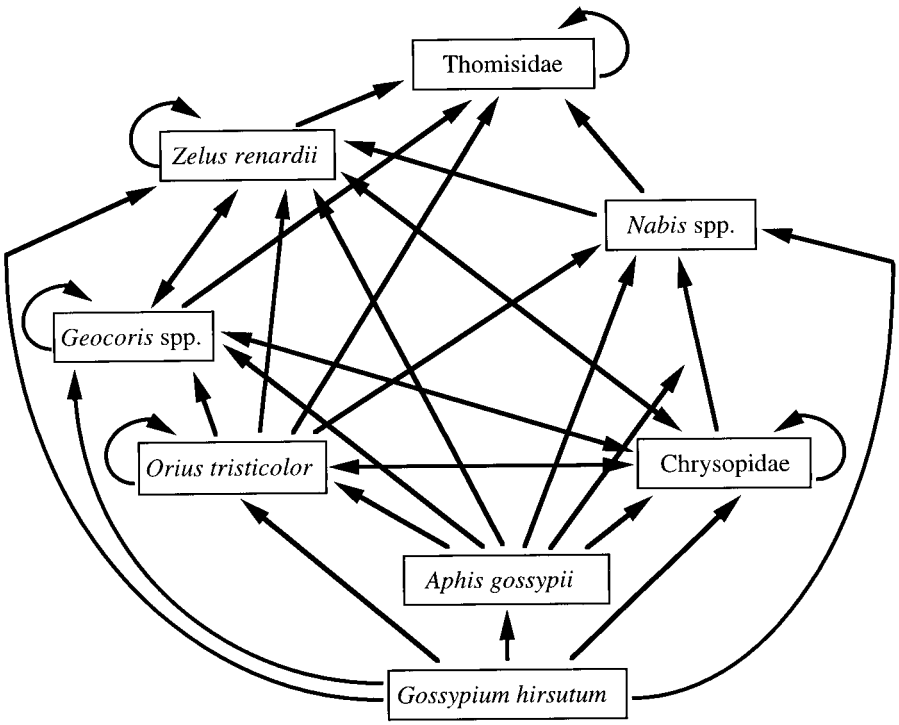

FIG. 1. Simplified trophic web of predatory arthropods associated with the cotton aphid, *Aphis gossypii*, on mid- and late season cotton grown in the Central Valley of California (Rosenheim et al. 1993; J. A. Rosenheim and D. D. Limburg, *unpublished data*).

spp. eggs and each of the larval stages, and higher densities of prepupae and pupae in cocoons. Insect ecologists have long recognized, however, that the age distribution of lacewing populations in cotton is often comprised of high densities of eggs, but low densities of larvae (Whitcomb and Bell 1964, Wilson and Gutierrez 1980). The rarity of the later instar larvae is a practical concern, because it is the second and especially third instars that have the largest capacities to consume prey (Principi and Canard 1984). A large drop in densities between the egg and larval stages could in principle be explained by heavy mortality occurring during the egg or the early larval stages. In either case, this age distribution suggests that local reproductive recruitment of lacewings in many cotton fields may be low, because very few individuals developing in cotton survive to reach the adult stage. Field surveys performed in California during 1993–1994 revealed that, whereas lacewing populations are comprised mostly of eggs and small larvae in fields harboring low to moderate densities of aphids, the age distribution often shifts towards a larger representation of late-instar larvae and pupae at sites harboring outbreak densities of aphids or spider mites (J. Rosenheim, *unpublished data*).

These curious age distributions of predatory lacewings motivated observational and experimental work addressing potential sources of lacewing mortality. Direct observations of predation within the arthropod community on cotton revealed that the trophic web was complex, with many generalist predators consuming not only herbivorous species but also each other (Whitcomb and Bell 1964, Rosenheim et al. 1993, 1995; Fig. 1). In particular, several predatory Hemiptera were observed consuming lacewing larvae in the field. Because these hemipteran predators also compete with lacewing larvae for prey, this form of higher-order predation can be defined more narrowly as intraguild predation (Polis and Holt 1992), but in the remainder of this paper I will retain the more general term ''higher-order predation.'' Inclusion/exclusion experiments conducted on a small spatial scale (single-plant enclosures), a short temporal scale ($\leq$10 d), and at sites harboring low to moderate aphid densities demonstrated that hemipteran predators can impose heavy mortality on *C. carnea* larvae, in some cases releasing aphid populations from effective suppression generated by *C. carnea* alone (Rosenheim et al. 1993, Cisneros and Rosenheim 1997). Focal observations on freely foraging neonate *C. carnea* larvae in the field confirmed the primary result of the field cage experiments: larvae were subject to intense predation by hemipterans, including *Orius tristicolor* (Anthocoridae), *Geocoris pallens* and *Geocoris punctipes* (Lygaeidae), *Nabis* spp. (Nabidae), and *Zelus renardii* (Reduviidae) (Rosenheim et al. 1999). The focal observations also demonstrated that neonate *C. carnea* achieve high and perhaps near maximal rates of aphid consumption when aphids are present at low

densities (as low as 3.9 aphids/leaf). Consistent with this result, the field cage experiments, initiated with ~5–10 aphids/leaf, showed relatively high *C. carnea* survival (~50%) when other predators were excluded, except in the few cases where *C. carnea* subsequently completely exhausted the aphid populations in the enclosures.

These results suggest that the age distribution of lacewings in cotton may be maintained by heavy mortality acting on lacewing larvae, and that in situ reproductive recruitment in cotton fields harboring low to moderate densities of aphid prey is minimal. What then is the source of the lacewing eggs? One possibility is that local recruitment to the adult stage, although low, is sufficient to maintain the observed densities of lacewing eggs. *Chrysoperla* spp. adults maintained under near optimal laboratory conditions can live for 2–3 mo and produce ~1000 eggs (Rousset 1984, Tauber et al. 1993, Zheng et al. 1993). Realized longevity and fecundity under field conditions are, however, unknown. Another possibility is that there is an external source of the adult lacewings observed in cotton fields with moderate prey resources; that is, these fields may be spatially subsidized by adult lacewing immigration (Polis et al. 1997). Candidate source habitats for lacewing populations include other agroecosystems in which higher-order predation is less intense, or perhaps those cotton fields in which herbivore outbreaks create conditions under which predation pressures experienced by lacewing larvae might be relaxed. *Chrysoperla carnea* adults are highly mobile and appear to disperse many kilometers upon eclosion and prior to reproduction (Duelli 1980*a*, *b*); furthermore, the movement pattern of ovipositing females has been described as nomadic, with short flights occurring between successive ovipositions (Duelli 1984). Thus, some cotton fields may be true sinks if immigration exceeds emigration and natality is insufficient to balance mortality over the full range of lacewing densities (Pulliam and Danielson 1991). Cotton fields may be pseudosinks if immigration exceeds emigration, thereby creating local lacewing densities that are so high that lacewing mortality rates are enhanced, exceeding natality (Watkinson and Sutherland 1995). Sink and pseudosink habitats can be distinguished by experimentally isolating them from immigrants: populations in true sink habitats will move to local extinction, whereas populations in pseudosink habitats will decline until they reach levels where density-dependent mortality factors have relaxed sufficiently that natality and mortality are balanced.

Manipulative field experiments conducted with complex communities are rarely subject to only a single interpretation. The experiments described above were conducted over small spatial and temporal scales, and are subject to all the limitations of such work, including in particular the possibility that insect foraging behavior or densities may have been modified by the artificial confinement. The focal observations circumvent the problem of confinement, but treat only one developmental stage (neonates) foraging at one time of the day (daylight hours). Kitchell and Carpenter (1993) and Polis (1994) have suggested that the ''indeterminacy'' of field experiments highlighted by Yodzis (1988) may be partly overcome, however, by combining natural history observation with experimentation conducted at a variety of spatial and temporal scales. In this study I attempt to follow this approach (Table 1).

The overall goal of this work was to test the hypothesis that higher-order predation produces source–sink dynamics in *Chrysoperla* spp. populations. First, I used small-scale experiments to quantify the impact of higher-order predators on *C. carnea* larval survivorship to determine if this predation could be a mechanism creating a sink habitat. This work extended previous results by including tests of additional groups of predators (*Orius tristicolor* and crab spiders, *Misumenops* sp., family Thomisidae) and, most critically, by testing the full, unmanipulated community of generalist predators. These small-scale experiments demonstrated that *C. carnea* larvae are subject to intense predation, and motivated experimentation to determine if higher-order predation could generate sink habitats. Thus, second, I employed larger scale and longer term experiments to test the hypothesis that cotton fields harboring moderate aphid populations are sink habitats for *Chrysoperla* spp. Third, based upon the age structure of *Chrysoperla* spp. populations observed during the large-scale experiments, I explored a second possible mechanism that could make cotton a sink habitat for lacewings: the impact of mortality factors on *Chrysoperla* spp. eggs. Finally, I investigated whether variation in the density of aphid prey can modulate the severity of higher-order predation experienced by *C. carnea* larvae, thereby producing a spatial mosaic of source and sink habitats in cotton agroecosystems.

METHODS

Higher-order predation on C. carnea *larvae: small field enclosures*

1993 Experiment.—This experiment employed small field enclosures to quantify predation on *C. carnea* larvae by five common generalist predators, and the resulting effects on aphid population growth. The experiment was conducted 3–10 August 1993 in an experimental planting of *G. hirsutum* cv. ''Maxxa'' grown at the University of California Shafter Research Station, Kern County, California. Plants were grown without insecticides but otherwise following standard commercial practices, with rows separated by 102 cm.

The top six or seven mainstem nodes of a plant were used as the experimental unit; the only criterion used to select plants for inclusion in the study was that they harbor >80 aphids in their top seven nodes. All plant structures were inspected in the field to (1) count *A. gossypii*; (2) visually estimate the proportion of the

TABLE 1. Overview of the experiments reported in this paper.

Study title	Objective	Date of replicates	Description	Key variables measured
Higher-order predation on *C. carnea* larvae	Quantify predation on larvae as a potential mechanism contributing to the creation of a sink habitat in cotton	1993, 1994	Experimental manipulations of predator communities in small field enclosures	*C. carnea* survival; rate of aphid population growth
Test for spatial subsidy of *Chrysoperla* spp. populations	Determine if cotton fields with moderate aphid densities are sink habitats for *Chrysoperla* spp.	1993, 1994	Experimental manipulations of *Chrysoperla* spp. migration into and out of large field enclosures	*Chrysoperla* spp. population size
Mortality factors acting on *Chrysoperla* spp. eggs	Quantify egg mortality as a potential mechanism contributing to the creation of a sink habitat in cotton	Sep 1994, Oct 1994, Aug 1995	Observational studies following the developmental fates of *Chrysoperla* spp. egg cohorts in the open field	Proportion of *Chrysoperla* spp. eggs hatching successfully
Influence of aphid prey availability and higher-order predation on *C. carnea larvae*	Determine if aphid prey availability modulates the intensity of predation on *C. carnea* larvae, thereby controlling whether cotton habitats act as sinks or sources for *Chrysoperla* spp.	1995	Experimental manipulations of aphid density and predators (fully crossed design) in small field enclosures	*C. carnea* survival, growth, and development

Note: The overall goal of the study was to evaluate the hypothesis that higher-order predation produces source–sink dynamics in populations of *Chrysoperla* spp. lacewings.

lower leaf surface harboring active colonies of spider mites, *Tetranychus* spp.; and (3) in some treatments, remove predatory arthropods. All predators were readily located except for the eggs of *O. tristicolor* and *Nabis* spp., which are imbedded in plant tissue and are therefore very difficult to detect in the field; we made no attempt to remove these eggs. (Because the experiment was short in duration, nymphal *O. tristicolor* and *Nabis* spp. hatching from eggs did not have enough time to grow to a size where they were likely to prey on the experimental lacewings.) The inspected portion of the plant was enclosed in a tapered polyester mesh sleeve (height 58 cm, width at base 50 cm, width at top 19 cm; ''Fibe-Air Sleeve'' [Kleen Test Products, Brown Deer, Wisconsin, USA]), which had an irregular weave with pores sufficiently small to confine insects (largest pores ~0.3 mm).

Plants were assigned sequentially to one of 14 treatments, each replicated 10 times. The first two treatments were controls: (1) no cage control, in which the full arthropod community was left uncaged and without any manipulation; (2) cage control, in which the full arthropod community was caged, but otherwise unmanipulated. In the remaining treatments, all predators were removed and different predator species reintroduced singly and in combination as follows: (3) no predators added; (4) two mid-instar immature crab spiders, *Misumenops* sp., added; (5) two adult *O. tristicolor* added; (6) two adult *Geocoris* sp. added; (7) two adult *Nabis* sp. added; (8) one mid-instar nymph and one adult *Z. renardii* added; (9) three second-instar *C. carnea* added. Treatments 10–14 were identical to treatments 4–8, except that in each case three second-instar *C. carnea* were added in combination with the other predators. *C. carnea* were obtained from the Rincon-Vitova insectary, and were fed on eggs of the moth *Anagasta kuehniella* prior to release into the field enclosures. All other predators were hand collected from *G. hirsutum* on the day of the experiment. No attempt was made to determine the sex of the predators. The densities of predators used in the enclosures were all within commonly observed field densities (which may vary dramatically both spatially and temporally) with two exceptions: densities of crab spiders and adult *Z. renardii* rarely reach the densities used here (J. Rosenheim, *unpublished data*). Nymphal *Z. renardii* can, however, be abundant (Rosenheim et al. 1993), and both nymphal and adult *Z. renardii* can have important impacts on lacewings (Cisneros and Rosenheim 1997). Achieving lower and more realistic densities of crab spiders would have required larger enclosures, but predator manipulations over larger arenas are difficult to establish; the abnormally high densities of spiders did not represent an interpretational problem, however, because they showed no impact on lacewings (see *Results*).

Plant stems were cut and the enclosures brought to the laboratory six days after the setup. Aphids were recounted and spider mite densities estimated as before, and all predators were identified to species. Most of the surviving *C. carnea* had completed the second in-

star and most of the third (final) instar; a few had spun cocoons.

1994 Experiment.—This experiment, conducted between 22 August and 2 September 1994 at the Kearney Agricultural Center, Fresno County, California was designed to replicate the 1993 experiment while employing a more realistic age distribution of *C. carnea* immatures. The methods were identical to those of the 1993 experiment except as noted here.

Cotton was grown on rows separated by 76 cm. The top 6–8 nodes of the plant were enclosed in each enclosure. Cages receiving *C. carnea* were stocked with one second-instar larva (5–7 d old), two first instar larvae (1–3 d old), and three eggs (3–4 d postlaying, and thus within 1–2 d of hatch). *Chrysoperla carnea* eggs and larvae were the offspring of adults collected in cotton and reared in the laboratory. Adults were provided with water and food (sugar and Wheast® [Stauffer Chemical, Visalia, California, USA], a combination of baker's yeast and whey). The *C. carnea* laid eggs on waxed paper which we used to line their cages. Small pieces of waxed paper bearing single eggs were pinned to the underside of leaves harboring aphids within the field enclosures. Larvae were raised in the laboratory by feeding them *A. gossypii* and/or lacewing eggs.

Plants were assigned sequentially to one of 11 treatments, each replicated 8–14 times. Treatment (1) was a no cage control, in which the full arthropod community was left uncaged and unmanipulated. For the remaining treatments, all predators were removed and different predator species reintroduced singly and in combination as follows: (2) no predators added; (3) four adult *O. tristicolor* added; (4) two adult *Geocoris* sp. added; (5) one adult *Nabis* sp. added; (6) one adult *Z. renardii* added; (7) *C. carnea* (six immatures, as described in the preceding paragraph) added. Treatments 8–11 were identical to treatments 3–6, except that in each case *C. carnea* were added in combination with the other predators. Spider mite densities were too low to be quantified accurately. The experiment was run for 10 days.

Test for spatial subsidy of Chrysoperla *spp. populations: large field enclosures*

1993 Experiment.—The goal of this experiment was to determine if cotton fields harboring intermediate densities of aphid prey can be sink or pseudosink habitats for *Chrysoperla* spp. populations. The basic approach was to experimentally isolate a subpopulation of *Chrysoperla* spp. in cotton by blocking adult migration, and to compare its dynamics with that of paired subpopulations that were open to migration. As negative internal controls, I also quantified the effect of blocking migration on populations of the dominant herbivores and hemipteran predators, for which there has never been a suggestion that in situ reproduction in cotton is insufficient to support local populations. The experiment was conducted from 24 August to 5 October 1993 in an experimental planting of *G. hirsutum* cv. ''Maxxa'' grown at the central location of the Shafter Research Station. Plants were grown as described above for the 1993 small field enclosures experiment.

The experimental units were small plots of *G. hirsutum* located within an unbroken larger planting. Plots, comprising two rows of plants, were 1.7 m wide and 9.5 m long and enclosed 204.5 $\pm$ 6.2 plants (mean $\pm$ 1 SE). Three experimental treatments, each replicated four times, were established. In the first treatment (closed cage) the plot was enclosed within a large field cage (1.7 m wide, 1.7 m tall, and 10.0 m long) completely screened with plastic mesh (pore size: 0.46 $\times$ 0.52 mm). Flashing attached to the bottom of the mesh was buried in the soil. Only the central furrow of the plot received irrigation water, which entered the cage through a screened aluminum pipe. The second treatment (open cage) was identical to the first treatment except that the cages had doors, openings 0.9 m wide and 1.7 m tall, at each end to allow lacewings and other arthropods to move through the cage. The third treatment (no cage) had no cage present. The treatments were chosen so that a comparison of the open cages vs. the closed cages would provide a test of the role of migration, and a comparison of the open cages vs. the no cage controls would provide a test of cage effects.

To install the cages with minimal disturbance to the resident predators, we used the following protocol. On the day prior to the start of the experiment, the metal framework of each cage was carried to the field and set in place. The mesh was placed alongside the length of the cage on the ground. The plots were then left undisturbed for ~24 h to allow the arthropods to redistribute themselves and recover from any disturbance caused by the cage transport. We then returned to the plots and gingerly lifted the mesh over the metal framework, attempting to minimize contact with the plants. Informal observations suggested that adult lacewings, which are the most easily disturbed of the mobile predators, were essentially unaffected by the process of setting up the mesh.

Upon the establishment of the treatments and at approximately weekly intervals thereafter each plot was sampled to quantify herbivore and predator densities. Twenty leaves from the fifth mainstem node position were sampled into alcohol and returned to the laboratory, where they were hand washed over a sieve (openings 75 μm^2) to collect all foliar arthropods. These samples were then counted under a stereoscope. Because *A. gossypii* exhibits a large amount of phenotypic plasticity (changing body size, color, and demographic parameters in response to changing climate and host plant condition; Wilhoit and Rosenheim 1993), aphid body length was measured for up to 10 haphazardly selected adult apterous *A. gossypii* per sample. Twenty plants were selected at regular inter-

vals across each plot, and the top six nodes carefully searched in the field to count all lacewing eggs and motile stages of hemipteran predators.

Informal observations revealed that some adult *Z. renardii* were foraging on both the plants and on the cage walls, and we observed an adult lacewing being captured on the cage. Other predators appeared to be foraging naturally on the plants. Although adult *Z. renardii* has been observed consuming adult lacewings in unmanipulated cotton plantings (Cisneros and Rosenheim 1998; J. A. Rosenheim, *unpublished data*), the cage walls might create unnatural opportunities for these predation events. At the end of the second week of the experiment, by which time treatment effects had already been established, two changes were therefore implemented. First, the two cage treatments were switched; that is, the cages that had been closed were opened, and the cages that had been open were sealed. This provided a second test of the influence of migration on *Chrysoperla* spp. egg densities. Second, at 1–3 d intervals for the remaining 4 wk of the experiment, the closed cages were searched, and any adult *Z. renardii* found on the cage walls (and a small number of adults found on the plants, where they were much more difficult to detect) were removed. A mean of 13.5 ± 1.3 adult *Z. renardii* were removed per cage. These removals were not attempted in the open cages (which would have been rapidly recolonized), and therefore should have made the experiment more conservative with respect to demonstrating that isolated *Chrysoperla* spp. populations would decline in density.

In the closed cage treatment only, adult lacewings were counted at the start of the experiment and at the end of the second week (before switching the cage treatments) by shaking all the plants in the cages and carefully hand capturing the lacewings in small vials when they flew to the cage walls. Lacewings were released back into the cage when the counts were complete. Although this procedure did not appear to affect the lacewings adversely, these counts were not repeated during the second phase of the experiment (after the treatments were switched).

To assess the effects of the cages on microclimatic conditions, I measured three parameters. First, plant canopy temperature readings were measured at three evenly spaced locations within each plot with an infrared thermometer during the normal weekly sampling. Second, I measured the number of nodes of new growth (regrowth) produced by 20 plants per plot at the end of the experiment. Cotton plants typically cease vegetative growth in August when fruit are maturing and undergo regrowth as fruit maturation is completed if growing conditions are suitable; regrowth is a useful index of late-season plant vigor. Third, as described above, aphid body size, which responds sensitively to abiotic and host plant conditions, was quantified.

The cotton field in which the experimental plots were located was sampled weekly to describe the predatory arthropod community. Five to ten randomly selected plants were clipped at the base, carried to the edge of the field, and all plant structures searched for lacewing eggs (singly deposited eggs from *Chrysoperla* spp. and group-deposited eggs from *C. nigricornis* were recorded separately), larvae, and cocoons; nymphal and adult Hemiptera; and spiders. These whole-plant searches underestimate the densities of adult *Nabis* spp. and *Zelus* spp., which tend to fly off plants being handled. As a complementary sampling approach, six to ten sweep-net samples, each comprised of ten sweeps of a 38.1 cm diameter insect net through the upper plant canopy, were taken weekly. On 31 August and 28 September, samples of adult lacewings were hand netted and identified in the laboratory to determine species composition.

1994 Experiment.—The experiment was repeated 17 August to 27 September 1994 in a cotton field located 1.5 km southwest of the location of the 1993 trial, using the same procedures except as noted here. Experimental plots contained 182.4 ± 3.2 plants (mean ± 1 SE). The lacewing species composition was determined by identifying adults captured in the closed cages during the initial lacewing census and, for the *Chrysoperla* spp., by rearing samples of singly laid eggs collected weekly in the experimental field for identification as first instar larvae. A mean of 41.5 ± 6.9 adult *Z. renardii* found on the walls of the closed cages were removed in searches conducted at intervals of 1–3 days throughout the trial. The open and closed cage treatments were not switched during the experiment, which was terminated unexpectedly when the plot was accidentally sprayed with a chemical defoliant. This precluded the final sampling of cages for adult lacewing densities.

Mortality factors acting on Chrysoperla *spp. eggs*

We followed the development of field cohorts of freshly laid *Chrysoperla* spp. eggs to quantify the impact of mortality factors. Between 12 and 20 plants were carefully searched on day 0 of each trial, and the locations of all *Chrysoperla* spp. eggs were marked with a paint pen near the base of the egg stalk. On day 1 the plants were searched again to find eggs that had been laid during the intervening night. These eggs were individually labeled and monitored daily for up to 14 d to record their fate. At the end of the trial, all eggs (or egg shells) were returned to the laboratory and inspected under a microscope to determine their fate. Parasitized eggs turned gray, and emerging parasitoids produced distinctive round exit holes. Eggs consumed by predators with piercing/sucking mouthparts appeared collapsed, with small traces of egg yolk remaining within. Inviable eggs did not go through the color changes (green to tan) that accompany normal embryogenesis, and after a long time in the field eventually collapsed. Egg chorions from which *Chrysoperla* spp. successfully emerged were devoid of residual yolk

TABLE 2. Results of the 1993 experiment: influence of predators on *C. carnea* survivorship and aphid population growth.

Treatment	Initial aphid density	Final aphid density	*Orius tristicolor* nymphs	*Orius tristicolor* adults	*Geocoris* spp. nymphs
No cage	131 ± 10	294 ± 41	0.4 ± 0.2	0.8 ± 0.4	0.5 ± 0.3
Cage without any manipulation	135 ± 11	487 ± 133	1.0 ± 0.8	0.2 ± 0.1	0.5 ± 0.2
Aphids only	155 ± 11	459 ± 65	0.8 ± 0.3	0.2 ± 0.1	0.3 ± 0.2
Thomisidae	131 ± 9	433 ± 51	1.2 ± 0.9	0.2 ± 0.1	0.1 ± 0.1
Orius	150 ± 10	397 ± 57	1.5 ± 0.6	0.9 ± 0.3	0.5 ± 0.2
Geocoris	152 ± 11	431 ± 89	0.2 ± 0.2	0.1 ± 0.1	0.2 ± 0.1
Nabis	157 ± 20	245 ± 38	1.3 ± 0.5	0.2 ± 0.1	0.1 ± 0.1
Zelus	142 ± 12	403 ± 53	0.9 ± 0.3	0.0 ± 0.0	0.3 ± 0.2
C. carnea	153 ± 10	151 ± 58	0.6 ± 0.3	0.1 ± 0.1	0.0 ± 0.0
C. carnea + Thomisidae	131 ± 8	66 ± 20	0.2 ± 0.2	0.1 ± 0.1	0.0 ± 0.0
C. carnea + *Orius*	144 ± 7	58 ± 24	0.5 ± 0.3	0.8 ± 0.3	0.2 ± 0.1
C. carnea + *Geocoris*	137 ± 8	104 ± 34	0.4 ± 0.3	0.3 ± 0.2	0.0 ± 0.0
C. carnea + *Nabis*	134 ± 10	162 ± 25	0.3 ± 0.2	0.0 ± 0.0	0.5 ± 0.2
C. carnea + *Zelus*	141 ± 9	382 ± 56	0.7 ± 0.2	0.0 ± 0.0	0.1 ± 0.1
P	0.6	<0.0001	0.4	0.01	0.1

Notes: Values shown are densities of live aphids (number per experimental unit; *see Methods: ...1993 experiment*) at the beginning and end of the experiment and densities of predators at the end of the experiment in the 14 experimental treatments (means ± 1 SE). *P* values are for a Kruskal-Wallis rank-sums test.

† This value may underestimate the true mean because this predator often flies off of plants being handled.

and exhibited distinctive, longitudinal tears. Trials were initiated on 12 September 1994 in the same Shafter field where the large field enclosure study was in progress; on 5 October 1994 at the University of California, Davis Student Experimental Farm, Yolo County, in an insecticide-free cotton planting (cv. ''Maxxa''); and on 9 August 1995 in an organic cotton field (cv. ''Maxxa'') in Merced County, California.

Influence of aphid prey availability and higher-order predation on C. carnea *larvae*

This experiment had three goals. First, the experiment was designed to assess the relative importance of bottom-up influences (using treatments with intermediate vs. high densities of aphid prey) and top-down influences (using treatments with higher-order predators present vs. absent) on the performance of *C. carnea* larvae. Second, by employing the fully crossed design advocated by Polis (1994) and Osenberg and Mittelbach (1996), the experiment provided a formal test of interaction of bottom-up and top-down effects. Third, the experiment evaluated the hypothesis that cotton fields with outbreak densities of aphid prey might be sites where *C. carnea* larval survivorship is enhanced, and which might therefore function as source habitats for *C. carnea.*

The experiment was performed from 24 July to 4 August 1995 at the Shafter Research Station in a cotton plot harboring an aphid outbreak. The techniques followed those described for the 1993 experiment on higher-order predation, with the following modifications. The top five or six nodes of plants that harbored high aphid densities were carefully searched to remove all predators, and enclosed in polyester mesh bags. Each cage received a single neonate (0–24 h old) *C. carnea* larva. Only a single *C. carnea* was released per cage to avoid confounding the effects of interspecific predation and cannibalism. The low *C. carnea* to aphid ratios, however, precluded the ability of *C. carnea* to suppress aphid population growth, and thus the focus of this experiment was on *C. carnea* performance rather than herbivore population dynamics. *Chrysoperla carnea* were the offspring of field-collected females, reared as described in *Methods: Higher-order predation on* C. carnea *larvae: small field enclosures: 1994 experiment,* and fed on either aphids or *C. carnea* eggs (larvae are cannibalistic) before release into the cages.

Plants were assigned sequentially to one of four treatments, each replicated 36 or 37 times: (1) intermediate aphid density, predators absent; (2) high aphid density, predators absent; (3) intermediate aphid density, predators present; and (4) high aphid density, predators present. For the high aphid density treatment, all aphids naturally present on the plants were retained. Initial aphid densities per cage were estimated by counting all aphids on one quartile of every other leaf in the enclosure (leaf veins divide the leaf into quartiles; within each cage, counts were rotated through quartiles 1, 2, 3, and 4). For the intermediate aphid density treatment, a paint brush was used to remove aphids until ~5–10 aphids remained on each leaf, and all remaining aphids were counted. Any mite colonies observed were also removed in the intermediate aphid density treatments by brushing. The predators present treatments received one adult *O. tristicolor,* one adult *G. pallens,* and one adult *Nabis* sp., all of which were collected in adjacent cotton or alfalfa within a few hours of release in the cages.

Cages were left in the field for 9 d, at which time the plant stems were cut, the cages brought to the laboratory, and their contents searched for all living and dead predators. Aphids were recounted using the same sampling procedure used at the start of the experiment. All surviving *C. carnea* had reached either the final

TABLE 2. Extended.

Geocoris spp. adults	*Nabis* spp. nymphs	*Nabis* spp. adults	*Zelus* nymphs	*Zelus* adults	Thomisidae
0.6 ± 0.3	0.1 ± 0.1	0.0 ± 0.0†	0.0 ± 0.0	0.0 ± 0.0†	0.0 ± 0.0
0.9 ± 0.4	0.3 ± 0.2	0.0 ± 0.0†	0.0 ± 0.0	0.0 ± 0.0†	0.0 ± 0.0
0.1 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.1 ± 0.1	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.6 ± 0.2
0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
2.1 ± 0.1	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	0.1 ± 0.1	1.7 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.2	0.0 ± 0.0
0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.6 ± 0.2
0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
1.8 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	0.0 ± 0.0	1.7 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	1.0 ± 0.0	0.0 ± 0.0
<0.0001	0.3	<0.0001	0.5	<0.0001	<0.0001

(third) larval stage or had recently spun a cocoon. *Chrysoperla carnea* developmental stage was recorded, and living larvae and cocoons were weighed to the nearest 10 μg. Thus, the experiment provided measures of *C. carnea* survival, development, and growth rate. In a few enclosures, I found lacewing larvae at the close of the experiment that I could infer were not the individuals I had released, because they were either other species or because they were much younger (the younger individuals probably developed from eggs that I failed to detect when cleaning the plants at the start of the experiment). I excluded from the analysis all *C. carnea* that weighed <5.00 mg (there was a pronounced discontinuity in the size distribution of *C. carnea* larvae at approximately 7.00 mg, with only two larvae weighing between 5.00 and 7.00 mg), and simply retained those few replicates in which two large *C. carnea* were found.

Statistical analyses

Chrysoperla carnea survival and aphid population growth (expressed as daily per capita change in population size: [(final aphid count − initial aphid count)]/[(initial aphid count)×(duration of experiment, in days)]) in the higher-order predation experiments (small field enclosures) were analyzed with Kruskal-Wallis rank-sum tests and planned pairwise contrasts using two-tailed Wilcoxon rank-sum tests. In analyzing aphid population growth, I allocated $\alpha = 0.05$ to tests of single predator species vs. the no-predator control, and an additional $\alpha = 0.05$ for tests of predator combinations vs. *C. carnea* alone; Bonferroni's inequality was used to correct for multiple comparisons. To test for interactions between the effects of predators on aphid population growth, I used the multiplicative risk model (Soluk and Collins 1988, Sih et al. 1998), implemented by transforming aphid population growth rates as ln[(final number of aphids + 1)/(initial number of aphids)] and conducting a fully crossed two-way ANOVA. The large field enclosure experiments were analyzed using multivariate repeated-measures ANOVA (von Ende 1993) implemented with JMP 3.1.5 (SAS Institute 1995). I used the sum response design to obtain a test of the overall treatment effect and the contrast response design to obtain a test of the treatment × time interaction. These tests were followed by planned two-tailed pairwise contrasts of open vs. closed cage treatments (migration effect) and open cage vs. no cage treatment (cage effect), again employing the Bonferroni correction to maintain overall $\alpha = 0.05$. I used stepwise polychotomous logistic regression to evaluate the main and interactive effects of aphid density and higher-order predation treatments on survivorship of larval *C. carnea* in the small field enclosures. Although I released only one *C. carnea* larva per cage, the response variable (number of *C. carnea* present at the end of the trial) was coded as 0, 1, or 2, to accommodate the few replicates in which I failed to exclude all naturally resident *C. carnea.* Stepwise dichotomous logistic regression was used to test the influences of aphid density treatment, predator presence, and the interaction of aphids and predators on the likelihood that *C. carnea* would reach the cocoon stage in the small cage enclosures in 1995. Throughout the text, summary statistics are presented as the mean ± 1 SE.

RESULTS

Higher-order predation on C. carnea *larvae: small field enclosures*

1993 Experiment.—The experimental manipulations successfully produced different densities of adult predators in different treatments (Table 2). Immature stages of hemipteran predators, which I had attempted to remove from the cages, were present at low densities in many treatments, due both to the difficulty of finding early instar nymphs during predator removals (for *Geocoris* spp.) and to recruitment from eggs laid in plant tissue (for *O. tristicolor* and *Nabis* spp.); in no case, however, were there significant differences in nymphal

TABLE 3. Results of the 1994 experiment; influence of predators on *C. carnea* survivorship and aphid population growth.

Treatment (no. replicates)	Initial aphid density	Final aphid density	*Orius tristicolor* nymphs	*Orius tristicolor* adults
No cage(10)†	116 ± 8	234 ± 54	…	…
Aphids only (14)	110 ± 8	247 ± 49	7.4 ± 1.0	0.3 ± 0.1
Orius (10)	123 ± 9	204 ± 49	10.8 ± 1.4	1.6 ± 0.5
Geocoris (10)	132 ± 12	273 ± 59	4.3 ± 0.6	0.0 ± 0.0
Nabis (10)	114 ± 11	204 ± 58	6.7 ± 1.4	0.4 ± 0.2
Zelus (9)	142 ± 11	388 ± 89	9.9 ± 2.4	0.3 ± 0.2
C. carnea (9)	123 ± 12	15 ± 6	1.3 ± 0.5	0.8 ± 0.5
C. carnea + *Orius* (10)	131 ± 11	18 ± 8	4.1 ± 1.1	0.8 ± 0.5
C. carnea + *Geocoris* (9)	131 ± 7	73 ± 29	0.6 ± 0.3	0.2 ± 0.1
C. carnea + *Nabis* (10)	141 ± 14	39 ± 9	3.2 ± 0.8	0.0 ± 0.0
C. carnea + *Zelus* (8)	123 ± 10	106 ± 33	6.0 ± 1.8	0.0 ± 0.0
P	0.3	<0.0001	<0.0001	0.0022

Notes: Values shown are densities of live aphids (number per experimental unit; see *Methods: ...1993 experiment*) at the beginning and end of the experiment and densities of predators at the end of the experiment in the 11 experimental treatments (means ± 1 SE). *P* values are for a Kruskal-Wallis rank-sums test.

† Predator densities not quantified for this uncaged treatment, because predator dispersal during plant handling would likely lead to consistent underestimates.

predator densities across treatments (Table 2). Nymphal *Z. renardii* did not survive in the *Z. renardii* treatment, perhaps as a result of cannibalism. Species composition of predators recovered from all enclosures at the end of the experiment was: for *Geocoris* spp., 97% *G. pallens* and 3% *G. punctipes*; for *Nabis* spp., 71% *N. alternatus* and 29% *N. americoferus.*

Chrysoperla carnea larval survival varied strongly across treatments (Fig. 2A; $\chi^2 = 36.3$, $P < 0.0001$), exhibiting a marginally nonsignificant decline in the presence of *Geocoris* spp. and a strong decline in the presence of *Nabis* spp. or *Z. renardii.* These declines occurred despite a greater availability of aphid prey in treatments where *C. carnea* were combined with *Nabis* spp. or *Z. renardii*, and thus appear to reflect direct predation on *C. carnea* rather than enhanced competition.

Final aphid densities varied strongly across treatments (Table 2), but at least moderate aphid populations persisted in all treatments, minimizing the likelihood of severe food limitation for predators. Aphid populations grew vigorously in the treatments where all predators were excluded (Fig. 2B, per capita aphid population growth rate per day = 0.34 ± 0.08, i.e., daily increase in aphid numbers of 34%). Aphid populations also grew rapidly, however, where the full predator community was left uncaged (population growth rate = 0.22 ± 0.05) or caged without manipulation (population growth rate = 0.38 ± 0.10), suggesting that the full predator community at this site was exerting minimal suppression on aphid populations. This result was observed despite the fact that the uncaged plants harbored a mean of 3.4 ± 0.9 *Chrysoperla* spp. eggs (total on top six to seven nodes) when censused at the close of the experiment, suggesting a substantial potential in the absence of higher-order predation for recruitment of *Chrysoperla* spp. larvae. The cage effect was nonsignificant (comparison of no cage vs. cage control, $\chi^2 = 2.3$, $P = 0.13$).

Of the predators tested singly, four species had minimal and nonsignificant influences on aphid dynamics: *Misumenops* sp., *O. tristicolor, Geocoris* spp., and *Z. renardii* (Fig. 2B, $\chi^2 \leq 0.4$, $P > 0.5$ in each case). *Nabis* spp. generated moderate suppression ($\chi^2 = 7.0$, $P = 0.008$), and *C. carnea* arrested aphid population growth almost entirely ($\chi^2 = 10.1$, $P = 0.002$). When predators were combined with *C. carnea* strong aphid population suppression was retained in all cases, with nonsignificant differences from the effects of *C. carnea* alone, with one exception: *Z. renardii* released aphid populations from the control exerted by *C. carnea* alone (Fig. 2B). Formal tests for statistical interaction using two-way ANOVA on ln-transformed data yielded evidence of significant interaction of *C. carnea* larvae only with *Z. renardii* ($F_{1,36} = 9.9$, $P = 0.003$). The interaction with *Nabis* spp. was marginally nonsignificant ($F_{1,36} = 6.8$, $P = 0.0133$, compared to the Bonferroni critical *P* value of 0.0125), and interaction terms for *Misumenops* sp., *O. tristicolor*, and *Geocoris* spp. were nonsignificant ($F_{1,36} \leq 1.9$, $P \geq 0.2$). Initial and final densities of spider mites, *Tetranychus* spp., were low (treatment means <3% leaf area with active mite colonies), and final densities did not vary significantly between treatments ($P = 0.6$).

1994 Experiment.—The experimental manipulations again produced distinctly different densities of predators in different treatments (Table 3). Nymphal *Geocoris* spp., *Nabis* spp., and *Z. renardii* were successfully excluded from the experimental cages, however a large number of *O. tristicolor* nymphs were found in cages at the end of the experiment, likely the result of hatching from eggs, which are laid in plant tissue. *Orius tristicolor* nymphal densities were, however, found to have nonsignificant effects on *C. carnea* survival and per capita aphid population growth rate, after controlling for treatment effects (ANCOVA, $F_{1,88} = 0.1$, $P = 0.8$; $F_{1,88} = 0.3$, $P = 0.6$, respectively). Species composition for predators sampled at the start of the ex-

TABLE 3. Extended.

Geocoris spp. nymphs	*Geocoris* spp. adults	*Nabis* spp. nymphs	*Nabis* spp. adults	*Zelus renardii* nymphs	*Zelus renardii* adults
…	…	…	…	…	…
0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.3 ± 0.2	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	1.9 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.1
0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.1 ± 0.1	1.7 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	1.0 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
0.3 ± 0.2	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	0.4 ± 0.4	1.0 ± 0.0
0.6	<0.0001	0.3	<0.0001	0.3	<0.0001

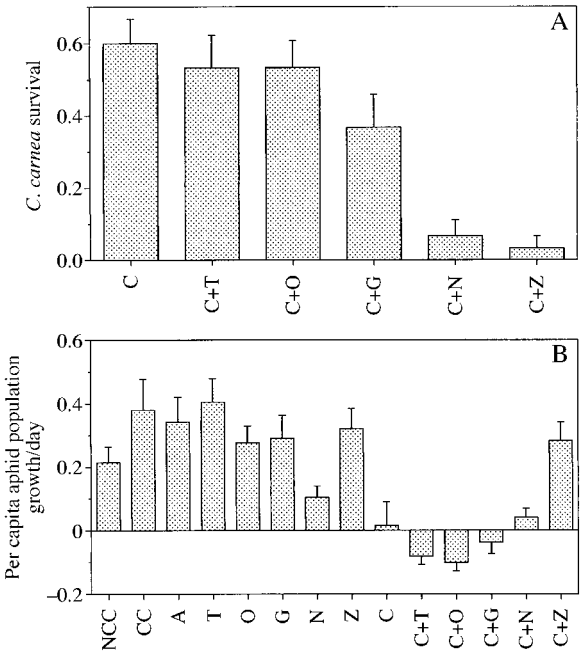

FIG. 2. Higher-order predation on *C. carnea* larvae by generalist predators in small field enclosures, 1993. (A) Mean + 1 SE proportion of *C. carnea* larvae surviving. Wilcoxon rank-sum tests comparing single predator species vs. the *C. carnea* only treatment, using Bonferroni's critical *P* value of 0.05/7 = 0.007: effect of Thomisidae, $\chi^2 = 0.4$, $P = 0.7$; *O. tristicolor*, $\chi^2 = 0.5$, $P = 0.6$; *Geocoris* spp., $\chi^2 = 4.3$, $P = 0.04$; *Nabis* spp., $\chi^2 = 14.1$, $P = 0.0002$; *Z. renardii*, $\chi^2 = 15.3$, $P = 0.0001$. (B) Mean + 1 SE per capita aphid population growth rate per day, calculated as (final aphid count − initial aphid count)/[(initial aphid count) × (duration of experiment, in days)]. Wilcoxon rank-sum tests comparing predator species combinations vs. the *C. carnea* only treatment, using Bonferroni's critical *P* value of 0.01: effect of Thomisidae, $\chi^2 = 0.8$, $P = 0.4$; *O. tristicolor*, $\chi^2 = 2.5$, $P = 0.11$; *Geocoris* spp., $\chi^2 = 0.0$, $P = 0.9$; *Nabis* spp., $\chi^2 = 1.5$, $P = 0.23$; *Z. renardii*, $\chi^2 = 7.0$, $P = 0.008$. Treatments: NCC, no cage control; CC, cage control; A, aphids only (no predators added); T, Thomisidae; O, *O. tristicolor*; G, *Geocoris* spp.; N, *Nabis* spp.; Z, *Z. renardii*; C, *C. carnea*; C+T, *C. carnea* + Thomisidae; C+O, *C. carnea* + *O. tristicolor*; C+G, *C. carnea* + *Geocoris* spp., C+N, *C. carnea* + *Nabis* spp.; C+Z, *C. carnea* + *Z. renardii*.

periment was: for *Geocoris* spp., 100% *G. pallens* and for *Nabis* spp., 100% *N. alternatus*.

Chrysoperla carnea larval survivorship was substantially depressed in those treatments that demonstrated relatively high survival in the 1993 experiment. The low survival appears to have been due to enhanced competition for prey. The mean aphid population growth rate in the absence of predators (0.12 ± 0.04) in 1994 was only 35% of that observed in 1993 (0.34 ± 0.08), which apparently allowed *C. carnea* to drive aphid populations to very low densities in those treatments where *C. carnea* survival was expected to be high (*C. carnea* only, *C. carnea* + *O. tristicolor*). In these treatments, final aphid densities were extremely low (Table 3), which may have led to starvation or, as was observed in casual field observations, cannibalism by the older instars on younger larvae. *Chrysoperla carnea* survival still exhibited significant variation across treatments (Fig. 3A, $\chi^2 = 9.3$, $P = 0.05$), due to a significant drop in survival in the presence of *Z. renardii*. The lower survival in the *C. carnea* + *Z. renardii* treatment occurred against a backdrop of higher availability of aphid prey (Table 3), suggesting that *Z. renardii* were preying on *C. carnea* rather than outcompeting them for food.

The cotton field in which this experiment was conducted had a naturally high density of *Chrysoperla* spp. eggs; at the initiation of the trial, the top of the plants used for the no-cage controls (encompassing the top six to eight nodes) harbored a mean of 9.5 ± 2.4 *Chrysoperla* spp. eggs. Nevertheless, the sampling revealed a mean of only 1.0 ± 0.7 lacewing larvae per plant; 8 of the 10 larvae found appeared to be neonates (2 mm long), and the other two were also first or early second instars (body lengths of 3 mm and 4 mm). Thus, despite high densities of *Chrysoperla* spp. eggs, recruitment of larvae to the later instars, which exert the predominant impact on aphid populations, appeared to be minimal under unmanipulated field conditions. The no-cage control demonstrated rates of aphid population growth that were not significantly lower than those observed in the aphids-only treatment (Fig. 3B, $\chi^2 = 0.2$, $P =$

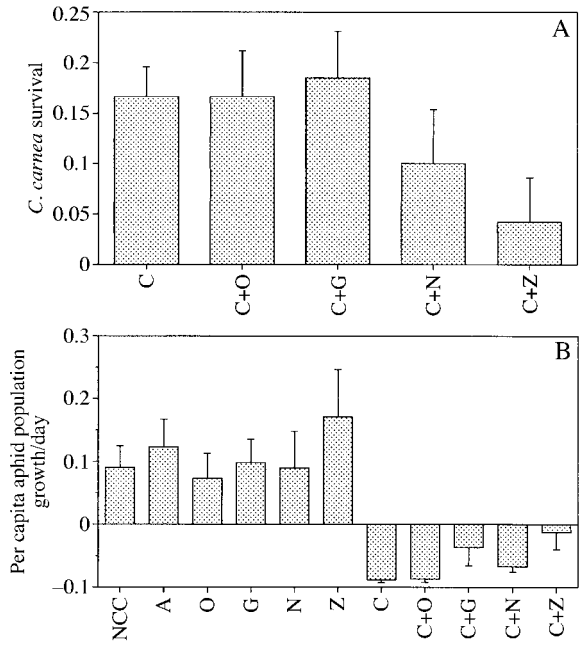

FIG. 3. Higher-order predation on *C. carnea* larvae by generalist predators in small field enclosures, 1994. (A) Mean + 1 SE proportion of *C. carnea* larvae surviving. Wilcoxon rank-sum tests comparing single predator species vs. the *C. carnea* only treatment, using Bonferroni's critical *P* value of 0.0125: effect of *O. tristicolor*, $\chi^2 = 0.0$, $P = 1.0$; *Geocoris* spp., $\chi^2 = 0.2$, $P = 0.7$; *Nabis* spp., $\chi^2 = 3.1$, $P = 0.08$; *Z. renardii*, $\chi^2 = 6.4$, $P = 0.011$. (B) Mean + 1 SE per capita aphid population growth rate per day, calculated as [(final aphid count) − (initial aphid count)]/[(initial aphid count) × (duration of experiment, in days)]. Wilcoxon rank-sum tests comparing predator species combinations versus the *C. carnea* only treatment, using Bonferroni's critical *P* value of 0.01: effect of *O. tristicolor*, $\chi^2 = 0.1$, $P = 0.7$; *Geocoris* spp., $\chi^2 = 3.6$, $P = 0.06$; *Nabis* spp., $\chi^2 = 3.5$, $P = 0.06$; *Z. renardii*, $\chi^2 = 9.2$, $P = 0.002$. See the legend to Fig. 2 for explanations of treatment abbreviations.

0.6), demonstrating that the full predator community was not generating substantial aphid suppression. This is a striking result, given the high density of *Chrysoperla* spp. eggs that were present naturally on these plants. None of the hemipteran predators tested singly produced significant suppression of aphid populations (Fig. 3B, $\chi^2 \leq 0.4$, $P \geq 0.5$ in each case). As observed in 1993, *C. carnea* when tested alone was the most effective control agent of aphids, in this case driving aphid populations to very low levels ($\chi^2 = 13.3$, $P = 0.0003$). Effective suppression of aphid populations was retained when *C. carnea* were combined with *O. tristicolor*. Strong suppression was also observed when *C. carnea* were combined with *Geocoris* spp. or *Nabis* spp., although with a marginally nonsignificant trend towards increased aphid densities. As observed in 1993, the effective suppression of aphids generated by *C. carnea* alone was significantly disrupted in the presence of *Z. renardii*. Formal statistical tests for predator interaction using two-way ANOVA yielded evidence of significant interactions of *C. carnea* only with *Z. renardii* ($F_{1,37} = 7.4$, $P = 0.01$). Interaction terms for *O. tristicolor*, *Geocoris* spp., and *Nabis* spp. were nonsignificant ($F_{1,39} = 0.2$, $P = 0.6$; $F_{1,39} = 3.3$, $P = 0.08$; and $F_{1,40} = 3.8$, $P = 0.06$, respectively).

Test for spatial subsidy of Chrysoperla *spp. populations: large field enclosures*

1993 Experiment.—The age structure of the lacewing population at the field site over the course of the six-week experiment was characterized by high densities of *Chrysoperla* spp. eggs, very few lacewing larvae, and no detectable lacewing pupae (Fig. 4). Egg-to-pupal developmental success rates in this population appeared, therefore, to be near zero. On 31 August the field harbored four lacewing species, *C. carnea* (29/51 = 57%), *C. comanche* (22%), *Chrysopa nigricornis* (18%), and *Chrysopa oculata* (4%). By 28 September, *C. comanche* had become the dominant species (41/66 = 62%), as occurs routinely towards the end of the growing season, with *C. carnea* (18%), *C. nigricornis* (18%), and *Chrysopa coloradensis* (2%) also present. A diverse community of hemipteran predators was also established at this site (Table 4A).

The closed cages contained a mean of 24.8 ± 2.8 lacewing adults when established on 24 August. During the first two weeks of the experiment, densities of *Chrysoperla* spp. eggs in the closed cages showed strong and highly significant declines relative to the open cages (Fig. 5A, Table 5). By week 2, a mean of 12.0 ± 3.5 adult lacewings remained per closed cage. When

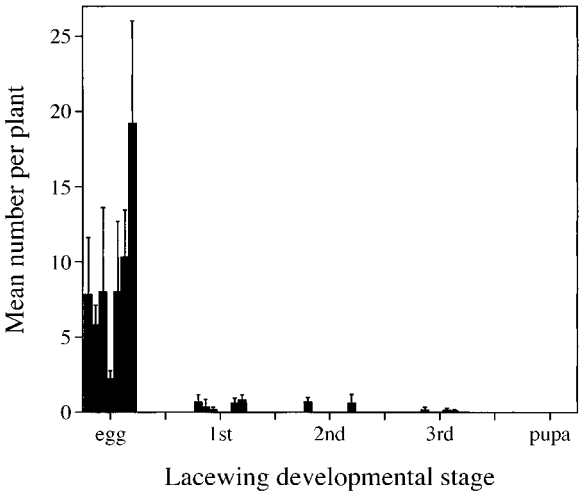

FIG. 4. Age structure of the lacewing community at the field site of the 1993 experiment on spatial subsidy of *Chrysoperla* spp. populations. Shown are the mean + 1 SE densities of lacewing eggs (singly laid *Chrysoperla* spp. eggs only), three larval instars, and pupae during seven weekly samples, 25 August–5 October 1993. Lacewing instars were estimated from body length (2–3 mm, first instar; 4–6 mm, second instar; ≥7 mm, third instar).

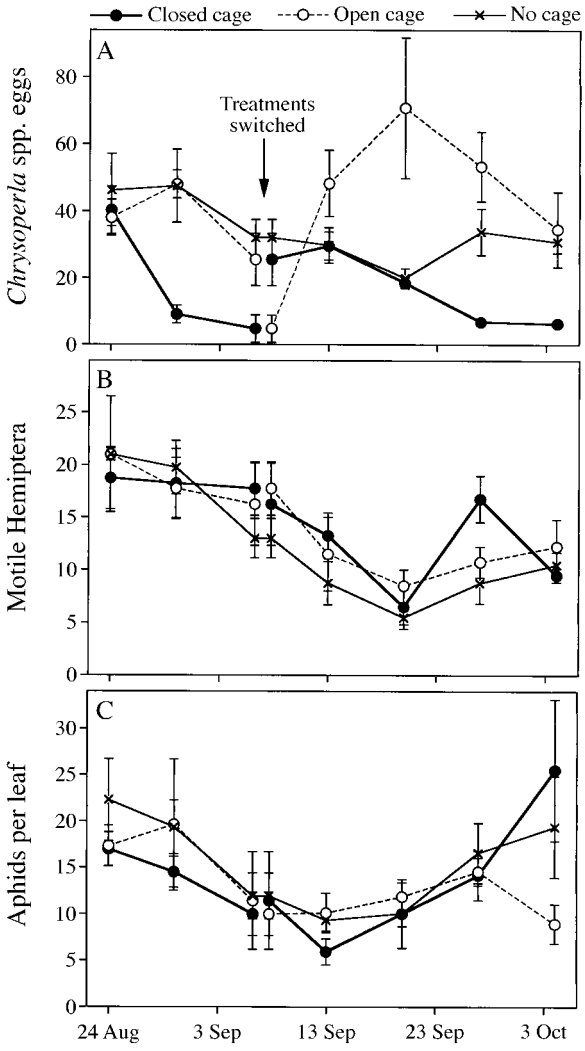

FIG. 5. Spatial subsidy of *Chrysoperla* spp. populations in the cotton agroecosystem: large enclosure experiment, 1993. The two cage treatments (open and closed) were switched after taking samples in week 2. Mean ± 1 SE density of (A) *Chrysoperla* spp. eggs and (B) nymphal and adult hemipteran predators, *O. tristicolor, Geocoris* spp., *Nabis* spp., and *Z. renardii*, in a sample of the top six nodes of 20 plants per plot. (C) Mean ± 1 SE number of aphids per leaf (sampled at the fifth mainstem node).

the cage treatments were switched after the second week's census, *Chrysoperla* spp. egg densities in the newly opened cages increased strongly, while the *Chrysoperla* spp. egg densities in the newly sealed cages again showed a large and highly significant decline (Fig. 5A). In both phases of this experiment, *Chrysoperla* spp. populations appeared to rely on spatial subsidy to maintain their naturally observed densities.

These strong and repeatable influences of migration on *Chrysoperla* spp. egg densities were not observed for hemipteran predators or aphids (Fig. 5B, C; Table 5). Densities of other herbivorous arthropods, including whiteflies, spider mites, and thrips, were also unaffected by the experimental treatments (data not shown).

What mechanism(s) might underlie the declining densities of *Chrysoperla* spp. eggs in subpopulations isolated from immigration? Prey did not appear to be limiting at any time during the experiment; aphid densities were always well above 3.9 aphids per leaf (Fig. 5C), a density at which aphid consumption rates by *C. carnea* appear to be nearly saturated (Rosenheim et al. 1999). Other potential prey were also present at moderate densities (Mean numbers per leaf across all treatments, weeks 0–2: thrips, 0.18 ± 0.04; mites, 1.1 ± 0.3; whiteflies, 1.9 ± 0.2. Mean numbers per leaf across all treatments, weeks 2–6, thrips, 0.05 ± 0.02; mites, 1.0 ± 0.2; whiteflies, 8.1 ± 0.6). Two sources of egg mortality appeared to be of minor importance: in samples of singly laid eggs collected weekly in the experimental field and reared in the laboratory, 7.6% (17/224) died without hatching and 0.9% (2/224) yielded parasitoid wasps.

Cage effects also appeared to be relatively minor. Although both the open and closed cages altered the daily temperature cycles when compared to the no cage controls (plant canopy temperatures were 0–4°C cooler during the midday hours and 1°C warmer in the early morning and evening), temperatures in the open and closed cages were nearly identical (data not shown). Aphid body size, a trait that responds to variation in abiotic conditions and host plant quality, did not vary between treatments during either phase of the experiment (data not shown). Plant regrowth varied significantly across treatments (Kruskal-Wallis rank-sum test, $\chi^2 = 6.0$, $P = 0.05$), with stronger regrowth in the closed cages (2.2 ± 0.5 nodes/plant) than in the no-cage treatment (0.7 ± 0.4 nodes/plant; $\chi^2 = 5.3$, $P = 0.02$), but once again the closed cages did not differ significantly from the open cages (1.5 ± 0.4 nodes/plant, $\chi^2 = 1.3$, $P = 0.25$). Informal observations suggested that humidity in the closed cages was somewhat higher than in the open cages, and substantially higher than in the no-cage controls; this appeared to enhance plant water status, and was probably responsible for the more vigorous regrowth.

1994 Experiment.—The age structure of the lacewing population was again characterized by high densities of *Chrysoperla* spp. eggs and few lacewing larvae, but in contrast to 1993 there was evidence of steady, low-level recruitment to the pupal stage (Fig. 6). The mean egg densities of 7.52 ± 1.68 eggs/plant and mean pupal densities of 0.19 ± 0.04 pupae/plant suggest an egg-to-pupal developmental success rate of ~1% (incorporating a correction for the longer development time of pupae, ~12 d, compared with eggs, ~4–5 d). At the start of the trial, the closed cages harbored a mean of 53.8 ± 15.6 lacewing adults, of which 69.8% were *C. comanche*, 17.7% *C. carnea*, 9.3% *C. nigricornis*, 2.3% *C. oculata*, and 0.9% *C. coloradensis. Chrysoperla comanche* was the dominant

TABLE 4. Densities of predatory arthropods in the fields where the large enclosure experiments were conducted: (A) 25 August–5 October 1993; (B) 15 August–27 September 1994.

Experiment	*Orius tristicolor* nymphs	*Orius tristicolor* adults	*Geocoris* spp. eggs	*Geocoris* spp. nymphs
A) 1993				
Whole-plant searches	0.25 ± 0.11	0.07 ± 0.05	0.60 ± 0.35	0.82 ± 0.25
Sweep net samples	0.14 ± 0.06	0.82 ± 0.30	···	4.56 ± 1.00
B) 1994				
Whole-plant searches	3.86 ± 1.29	0.86 ± 0.26	2.11 ± 1.16	0.58 ± 0.12
Sweep net samples	1.64 ± 0.45	2.84 ± 1.01	···	0.86 ± 0.23

Note: Values are numbers per plant and per sweep sample (means ± 1 SE) (each sample composed of ten sweeps) across seven weekly samples.

species throughout the experiment; 83.3% (145/174) of singly laid eggs reared in the laboratory yielded *C. comanche*. As in 1993, a diverse community of hemipteran predators was established in the field (Table 4B).

Densities of *Chrysoperla* spp. eggs in closed cages declined significantly in comparison with the open cages or the no cage controls (Fig. 7A, Table 5). *Chrysoperla* spp. eggs in the closed cages appeared, however, to stabilize at a new, reduced density, ~40% of that observed in the open cages and the no cage controls. In this population, in situ reproductive recruitment appeared sufficient to maintain *Chrysoperla* spp. populations, albeit at a diminished density.

As in 1993, *Chrysoperla* spp. were unique among the herbivorous and predatory arthropods sampled in demonstrating decreased densities in the closed cages compared to the open cages (Fig. 7B, C; Table 5). Aphid densities increased dramatically in the closed cages during the latter half of the experiment, while densities in the open cages and no cage controls declined. The basis of this result is unclear; aphid body size did not differ significantly between treatments (Wilks' $\lambda = 0.72$, $P = 0.3$); a trend towards increasing aphid populations in the closed cages was also observed at the end of the 1993 trial (Fig. 5B), suggesting that some aspect of the caging treatment had a consistently positive influence on aphid populations. Densities of spider mites and thrips were not significantly influenced by the experimental treatments (data not shown). At the start of the experiment, densities of whiteflies were by chance higher in the open cage treatment (0.75 ± 0.26 whitefly per leaf) than in the closed cages (0.34 ± 0.07 per leaf), and this difference persisted throughout the experiment (MANOVA, pairwise contrast of open vs. closed cages, Wilks' $\lambda = 0.46$, $P = 0.01$). Whitefly populations grew strongly in all treatments, however, and the proportional difference between the cage treatments did not increase (densities on week 6, open cages 10.9 ± 1.8, closed cages 7.9 ± 1.4). Thus, there was no suggestion that immigration was required to support local whitefly populations.

Prey were more abundant in this 1994 trial than in 1993, and thus were again unlikely to be limiting for *Chrysoperla* spp. Aphids were present at consistently high densities in the closed cage treatment (Fig. 7C), and were supplemented by moderate densities of other potential prey (mean density per leaf across all sampling dates and treatments: thrips, 2.2 ± 0.3; mites, 31.5 ± 4.9; whiteflies, 2.4 ± 0.2). Singly-laid *Chrysoperla* spp. eggs collected on 23 August and 6 September and reared in the laboratory showed that rates of inviability (5/75 = 6.7%) and egg parasitism (0/75 = 0%) were low, as observed in 1993. Thus, these sources of egg mortality appeared unlikely to be responsible for the drop in *Chrysoperla* spp. egg densities in the closed cage treatments.

Mortality factors acting on Chrysoperla *spp. eggs*

All freshly laid lacewing eggs discovered on previously searched cotton plants were deposited singly; that is, they were oviposited by either *C. comanche* or *C. carnea*. The developmental fates of cohorts of *Chrysoperla* spp. eggs studied during August (at Merced) and September (at Shafter) revealed relatively high rates of successful hatch (69% and 76%; Table 6). The egg cohort studied at Davis during October experienced an early winter storm, with lower temperatures and heavy winds; this resulted in longer development times for the *Chrysoperla* spp. eggs and may have contributed to the lower rate of successful hatch (Table 6). The cause(s) of egg disappearance are unknown; it is possible that eggs were entirely consumed by predators with chewing mouthparts, but this has not been observed during the course of these studies. Eggs might also have been dislodged by plants rubbing against each other in the wind; in this case, their likelihood of survival is unknown. In either case, field conditions leading to the higher estimates of successful hatch seen in the Shafter and Merced cohorts are more representative of growing season conditions, including those occurring during the 1993 and 1994 large field enclosure experiments. It appears that egg mortality contributes only modestly to the sharp decline in *Chrysoperla* spp. densities in the egg versus the early larval stages.

Influence of aphid prey availability and higher-order predation on C. carnea *larvae*

The experimental treatments successfully produced large differences in the initial and final aphid densities

TABLE 4. Extended.

Geocoris spp. adults	*Nabis* spp. nymphs	*Nabis* spp. adults	*Zelus renardii* nymphs	*Zelus renardii* adults	Thomisidae (all stages)
0.48 ± 0.17	0.08 ± 0.05	0.02 ± 0.02	0.49 ± 0.15	0.05 ± 0.03	0.13 ± 0.07
4.75 ± 1.21	1.25 ± 0.36	1.24 ± 0.28	0.12 ± 0.07	0.52 ± 0.21	0.34 ± 0.10
0.22 ± 0.11	0.51 ± 0.12	0.20 ± 0.09	0.72 ± 0.22	0.03 ± 0.02	0.04 ± 0.03
1.13 ± 0.47	1.50 ± 0.37	0.92 ± 0.28	0.10 ± 0.06	0.25 ± 0.07	0.16 ± 0.07

and the final densities of adult *G. pallens* and *Nabis* sp. predators per enclosure (Table 7). *Orius tristicolor* and *Nabis* sp. nymphs were found in the no predator treatments, presumably having emerged from eggs that had been oviposited in plant tissues before the cages were put in place. In no case, however, did hemipteran nymph densities vary significantly across treatments.

Chrysoperla carnea survivorship varied strongly across treatments, revealing a strong interaction between the availability of aphid prey and the impact of higher-order predation (Fig. 8, Table 8). When the availability of aphid prey was intermediate, the addition of hemipteran predators depressed *C. carnea* survival by ~90% (5.6% survival with predators vs. 54.1% survival without predators), but when the availability of aphid prey was very high, the addition of hemipteran predators depressed *C. carnea* survival only modestly, by 40% (40.5% vs. 67.6% survival). The main effect of higher-order predation and the interaction of higher-order predation with aphid density were highly significant, whereas the main effect of aphid availability was nonsignificant (Table 8). Because the procedure of brushing the cotton foliage to remove aphids also probably made it more likely that any cryptic lacewing eggs or neonate larvae would be detected and removed in the intermediate aphid density treatment, I think it is likely that the high aphid density treatment replicates, which were not brushed, were more likely to be have extra *C. carnea* larvae that I failed to exclude. This would tend to bias the experiment towards an apparent increase in *C. carnea* survival in the high aphid density treatments; that no such effect was observed suggests that the lack of a main effect of aphid density may be relatively robust.

Patterns of *C. carnea* growth and development reinforce the conclusion that the aphid density treatments had no main effect on *C. carnea* performance. Approximately 60% (37/62) of the *C. carnea* larvae de-

TABLE 5. Multivariate repeated-measures ANOVA for the effects of migration and caging on densities of *Chrysoperla* spp., motile hemipteran predators (*O. tristicolor, Geocoris* spp., *Nabis* spp., and *Z. renardii*), and aphids in large field enclosures, 1993 and 1994.

Source	*Chrysoperla* spp. eggs		Motile Hemiptera		Aphids	
	λ	*P*	λ	*P*	λ	*P*
1993, weeks 0–2						
Main effect of treatments	0.24	0.0017	1.00	0.98	0.75	0.28
Open vs. closed cages	0.32	0.0018	···	···	···	···
No cage vs. open cage	0.98	0.70	···	···	···	···
Time × treatment effect	0.16	0.0034	0.69	0.53	0.85	0.85
Open vs. closed cages	0.19	0.0013	···	···	···	···
No cage vs. open cage	0.89	0.64	···	···	···	···
1993, weeks 2–6						
Main effect of treatments	0.24	0.0016	0.75	0.28	0.92	0.70
Open vs. closed cages	0.33	0.0023	···	···	···	···
No cage vs. open cage	0.94	0.48	···	···	···	···
Time × treatment effect	0.01	<0.0001	0.33	0.42	0.22	0.20
Open vs. closed cages	0.07	0.0015	···	···	···	···
No cage vs. open cage	0.14	0.011	···	···	···	···
1994, weeks 0–6						
Main effect of treatments	0.20	0.0007	0.76	0.30	0.74	0.25
Open vs. closed cages	0.23	0.0004	···	···	···	···
No cage vs. open cage	0.96	0.55	···	···	···	···
Time × treatment effect	0.04	0.076	0.24	0.72	0.04	0.08
Open vs. closed cages	···	···	···	···	···	···
No cage vs. open cage	···	···	···	···	···	···

Note: The table reports Wilk's λ and associated *P* values.

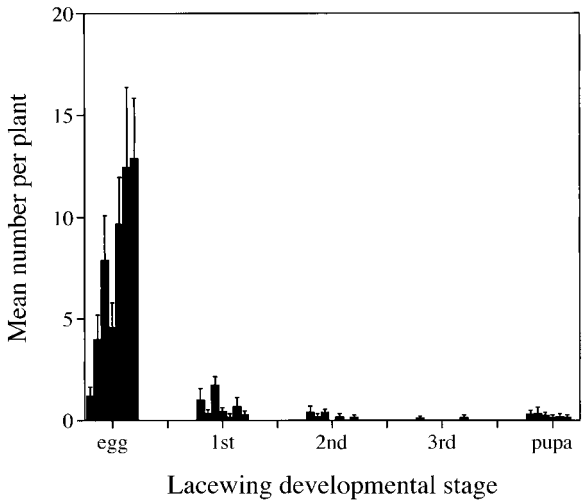

FIG. 6. Age structure of the lacewing community at the field site of the 1994 experiment on spatial subsidy of *Chrysoperla* spp. populations. Shown are the mean + 1 SE densities of lacewing eggs (singly laid *Chrysoperla* spp. only), three larval instars, and pupae during seven weekly samples, 15 August to 27 September 1994. Lacewing instars were estimated from body length (2–3 mm, first instar; 4–6 mm, second instar; ≥7 mm, third instar).

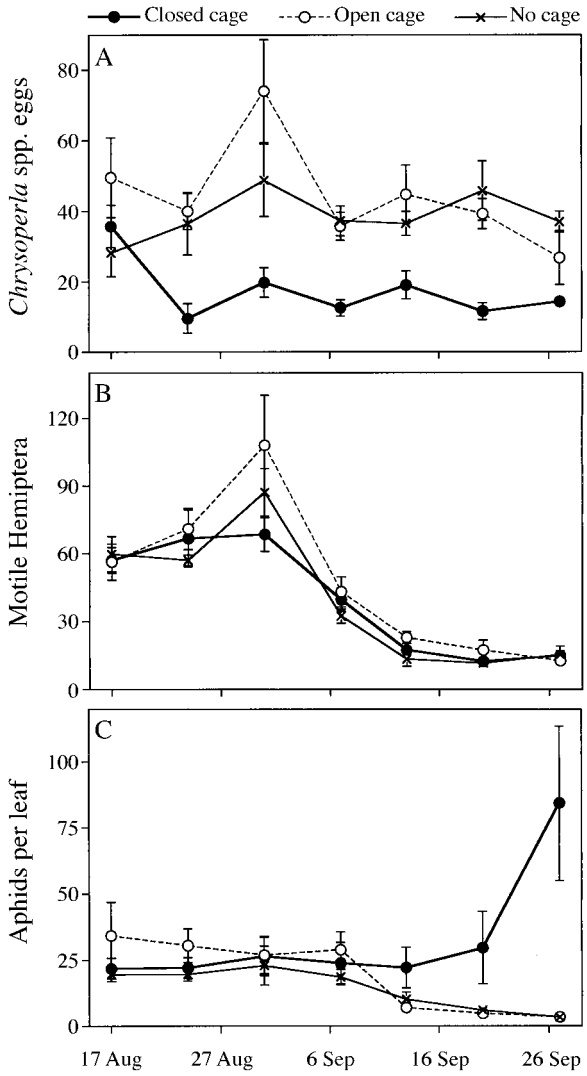

FIG. 7. Spatial subsidy of *Chrysoperla* spp. populations in the cotton agroecosystem: large enclosure experiment, 1994. Mean ± 1 SE numbers of (A) *Chrysoperla* spp. eggs and (B) nymphal and adult hemipteran predators, *O. tristicolor, Geocoris* spp., *Nabis* spp., and *Z. renardii,* in a sample of the top six nodes of 20 plants per plot. (C) Mean ± 1 SE number of aphids per leaf (sampled at the fifth mainstem node).

veloped through the three larval instars and spun cocoons during the 9-d experiment (Table 9). The aphid density treatment had no significant effect on the probability that *C. carnea* reached the cocoon stage (stepwise logistic regression; *F*-to-enter = 0.4, *P* = 0.55). The predator treatment and the interaction of aphid density and predators likewise had nonsignificant effects (*F*-to-enter = 0.7, *P* = 0.4, and *F*-to-enter = 0.2, *P* = 0.7, respectively). Furthermore, there were no significant effects of either the aphid density or predator presence treatments on the final live weights attained by *C. carnea* larvae or cocoons (two-way ANOVA: *P* ≥ 0.2 for all tests). Thus, I conclude that although *C. carnea* performance (including growth, development, and survivorship) was not directly constrained by food limitation in the intermediate aphid density treatment, the relative scarcity of aphid prey substantially amplified the importance of higher-order predation.

DISCUSSION

The cotton agroecosystem hosts a diverse and abundant community of generalist predators. Although one predator, *C. carnea,* can in isolation consistently produce strong top-down suppression of a key herbivore, *A. gossypii,* the full community of predators when tested together exerts minimal aphid suppression. Predator–predator interactions appear to be at the heart of this result. The age structure of *Chrysoperla* spp. populations in cotton fields harboring low to moderate aphid densities is often characterized by a sharp drop in densities from the egg to the first larval stage; this observation is consistent with heavy mortality during

TABLE 6. Impact of mortality factors on unmanipulated cohorts of *Chrysoperla* spp. eggs in the field.

Outcome	1994 Shafter (*N* = 25)	1994 Davis (*N* = 13)	1995 Merced (*N* = 32)
Parasitized	0.00	0.15	0.00
Preyed upon	0.08	0.15	0.16
Inviable	0.04	0.00	0.03
Missing	0.12	0.31	0.13
Hatched	0.76	0.38	0.69
Mean no. days to hatch	5.0 ± 0.3	8.4 ± 1.3	5.0 ± 0.1

Note: Values shown in the first five rows are the proportion of the initial egg cohort with the indicated developmental outcome; *N* = sample size.

either the egg or early larval stage. Egg cohorts followed under unmanipulated field conditions showed relatively high rates of successful hatch, suggesting that the vulnerable developmental stage is the young larva. Larval survival is relatively high in the absence of hemipteran predators, and much higher than the 0% or 1% survival rates derived from the observations of *Chrysoperla* spp. age structure (Figs. 4 and 6), suggesting that prey availability is not the primary limiting factor. Depressed survival is, however, observed in the presence of *Geocoris* spp., *Nabis* spp., and *Z. renardii*, all common inhabitants of cotton. The overall interpretation of these results, derived from field observations and small-scale and short-term experimentation, is that higher-order predation on lacewing larvae disrupts the strong top-down control of aphid populations in cotton.

A corollary hypothesis emerging from this interpretation is that *Chrysoperla* spp. populations have minimal in situ reproductive recruitment in many cotton fields. Larger scale, longer term field experiments were conducted to provide an independent test of the interpretation that higher-order predation is an organizing force in this system. *Chrysoperla* spp. subpopulations that were experimentally isolated from immigration experienced declining densities, in one year (1993) reaching very low densities and in another year (1994) declining to a low but apparently stable density. Thus, cotton fields harboring aphid populations of low to moderate density appear to be sink or pseudosink habitats for *Chrysoperla* spp. populations, in which natality is insufficient to balance mortality, and immigration is greater than emigration, producing a positive net spatial subsidy. It was this spatial subsidy that made the presence of higher-order predation conspicuous in this agroecosystem, by constantly infusing prey (*Chrysoperla* spp.) into a habitat where they were subject to intense attack. An experiment that simultaneously manipulated aphid prey availability (a bottom-up effect) and the presence of higher-order predators (a top-down effect) demonstrated that although *C. carnea* performance was not directly constrained by prey limitation, there was a strong interaction of aphid availability and the intensity of higher-order predation. Hemipteran predators killed ~90% of *C. carnea* larvae when aphid densities were intermediate, but killed only 40% of *C. carnea* larvae on plants with aphid outbreaks. Thus, cotton fields harboring aphid outbreaks may be source habitats for *Chrysoperla* spp., and spatial heterogeneity in the intensity of higher-order predation appears to generate source–sink dynamics in *Chrysoperla* spp. populations.

Higher-order predation on C. carnea *larvae*

Two small-scale field experiments were conducted in fields harboring large densities of *Chrysoperla* spp. eggs along with a diverse community of generalist hemipteran predators. These experiments showed, first, that when all predators were excluded, aphid populations grew at moderate to rapid rates. This is perhaps not an unexpected result, because natural enemies are thought by many to be important regulators of aphid populations (Hagen and van den Bosch 1968, Frazer 1988, Stary 1988, Morris 1992; but see Dixon 1998). Second, when the full predator community, including lacewings and hemipterans, was retained in a completely unmanipulated condition (the no-cage control) or manipulated only through caging (the cage control; 1993 only), aphid populations grew at moderate to rapid rates—indeed at rates that were statistically indistinguishable from that observed when all predators were excluded. This is perhaps a less expected result, given the high density and diversity of predators present in cotton (van den Bosch and Hagen 1966). This result becomes germane to the importance of higher-order predators in light of the third result: when just one member of the predator community, the lacewing *C. carnea*, was tested singly at densities that are commensurate with the natural field densities of *Chrysoperla* spp. eggs, it generated excellent aphid suppression, with aphid population growth either arrested (1993) or strongly reversed (1994). When tested in isolation, *C. carnea* showed survival rates that were sometimes higher (60%, 1993) and sometimes lower (17%, 1994), but in both cases high enough that naturally present densities of eggs would be expected to suppress aphid populations. These three results together suggest that other generalist predators interfere with the ability of lacewings to suppress aphids. Thus, the promise of aphid control inherent in the high density of lacewing eggs typically observed in cotton fields during the mid-to-late season is not realized.

The experimental treatments combining *C. carnea* with hemipteran predators showed that *Geocoris* spp., *Nabis* spp., and *Z. renardii* may each contribute to preventing *C. carnea* larvae from suppressing aphid populations. These hemipteran predators are ineffective, or at best mediocre (*Nabis* spp. during the 1993 trial), biological control agents for *A. gossypii*, but they can and do impose mortality on *C. carnea* larvae. Although the evidence that these predators, when combined with *C. carnea*, can release aphid populations from control is ostensibly mixed (Figs. 2B, 3B), these experiments likely underestimate the potential of hemipterans to disrupt the action of *C. carnea*. Both experiments were initiated with at least some second instar *C. carnea*, which are already capable of consuming substantial numbers of aphids (Principi and Canard 1984). What the experimental treatments that combined *C. carnea* with *Nabis* spp. showed, for example, was that these hemipteran predators did not kill the *C. carnea* fast enough to block a substantial degree of aphid control. However, in the field, lacewings must survive for 4–5 d as first instars, which are highly susceptible to predators (Rosenheim et al. 1999) but eat very few aphids (Principi and Canard 1984), before molting to the sec-

TABLE 7. Numbers of live aphids and hemipteran predators per experimental enclosure in the four treatments comprising the experiment examining the influence of aphid prey availability and higher-order predation on *C. carnea* larvae.

Treatment (*N*)	Initial aphid densities	Final aphid densities	*Orius tristicolor* nymphs
Low aphids, no predators (37)	81.8 ± 4.0	1117 ± 313	1.92 ± 0.35
Low aphids, predators (36)	78.1 ± 3.5	475 ± 110	1.28 ± 0.37
High aphids, no predators (37)	2654 ± 250	9431 ± 712	3.03 ± 0.70
High aphids, predators (37)	2378 ± 234	9869 ± 1063	1.49 ± 0.43
P	***	***	NS

Notes: Values shown are the means ± 1 SE. *P* values are for a Welch ANOVA for unequal variances on untransformed data.

*** $P < 0.001$; NS, $P < 0.05$

ond instar. I suggest that under natural field conditions, the collective effect of the hemipteran community is to prevent most lacewing larvae from surviving long enough to grow to a stage that can suppress aphid populations. This interpretation is consistent with and extends previous observations and experimentation showing that hemipteran predators attack and consume neonate *C. carnea* foraging freely in the field, and that predator–predator interactions can disrupt biological control of the cotton aphid (Rosenheim et al. 1993, Cisneros and Rosenheim 1997, Rosenheim et al. 1999).

Neither *O. tristicolor* nor crab spiders had detectable effects on *C. carnea* larval survivorship in the experiments reported here. *Orius tristicolor* is the smallest of the common hemipteran predators in cotton (adult body length 2 mm), and it is possible that its potential role as a predator of *C. carnea* might therefore be restricted to the youngest *C. carnea* larvae. The 1993 trial was initiated, however, with second instars, and overall *C. carnea* survivorship in the 1994 trial was sufficiently low because of exploitation of the aphid prey population to mask anything but a very strong mortality force. Additional work is therefore needed to quantify the impact of this predator on first instar *C. carnea*, which are known from field observations to be potential prey for *O. tristicolor* (Rosenheim et al. 1999). Crab spiders, although tested at densities higher than those typically observed, did not exert a detectable influence on *C. carnea* survival. These predators have, however, been observed in cotton consuming diverse arthropods, including *Nabis* spp. and *Z. renardii* (J. Rosenheim, *unpublished data*), and it is possible therefore that they may exert indirect, if not direct, influences on lacewing dynamics.

The dynamic significance of higher-order predators is becoming increasingly well-documented in natural terrestrial ecosystems (Polis 1991, Wise 1993, Schoener and Spiller 1995, 1996, Moran et al. 1996, Fagan 1997, Janssen et al. 1998, Letourneau and Dyer 1998, Moran and Hurd 1998, Polis et al. 1998, Rosenheim 1998, Spiller and Schoener 1998, Fincke 1999, Palomares and Caro 1999, Schellhorn and Andow 1999, Schoener and Spiller 1999, Wise and Chen 1999). Although less intensively studied in agricultural ecosystems, the potential importance of higher-order predators is of direct relevance to the design and implementation of biological pest control. Ecologists undertaking the introduction of predators or parasitoids to new habitats are essentially engaged in the engineering of new food webs (Ehler 1992). A sound understanding of terrestrial food web ecology will be of great importance to the deployment of control agents capable of exerting strong top-down influences on damaging herbivore populations. It will be important both from the perspective of avoiding the introduction of species likely to act as higher-order predators and from the perspective of introducing species whose action is less likely to be impeded by higher-order predators already present in the target ecosystem.

Spatial subsidy of Chrysoperla *spp. populations*

Both sink and pseudosink habitats are spatially subsidized, with immigration exceeding emigration and in situ mortality exceeding natality (Pulliam and Danielson 1991, Watkinson and Sutherland 1995). In pseudosink habitats, however, density-dependent regulatory influences relax when the spatial subsidy is removed and local densities decline, and natality and mortality come into eventual balance. The 1994 experiment on spatial subsidy was highly suggestive of pseudosink dynamics. There has, however, been no work conducted on the relationship between local lacewing densities and birth or death rates. Cannibalism, a source of mortality that is often strongly density-dependent, is known for lacewing larvae in laboratory settings and has been suggested to be an important influence on lacewing dynamics in the field (Canard and Duelli 1984, Dixon 1998; see also Ruzicka 1994). Nevertheless, cannibalism is unlikely to be important when larval densities are as low as those studied here (Figs. 4 and 6); direct observations of freely foraging neonate *C. carnea* larvae demonstrated that lacewing–lacewing encounters were rare, and cannibalism was never observed (Rosenheim et al. 1999). Additional work on density-dependent influences on lacewing demography will be valuable in further exploration of the pseudosink hypothesis.

In the 1993 trial, local *Chrysoperla* spp. populations declined strongly, indicating that the site was a true sink or perhaps a pseudosink with a very low equilib-

TABLE 7. Extended.

Orius tristicolor adults	*Geocoris* spp. nymphs	*Geocoris palens* adults	*Nabis* spp. nymphs	*Nabis* spp. adults
0.24 ± 0.12	0.05 ± 0.04	0.03 ± 0.03	0.22 ± 0.10	0.00 ± 0.00
0.22 ± 0.08	0.31 ± 0.10	0.86 ± 0.12	0.61 ± 0.18	0.81 ± 0.07
0.68 ± 0.22	0.11 ± 0.05	0.00 ± 0.00	0.59 ± 0.36	0.00 ± 0.00
0.49 ± 0.11	0.22 ± 0.10	0.92 ± 0.11	0.22 ± 0.08	0.78 ± 0.07
NS	NS	***	NS	***

rium density. Although these two possibilities might have been distinguished by a longer duration experiment, the closed cages appeared to create conditions under which aphid populations eventually showed abnormally high population growth (Figs. 5C and 7C), which might hamper the interpretation of a longer duration experiment. Informal observations suggest that high humidity in the closed cages alleviated plant water stress, producing conditions under which aphid growth rates are known to be enhanced (Wilhoit and Rosenheim 1993).

Why did *Chrysoperla* spp. densities decline more precipitously during the 1993 trial than during the 1994 trial? Variation in the densities of key predators might have played a role, but this is difficult to evaluate. *Geocoris* spp. were more abundant, but *O. tristicolor* was much less abundant in 1993 (Table 4). Perhaps more importantly, densities of aphids and alternate prey were greater during 1994. Although prey did not appear to be directly limiting during either year, the more abundant aphid prey present in 1994 may have significantly relaxed the intensity of higher-order predation. Whatever the cause of the differences between the two trials, the eventual outcome was clearly anticipated in the *Chrysoperla* spp. age structure at the two field sites: no in situ reproduction was detected in 1993 (Fig. 4), but consistent recruitment to the pupal stage occurred in 1994 (Fig. 6).

Because the singly laid eggs of the two commonest lacewing species, *C. comanche* and *C. carnea,* cannot be distinguished morphologically, and because these species are ecologically similar, I have focused in this study on the combined dynamics of these two species. What can be said, however, about the status of some cotton fields as sink habitats for each species considered in isolation? *Chrysoperla comanche* was the dominant lacewing species throughout the 1994 trial; thus, the conclusion from the 1994 trial that cotton may be a pseudo sink habitat for *Chrysoperla* spp. applies specifically to *C. comanche.* During the 1993 trial, however, the lacewing community shifted from one dominated by *C. carnea* to one dominated by *C. comanche*;

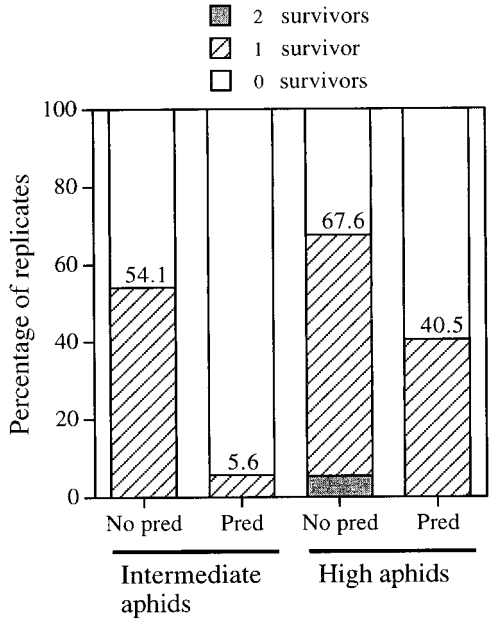

FIG. 8. Influences of aphid prey availability (bottom-up effect) and higher-order predators (top-down effect) on the survivorship of *C. carnea* larvae in small field enclosures. Shown are the percentages of replicates (n = 36–37 per treatment) in which 0, 1, or 2 *C. carnea* larvae survived over the 9-d experiment.

TABLE 8. Stepwise polychotomous logistic regression of factors influencing survivorship of larval *C. carnea*.

Step	Variable entered†	Coefficient (± 1 SE)‡	df	χ^2§	*P*
1	Predators	−3.29 ± 0.77	1	22.4	<0.0001
2	Aphids × predators	2.44 ± 0.80	1	13.7	0.0002

Variables not entered

Variable	df	Approximate χ^2 to enter	*P*
Aphids	1	2.1	0.15

Notes: The number of surviving *C. carnea* was coded as an ordered variable with three discrete states for zero, one, or two survivors per replicate. Total number of replicates = 147. Goodness of fit $\chi^2 = 4.7$, df = 4, $P = 0.32$, indicating good model fit.

† Predator treatment was coded as 0 for no predators and 1 for predators present. Aphid treatment was coded as 0 for low aphid density, 1 for high aphid density.

‡ Coefficients (b_i) of the logistic equation. Probability that more than i *C. carnea* survive: P(number of survivors $> i$) $= e^u/(1 + e^u)$, where $u = b_0 + b_1x_1 + b_2x_2 + \ldots + b_nx_n$, and x_i is an independent variable. The constant, b_0, has value 0.45 for $i = 0$ and −3.80 for $i = 1$.

§ Improvement chi-square statistic.

TABLE 9. Influence of aphid prey availability (bottom-up effect) and higher-order predation (top-down effect) on the numbers and mass (mean ± 1 SE) of surviving *C. carnea* reaching the larval and cocoon stages.

Treatment	No. in larval stage	Mass of larvae (mg)	No. in completed cocoon	Mass of larvae in cocoons (mg)
Low aphids, no predators	10	9.49 ± 0.68	10	9.26 ± 0.42
Low aphids, predators	0	···	2	10.54 ± 0.55
High aphids, no predators	10	10.69 ± 0.70	16	9.90 ± 0.36
High aphids, predators	5	10.68 ± 1.03	9	9.89 ± 0.53

Notes: For the two replicates where two *C. carnea* survived, both observations were used. *Chrysoperla carnea* development to the cocoon stage was analyzed with stepwise logistic regression. Effect of aphid treatment is not statistically significant (NS) (F-to-enter = 0.36, P = 0.55); effect of predator treatment is NS (F-to-enter = 0.72, P = 0.40); the interaction of aphids × predators is NS (F-to-enter = 0.15, P = 0.70).

this seasonal shift is the norm in California cotton, and appears to reflect the declining production of attractive volatile chemicals by cotton plants as they cease vegetative growth (Hagen 1986). Because the closed cages prevented adult *C. carnea* from emigrating from cotton plants of increasing maturity and declining attractiveness, whereas *C. carnea* were free to emigrate from the open cages, the 1993 trial was a conservative test of cotton's status as a sink habitat. The observation that *C. carnea* populations in the closed cages collapsed in the 1993 trial suggests that cotton is also a sink habitat for this species. The increasing densities of *C. comanche* observed in the open cages in 1993 appear to reflect a spatial subsidy rather than in situ reproductive recruitment, because similar increases in density did not occur in the closed cages. Thus, in summary, I suggest that the inference that cotton habitats can be sinks or pseudosinks for *Chrysoperla* spp. appears likely to apply to each of the *Chrysoperla* species studied here.

Chrysoperla carnea populations inhabiting irrigated agroecosystems in California's San Joaquin Valley are characterized by multivoltinism and an absence of aestival diapause (Tauber and Tauber 1986, 1992). Diapausing females, which generally change color from light green to reddish brown, were never observed in this study. Thus aestival diapause, which occurs in some western populations of *C. carnea* inhabiting natural ecosystems under long-day photoperiods and in the absence of aphid prey, appears unlikely to have contributed to the changes in lacewing egg densities observed here.

Although both the 1993 and 1994 trials suggest that some cotton fields are spatially subsidized by *Chrysoperla* spp. immigration, I emphasize that the experiments have not revealed the mechanism(s) underlying this result. To demonstrate conclusively that predation on *Chrysoperla* spp. larvae by hemipteran predators was responsible for creating a sink habitat, it would be necessary to conduct an experiment in which the immigration treatments were fully crossed with a predator removal treatment. Unfortunately, establishing and maintaining predator removal treatments over experimental plots large enough to test the spatial subsidy hypothesis is logistically very difficult. Although I have argued that predation on *Chrysoperla* spp. larvae is a key source of mortality, other factors are almost certainly important as contributory factors. Egg mortality has been quantified, and is nontrivial. Lacewings are attacked by larval-pupal and pupal parasitoids (Clancy 1946, Alrouechdi et al. 1984), and lacewing pupae within cocoons are also subject to predation; field data from California suggest that these factors kill a mean of ~30% of all lacewings that spin cocoons (J. A. Rosenheim and D. D. Limburg, *unpublished data*). Furthermore, we know very little about factors determining the extent to which adult lacewings realize their full potential for reproduction in nature. Predation on adult lacewings by *Z. renardii,* damselflies (family Coenagrionidae), and orb-web spiders (family Araneidae) has been observed (J. Rosenheim, *unpublished data*). Furthermore, foods for the nonpredatory adults, including pollen, floral and extrafloral nectar, and honeydew, may in some cases be limiting (Hagen 1986). It is possible that densities of aphids that are sufficient to satiate lacewing larvae do not produce sufficient honeydew to satiate lacewing adults, or there may be competition among diverse arthropods, including lacewings and native ants, such as *Solenopsis xyloni,* for honeydew resources (J. Rosenheim, *personal observation*). These possibilities all define areas for future research.

Pulliam (1996) has suggested that some anthropogenic habitats, including agroecosystems, may provide cues that indicate suitability but may, for a number of reasons including strong predation, prove to be sink habitats. Cotton fields harboring low-to-moderate densities of aphid prey may be such a ''trap habitat'' for *Chrysoperla* spp. populations. Gravid female *C. carnea* are attracted by chemical cues released by cotton plants (caryophyllene) and honeydew from aphids (indole acetaldehyde, a breakdown product of tryptophan), and are arrested by feeding on the sugars found in the honeydew (Hagen et al. 1976, van Emden and Hagen 1976, Flint et al. 1979, Hagen 1986). Heavy oviposition is thus elicited in a habitat where offspring survival probability is very low. Although all of the predatory arthropods considered in this study are native to North America, the irrigated cotton ecosystem is a novel habitat.

Interaction of bottom-up and top-down effects on lacewing populations

If cotton fields harboring low to moderate densities of aphid prey are sink or pseudosink habitats for *Chry-*

soperla spp., where are the source habitats? Following the observation of greater proportions of lacewings in late-instar larval and pupal stages at field sites harboring outbreaks of either aphids or mites (J. Rosenheim, *unpublished data*), I tested the main and interactive effects of aphid prey availability (a bottom-up effect) and higher-order predation (a top-down effect) on *C. carnea* performance. Although aphid prey availability did not have a direct effect on *C. carnea* performance, it had a strong indirect effect mediated through the impact of higher-order predation. The duration of the experiment was too short for aphid availability to influence the density of late-instar or adult hemipteran predators (i.e., the stages that can prey on *C. carnea*) through reproduction (Table 7). Thus, the indirect effect was not the result of aphids supporting the buildup of hemipteran predators which could then suppress *C. carnea* (i.e., an ''interaction chain'' sensu Wootton [1994] or a ''density-mediated indirect effect'' sensu Abrams et al. [1996]). Rather, the presence of abundant aphids appears to decrease the per capita strength of the interaction between hemipterans and *C. carnea* (i.e., an ''interaction modification'' sensu Wootton [1994] or a ''trait-mediated indirect effect'' sensu Abrams et al. [1996]). This is the first field study with terrestrial insects to demonstrate that the presence of alternate prey relaxes the intensity of higher-order predation, a result that has been observed frequently in simplified laboratory settings (Rosenheim et al. 1995, Lucas et al. 1998; but see Fincke 1994). To demonstrate conclusively that cotton fields harboring aphid outbreaks can be source habitats for *Chrysoperla* spp., it would be necessary to show that subpopulations of *Chrysoperla* spp. isolated from immigration can expand in the face of higher-order predation in such sites. Although this has not been demonstrated here, the survivorship of *C. carnea* larvae is sufficiently enhanced by the presence of superabundant aphid prey (Fig. 8) that cotton fields with aphid outbreaks are at least strong candidates for *Chrysoperla* spp. source habitats. Spatial heterogeneity in aphid densities may modulate the intensity of higher-order predation experienced by *Chrysoperla* spp. larvae, creating a mosaic of source and sink habitats for *Chrysoperla* spp. populations in cotton fields. It is also possible, and indeed likely, that other crops or natural habitats in the diverse agricultural landscape of California's Central Valley may be source habitats for *Chrysoperla* spp., because *Chrysoperla* spp. are common and indeed nearly omnipresent in California's Central Valley.

This study is one of many suggesting that top-down and bottom-up effects can interact, and that therefore it may be most useful to consider their joint effects rather than attempting to study them in isolation (Polis 1994, Krebs et al. 1995, Osenberg and Mittelbach 1996, Benrey and Denno 1997). Although most of the research examining interacting top-down and bottom-up effects in terrestrial arthropod communities has been focused on the slow-growth–high-mortality hypothesis for insect herbivores (reviewed by Benrey and Denno [1997]), this study shows that the same sort of interactive effects may also be important for predators (see also Estes et al. 1998).

What mechanisms might underlie the effect of aphid density on the intensity of higher-order predation? First, aphid availability might influence the rate of encounter between *C. carnea* larvae and higher-order predators. *Chrysoperla carnea* larvae are 4.3 times as likely to encounter a potential predator when foraging then when resting or feeding (Rosenheim et al. 1999), and *C. carnea* larvae spend more time foraging as aphid density declines. Second, aphid availability might influence the likelihood that an encounter between a *C. carnea* larva and a higher-order predator would lead to an actual predation event. Hemipteran predators in cotton do feed on aphids (Fig. 1) and might often be satiated at sites harboring superabundant aphid populations. The small observational data set presented in Rosenheim et al. (1999) does not provide any support for the idea that aphid density modulates the likelihood of an encounter leading to a predation event (logistic regression, $\chi^2 = 1.1$, $P = 0.30$), but additional work is needed to evaluate this hypothesis carefully.

Although *C. carnea* were not adversely affected by prey limitation in the intermediate aphid density treatment used in this study, the ability of *C. carnea* to harvest low-density prey is, of course, finite. An observational study demonstrated that when aphid densities are very low ($\leq \sim 1$ aphid per leaf), neonate *C. carnea* show decreased rates of aphid consumption and spend less total time consuming arthropod prey (Rosenheim et al. 1999). *Chrysoperla carnea* larvae consume more extrafloral nectar at sites with low aphid availability; this carbohydrate-rich food sustains *C. carnea* larvae for long periods (up to 19 d), but does not permit *C. carnea* to develop. By extending the duration of the highly vulnerable larval stages, low prey availability is likely to amplify the total impact of higher-order predators. Thus, it seems likely that the interaction between prey availability and higher-order predation will be maintained or even intensified at lower prey densities, where these interactive effects would complement a direct effect of food resources on lacewing performance.

Why is it important to recognize that source–sink dynamics may be imposed on *Chrysoperla* spp. populations by spatially heterogeneous higher-order predation? First, this result is relevant to the theory and practice of biological control. This study is the first experimental test of the oft-expressed hypothesis that higher-order predators may drive local populations of introduced biological control agents extinct (Stiling 1993). An understanding of factors underlying the failure of introduction programs to result in the permanent establishment of a biological control agent in a new environment will be critical to ongoing efforts to im-

prove success rates of classical biological control. Source–sink dynamics of natural enemies (predators, parasitoids, and pathogens) are also directly relevant to developing strategies for local and regional agricultural practices that maximize the contribution of biological control to the overall suppression of herbivore populations (Corbett and Plant 1993, Ives and Settle 1997). Researchers are currently exploring modifications of the agricultural landscape that move natural enemy source habitats closer to agricultural fields or that provide key resources for natural enemies that move between local habitats (Corbett and Rosenheim 1996, Marino and Landis 1996, Murphy et al. 1998). An understanding of the ecological processes that produce source and sink habitats will be pivotal to the success of these efforts. Finally, the movement of natural enemies between different agricultural fields can create a metapopulation structure that influences the ability of natural enemies to evolve key adaptations in response to pesticides and other novel selective agents operating in agroecosystems (Caprio and Hoy 1994, Peck and Ellner 1997).

The observation of source–sink dynamics generated by higher-order predation also has implications for a general theory of terrestrial arthropod community structure. The relative magnitudes of bottom-up and top-down forces acting on *Chrysoperla* spp. are not static, but rather are spatially heterogeneous. In habitats where aphid prey are not sufficiently abundant to ameliorate the intense higher-order predation experienced by *Chrysoperla* spp. larvae, local reproduction does not balance natality, and it is only through immigration that *Chrysoperla* spp. populations persist. Thus, although much of the work on spatial subsidies in food webs has emphasized transfers at the lower trophic levels (nutrients, herbivores, detritivores; e.g., Polis and Strong 1996, Huxel and McCann 1998, Polis et al. 1998), movement may also be important at higher positions in food webs (see review in Polis et al. 1997).

Perhaps most importantly, this work suggests that a casual inspection of terrestrial ecosystems may yield an underestimate of the importance of higher-order predation. The attractiveness of the cotton agroecosystem to adult lacewings produced a setting in which the impact of higher-order predators was conspicuous to ecologists. Now, as we attempt to determine the prevalence and general importance of higher-order predators, it is sobering to consider that the importance of predation on lacewings in this system would likely never have been detected were lacewings adults not so mobile and so strongly attracted to cotton. Predators that are vulnerable to higher-order predation may simply be excluded from many habitats, and in coevolved communities predators may avoid ovipositing in habitats where their offspring face strong risks of predation (e.g., Ruzicka 1994, Dixon 1998). Thus, manipulative experiments are essential to determining whether the absence of a predator from a given habitat is due to the potentially cryptic influences of higher-order predation.

Acknowledgments

For dedicated assistance in the field, I thank Jane Adams, Judy Andrade, Christine Armer, Marilys Brustel, Jorge Cisneros, Ramana Colfer, Franck Curk, Jason Edwards, David Hongkham, David Limburg, Erick Oshel, Laura Peck, Lawrence Wilhoit, and Paul Wynholds. Joel Ledford kindly identified the crab spiders. I wish to acknowledge the valuable suggestions made by Keith Hopper regarding experimental designs and the helpful input of several reviewers: R. G. Colfer, A. Corbett, V. Fournier, K. Laughlin, T. E. Leonardo, E. H. Nelson, D. A. Spiller, C. A. Tauber, M. J. Tauber, and two anonymous referees. This work was supported by grants from the California State Support Board of Cotton Incorporated, the University of California Statewide IPM program, the California Crop Improvement Association, and the USDA NRICGP (grants 94-37302-0504 and 96-35302-3816).

Literature Cited

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. Pages 371–395 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman & Hall, New York, New York, USA.

Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999. Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. Ecology **80**:518–523.

Alomar, O., and R. N. Wiedenmann, editors. 1996. Zoophytophagous Heteroptera: implications for life history and integrated pest management. Thomas Say Publications in Entomology. Entomological Society of America, Lanham, Maryland, USA.

Alrouechdi, K., Y. Séméria, and T. R. New. 1984. Ecology of natural enemies. Pages 187–193 *in* M. Canard, Y. Séméria, and T. R. New, editors. Biology of Chrysopidae. Dr. W. Junk, The Hague, The Netherlands.

Barkai, A., and C. McQuaid. 1988. Predator–prey role reversal in a marine benthic ecosystem. Science **242**:62–64.

Benrey, B., and R. F. Denno. 1997. The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. Ecology **78**:987–999.

Canard, M., and P. Duelli. 1984. Predatory behavior of larvae and cannibalism. Pages 92–100 *in* M. Canard, Y. Séméria, and T. R. New, editors. Biology of Chrysopidae. Dr. W. Junk, The Hague, The Netherlands.

Canard, M., and M. M. Principi. 1984. Development of Chrysopidae. Pages 57–75 *in* M. Canard, Y. Séméria, and T. R. New, editors. Biology of Chrysopidae. Dr. W. Junk, The Hague, The Netherlands.

Caprio, M. A., and M. A. Hoy. 1994. Metapopulation dynamics affect resistance development in the predatory mite, *Metaseiulus occidentalis* (Acari: Phytoseiidae). Journal of Economic Entomology **87**:525–534.

Cisneros, J. J., and J. A. Rosenheim. 1997. Ontogenetic change of prey preference in a generalist predator, *Zelus renardii,* and its influence on the intensity of predator–predator interactions. Ecological Entomology **22**:399–407.

Cisneros, J. J., and J. A. Rosenheim. 1998. Changes in the foraging behavior, within-plant vertical distribution and micro-habitat selection of a generalist predator: an age analysis. Environmental Entomology **27**:949–957.

Clancy, D. W. 1946. The insect parasites of the Chrysopidae (Neuroptera). University of California Publications in Entomology **7**:403–496.

Coll, M. 1998. Living and feeding on plants in predatory Heteroptera. Pages 89–129 *in* M. Coll and J. R. Ruberson, editors. Predatory Heteroptera in agroecosystems: their

ecology and use in biological control. Thomas Say Publications in Entomology. Entomological Society of America, Lanham, Maryland, USA.
Corbett, A., and R. E. Plant. 1993. Role of movement in the response of natural enemies to agroecosystem diversification—a theoretical evaluation. Environmental Entomology **22**:519–531.
Corbett, A., and J. A. Rosenheim. 1996. Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. Ecological Entomology **21**:155–164.
Dixon, A. F. G. 1998. Aphid ecology. Second edition. Chapman & Hall, London, UK.
Duelli, P. 1980*a*. Adaptive dispersal and appetitive flight in the green lacewing, *Chrysopa carnea*. Ecological Entomology **5**:213–220.
Duelli, P. 1980*b*. Preovipository migration flights in the green lacewing, *Chrysopa carnea* (Planipennia, Chrysopidae). Behavioral Ecology and Sociobiology **7**:239–246.
Duelli, P. 1984. Oviposition. Pages 129–133 *in* M. Canard, Y. Séméria, and T. R. New, editors. Biology of Chrysopidae. Dr. W. Junk, The Hague, The Netherlands.
Ehler, L. E. 1992. Guild analysis in biological control. Environmental Entomology **21**:26–40.
Eisner, T., A. B. Attygalle, W. E. Conner, M. Eisner, E. MacLeod, and J. Meinwald. 1996. Chemical egg defense in a green lacewing (*Ceraeochrysa smithi*). Proceedings of the National Academy of Sciences USA **93**:3280–3283.
Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473–476.
Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. American Naturalist **150**:554–568.
Fincke, O. M. 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. Oecologia **100**: 118–127.
Fincke, O. M. 1999. Organization of predator assemblages in Neotropical tree holes: effects of abiotic factors and priority. Ecological Entomology **24**:13–23.
Flint, H. M., S. S. Salter, and S. Walters. 1979. Caryophyllene: an attractant for the green lacewing. Environmental Entomology **8**:1123–1125.
Frazer, B. D. 1988. Predators. Pages 217–230 *in* A. K. Minks and P. Harrewijn, editors. Aphids: their biology, natural enemies and control, Volume B. Elsevier, Amsterdam, The Netherlands.
Greathead, D. J., and A. H. Greathead. 1992. Biological control of insect pests by insect parasitoids and predators: the BIOCAT database. Biocontrol News and Information **13**: 61N–68N.
Hagen, K. S. 1986. Ecosystem analysis: plant cultivars (HPR), entomophagous species and food supplements. Pages 151–197 *in* D. J. Boethel and R. D. Eikenbary, editors. Interactions of plant resistance and parasitoids and predators of insects. Ellis Horwood, Chichester, UK.
Hagen, K. S., P. Greany, E. F. Sawall, Jr., and R. L. Tassan. 1976. Tryptophan in artificial honeydews as a source of an attractant for adult *Chrysopa carnea*. Environmental Entomology **5**:458–468.
Hagen, K. S., and R. van den Bosch. 1968. Impact of pathogens, parasites, and predators on aphids. Annual Review of Entomology **13**:325–384.
Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause–effect relationships in energy flow, trophic structure and interspecific interactions. American Naturalist **142**:379–411.
Hairston, N. G., Jr., and N. G. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? American Naturalist **149**:1001–1007.
Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.
Hassell, M. P. 1978. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, New Jersey, USA.
Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist **149**:745–764.
Huxel, G. R., and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. American Naturalist **152**:460–469.
Ives, A. R., and W. H. Settle. 1997. Metapopulation dynamics and pest control in agricultural systems. American Naturalist **149**:220–246.
Janssen, A., A. Pallini, M. Venzon, and M. W. Sabelis. 1998. Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. Experimental and Applied Acarology **22**:497–521.
Kitchell, J. F., and S. R. Carpenter. 1993. Cascading trophic interactions. Pages 1–14 *in* S. R. Carpenter and J. R. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.
Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**:1112–1115.
Letourneau, D. K., and L. A. Dyer. 1998. Experimental test in lowland tropical forest shows top-down effects through four trophic levels. Ecology **79**:1678–1687.
Losos, J. B., and D. A. Spiller. 1999. Differential colonization success and asymmetrical interactions between two lizard species. Ecology **80**:252–258.
Lucas, E., D. Coderre, and J. Brodeur. 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey. Ecology **79**:1084–1092.
Marino, P. C., and D. A. Landis. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. Ecological Applications **6**:276–284.
Moran, M. D., and L. E. Hurd. 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. Oecologia **113**:126–132.
Moran, M. D., T. P. Rooney, and L. E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. Ecology **77**:2219–2227.
Morris, W. F. 1992. The effects of natural enemies, competition, and host plant water availability on an aphid population. Oecologia **90**:359–365.
Murphy, B. C., J. A. Rosenheim, R. V. Dowell, and J. Granett. 1998. Testing a habitat diversification tactic for improving biological control: parasitism of the western grape leafhopper, *Erythroneura elegantula* (Homoptera: Cicadellidae). Entomologia Experimentalis et Applicata **87**:225–235.
Osenberg, C. W., and G. G. Mittelbach. 1996. The relative importance of resource limitation and predator limitation in food chains. Pages 134–148 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman & Hall, New York, New York, USA.
Palomares, E., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist **153**: 492–508.
Peck, S. L., and S. P. Ellner. 1997. The effect of economic thresholds and life-history parameters on the evolution of pesticide resistance in a regional setting. American Naturalist **149**:43–63.
Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist **138**:123–155.
Polis, G. A. 1994. Food webs, trophic cascades and com-

munity structure. Australian Journal of Ecology **19**:121–136.
Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics **28**:289–316.
Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution **7**:151–154.
Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. Ecology **79**:490–502.
Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.
Polis, G. A., and K. O. Winemiller, editors. 1996. Food webs: integration of patterns and dynamics. Chapman & Hall, New York, New York, USA.
Principi, M. M., and M. Canard. 1984. Feeding habits. Pages 76–92 *in* M. Canard, Y. Séméria, and T. R. New, editors. Biology of Chrysopidae. Dr. W. Junk, The Hague, The Netherlands.
Pulliam, H. R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45–69 *in* O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, Illinois, USA.
Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist **137**:S50–S66.
Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. Annual Review of Entomology **43**:421–447.
Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological control agents: theory and evidence. Biological Control **5**: 303–335.
Rosenheim, J. A., D. D. Limburg, and R. G. Colfer. 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. Ecological Applications **9**:409–417.
Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia **96**:439–449.
Rousset, A. 1984. Reproductive physiology and fecundity. Pages 116–129 *in* M. Canard, Y. Séméria, and T. R. New, editors. Biology of Chrysopidae. Dr. W. Junk, The Hague, The Netherlands.
Ruzicka, Z. 1994. Oviposition-deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). European Journal of Entomology **91**:361–370.
SAS Institute. 1995. JMP 3.1.5. SAS Institute, Inc., Cary, North Carolina, USA.
Schellhorn, N. A., and D. A. Andow. 1999. Cannibalism and interspecific predation: role of oviposition behavior. Ecological Applications **9**:418–428.
Schoener, T. W., and D. A. Spiller. 1995. Effect of predators and area on invasion: an experiment with island spiders. Science **267**:1811–1813.
Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. Nature **381**:691–694.
Schoener, T. W., and D. A. Spiller. 1999. Indirect effects in an experimentally staged invasion by a major predator. American Naturalist **153**:347–358.
Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution **13**:350–355.
Slobodkin, L., F. Smith, and N. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. American Naturalist **101**:109–124.
Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and invertebrate predators: facilitation and interference among stream predators. Oikos **52**:94–100.
Spiller, D. A., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. Ecology **79**:503–516.
Stary, P. 1988. Aphidiidae. Pages 171–184 *in* A. K. Minks and P. Harrewijn, editors. Aphids: their biology, natural enemies and control, Volume B. Elsevier, Amsterdam, The Netherlands.
Stiling, P. 1993. Why do natural enemies fail in classical biological control programs? American Entomologist **39**: 31–37.
Tauber, C. A., and M. J. Tauber. 1986. Ecophysiological responses in life-history evolution: evidence for their importance in a geographically widespread insect species complex. Canadian Journal of Zoology **64**:875–884.
Tauber, C. A., and M. J. Tauber. 1992. Phenotypic plasticity in *Chrysoperla*: genetic variation in the sensory mechanism and in correlated reproductive traits. Evolution **46**:1754–1773.
Tauber, M. J., C. A. Tauber, and S. Gardescu. 1993. Prolonged storage of *Chrysoperla carnea* (Neuroptera: Chrysopidae). Environmental Entomology **22**:843–848.
van den Bosch, R., and K. S. Hagen. 1966. Predaceous and parasitic arthropods in California cotton fields. California Agricultural Experiment Station Bulletin 820. Division of Agricultural Sciences, University of California, Oakland, California, USA.
van Emden, H. F., and K. S. Hagen. 1976. Olfactory reactions of the green lacewing, *Chrysopa carnea*, to tryptophan and certain breakdown products. Environmental Entomology **5**: 469–473.
von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 *in* S. S. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, New York, New York, USA.
Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology **64**:126–130.
Whitcomb, W. H., and K. Bell. 1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. Bulletin 690. University of Arkansas Agricultural Experiment Station, Fayetteville, Arkansas, USA.
Wilhoit, L. R., and J. A. Rosenheim. 1993. The yellow dwarf form of the cotton aphid, *Aphis gossypii*. Pages 969–972 *in* Proceedings Beltwide Cotton Conferences. National Cotton Council of America, Memphis, Tennessee, USA.
Wilson, L. T., and A. P. Gutierrez. 1980. Within-plant distribution of predators on cotton: comments on sampling and predator efficiencies. Hilgardia **48**(2):3–11.
Wise, D. H. 1993. Spiders in ecological webs. Cambridge University Press, Cambridge, UK.
Wise, D. H., and B. Chen. 1999. Impact of intraguild predators on survival of a forest-floor wolf spider. Oecologia **121**:129–137.
Wissinger, S. A., G. B. Sparks, G. L. Rouse, W. S. Brown, and H. Steltzer. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. Ecology **77**:2421–2430.
Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics **25**:443–466.
Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508–515.
Zheng, Y., K. M. Daane, K. S. Hagen, and T. E. Mittler. 1993. Influence of larval food consumption on the fecundity of the lacewing *Chrysoperla carnea*. Entomologia Experimentalis et Applicata **67**:9–14.