

IMPACT OF GENERALIST PREDATORS ON A BIOLOGICAL CONTROL AGENT, *CHRYSOPERLA CARNEA*: DIRECT OBSERVATIONS

JAY A. ROSENHEIM,¹ DAVID D. LIMBURG, AND RAMANA G. COLFER

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

Abstract. Generalist predators in terrestrial arthropod communities have traditionally been viewed as predators whose dynamics are less tightly coupled to any particular prey species, but whose ecological roles are in other respects analogous to those of specialist predators. Biological-control theory for predator–prey interactions has been based upon a model of communities composed of three discrete trophic levels—plants, herbivores, and predators—in which biological control agents are top consumers and in which different species of predators interact only through competition for shared prey. Experiments employing single-plant field enclosures have suggested, however, that some generalist predators in the cotton agroecosystem function as higher-order predators, releasing populations of an herbivore, the cotton aphid *Aphis gossypii*, from control by another predator, the lacewing *Chrysoperla carnea*. Here we demonstrate through focal observations of neonate *C. carnea* foraging freely in the field that the high levels of mortality observed experimentally are not an artifact of cage confinement. Five generalist predators in the order Hemiptera were observed preying on neonate *C. carnea*. Neither cannibalism nor predation by heterospecific chrysopids was observed. The only other potential source of lacewing mortality observed was dislodgment from the plant, which occurred primarily on trichome-rich plant structures. A model of terrestrial arthropod communities incorporating higher-order predators may provide valuable insights into the regulation of herbivore populations and suggest useful avenues for biological-control research.

Key words: *agroecosystem, cotton; Aphis gossypii; arthropod predator–prey systems; biological control, disruption of; Chrysoperla carnea; cotton agroecosystem; generalist predators; higher-order predators; intraguild predation; top-down herbivore regulation.*

INTRODUCTION

Increased attention has recently been directed to the role of generalist predators as regulators of insect herbivore populations in agricultural ecosystems. Biological control theory and practice have traditionally emphasized the role of specialist natural enemies, whose dynamics are tightly linked to those of a target pest (Doutt 1964, Beddington et al. 1978, Hassell 1978). Several influential authors have, however, recently stressed the ability of generalist predators to establish populations in highly disturbed ecosystems, such as annual cropping systems, by exploiting alternative resources (Ehler and Miller 1978, Riechert and Lockley 1984, Murdoch et al. 1985, Wiedenmann and Smith 1997). Alternative resources may include plant material (Alomar and Wiedenmann 1996) or alternative prey, including detritivores (Settle et al. 1996), less-damaging herbivores (Karban et al. 1994), or even potentially other species of predators (Sunderland et al.

1997). Thus, generalist predators may establish or sustain population densities capable of controlling incipient pest outbreaks early in the season following the initial colonization of the crop by pests or later in the season following a period of pest scarcity.

Generalist predators have also recently been placed at the center of an acrimonious debate over the environmental risks associated with classical biological control, the importation of exotic species of predators to control invasive, usually non-native species of herbivores (Howarth 1991, McEvoy 1996, Simberloff and Stiling 1996). Generalist predators may pose substantially enhanced risks of non-target impacts on endemic faunas. The very characteristics that make generalists attractive as pest-control agents, and in particular their ability to support significant populations by consuming alternate prey, may increase their likelihood of producing localized or regional extinctions (Holt and Lawton 1994).

Relatively little attention has been devoted, however, to developing theory for the action of generalist predators within the context of rich terrestrial arthropod communities. Traditionally, generalist predators have been analyzed as predators whose dynamics were less

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¹ E-mail: jarosenheim@ucdavis.edu

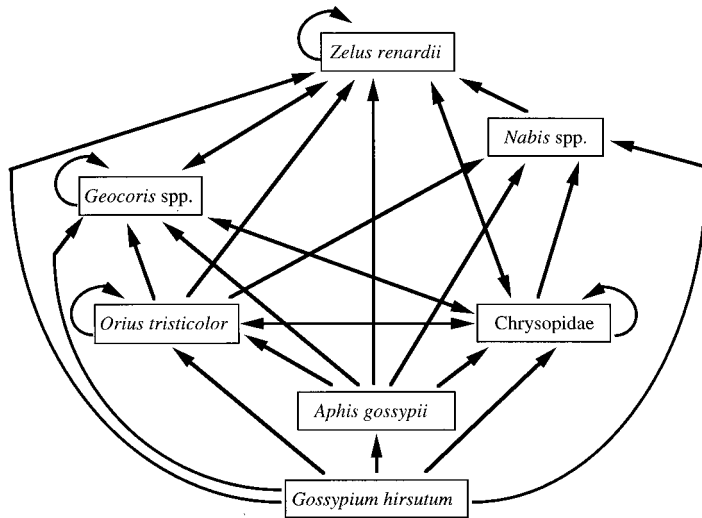


FIG. 1. Simplified trophic web of predatory arthropods associated with the cotton aphid, *Aphis gossypii*, on mid- and late-season cotton grown in the Central Valley of California, USA (Rosenheim et al. 1993; J. A. Rosenheim and D. D. Limberg, unpublished data).

tightly coupled to those of their target prey, but whose ecological roles were in other respects directly analogous to those of specialists (Murdoch et al. 1985, Hassell and May 1986). Biological control has adopted the community-ecology context for predator-prey interactions that was originally proposed by Hairston et al. (1960; see also Slobodkin et al. 1967) and subsequently extended by Fretwell (1977), Oksanen et al. (1981), and Hairston and Hairston (1993, 1997): that of three discrete trophic levels (predators, herbivores, and plants) in which biological control agents are top predators and in which different species of predators interact only through competition for shared prey. Recently, however, an alternative model has been proposed in which arthropod communities may comprise more than three trophic levels; trophic levels may be indistinct; predators may consume not only herbivores but also other predators; biological control agents may therefore be intermediate rather than top predators; and omnivory, cannibalism, and intraguild predation are widespread (Polis 1991, 1994, Wise 1993, Rosenheim et al. 1995, Polis and Strong 1996, Rosenheim 1998). Theoretical and empirical evidence suggests that higher-order consumers, including generalist predators, may disrupt what would otherwise be effective herbivore suppression by biological control agents (Holt and Polis 1997, Rosenheim 1998).

Biological control of Aphis gossypii by generalist predators

Previous work on the population dynamics of the cotton aphid, *Aphis gossypii*, in insecticide-free plantings of upland cotton, *Gossypium hirsutum*, has supported the hypothesis that higher-order predators are disrupting biological control. The cotton aphid is a dominant herbivore of *Gossypium* spp. worldwide (Leciant and Deguine 1994). Aphids exhibit irruptive dynamics in cotton grown in California's Central Valley,

despite the presence of a diverse community of generalist predators (University of California 1996). Populations of several species of predatory green lacewings, the most common of which is *Chrysoperla carnea* (family Chrysopidae), are common in mid- to late-season cotton (University of California 1996). Lacewings are known as potentially effective aphid predators, but larval stages are often rare in cotton fields that harbor non-outbreak aphid populations even when lacewing adults and eggs are common (Rosenheim et al. 1993). This curious age structure, combined with field studies documenting relatively high egg survivorship (J. A. Rosenheim, unpublished data), suggest that some strong mortality agent is acting on young lacewing larvae.

Field observations conducted from 1991 through 1996 have revealed a trophic web in California cotton in which lacewing larvae are subject to predation by a group of generalist predators in the order Hemiptera (Fig. 1). When different members of cotton's community of generalist predators, including lacewings and several predatory Hemiptera, were tested singly in field enclosures, only lacewing larvae effectively suppressed aphid population growth (Rosenheim et al. 1993). However, short-term field experiments employing single-plant enclosures suggested that hemipteran predators can impose heavy mortality (often $\geq 90\%$) on lacewing larvae, thereby releasing aphid populations from effective control (Rosenheim et al. 1993, Cisneros and Rosenheim 1997). When predators were experimentally excluded, lacewing developmental success was generally near 50%, and lacewing survival in the absence of predators was not significantly enhanced by increasing aphid densities from our standard experimental densities (~ 5 – 10 aphids per leaf) to outbreak densities (~ 100 – 200 aphids per leaf; J. A. Rosenheim, unpublished data). Thus, food limitation, the traditional explanation for predator death in the field, does not

appear to be a major source of mortality when aphid densities are ≥ 5 –10 aphids per leaf. Instead it is hemipteran predators, functioning as higher-order predators, that appear primarily to be responsible for the suppression of lacewings.

Experiments employing field enclosures may, however, distort the impact of predators if the cages alter the foraging behavior of the confined arthropods. Although a review of field experiments on predator–prey interactions suggested that caging treatments did not generally amplify the impact of predators (Sih et al. 1985), insect ecologists and biological-control researchers have a deep-seated and perhaps appropriate skepticism regarding results obtained with confined arthropods.

The primary goal of this study was therefore to provide an independent test of the hypothesis that young lacewing larvae foraging in cotton experience a high risk of predation. Our approach was to release neonate lacewing larvae in the open field and conduct focal observations to obtain direct estimates of lacewing mortality from predation. This approach is perhaps too labor intensive to have been adopted widely, but has been applied successfully to studies of freely foraging insect herbivores and parasitoids (e.g., Völkl and Kraus 1996, Bernays 1997, Heimpel et al. 1997); we are not aware of any observational studies quantifying predation on predatory insects. Direct observations also enabled us to differentiate between putative sources of mortality in the field, including (1) dislodgment from the plant, (2) predation by either heterospecific or conspecific lacewing larvae, whose cannibalistic behavior is routinely observed in laboratory studies (Canard and Duelli 1984), and (3) the impact of generalist predators in the order Hemiptera. Although an observational data set cannot definitively evaluate the importance of food limitation (experimental treatments excluding predators and manipulating prey availability are required to quantify mortality due to food limitation), we also report observed rates of lacewings feeding on arthropod prey and extrafloral nectar to define potentially important food resources.

METHODS

We released and observed neonate larvae of *Chrysoperla carnea* foraging freely in 10 field plantings of upland cotton that were grown without the use of insecticides, 1995–1996 (Table 1). Lacewing larvae were the offspring of field-collected adult *C. carnea*, which were hand-collected in cotton fields and returned to the laboratory. Adult lacewings were housed in 470-mL plastic containers lined with waxed paper (an oviposition substrate) and provided with water (delivered using a vial fitted with a wick) and food (an equal weight mixture of Wheat, which is a combination of baker's yeast and whey, and sugar). Waxed paper bearing eggs was harvested daily, and strips of the paper

bearing single eggs were held individually in 20-mL plastic vials to await egg hatch. Only neonate larvae that had descended from the egg, which is borne on a stalk, and initiated foraging no more than 3 h previously were used in the field observations.

To choose a natural location to release neonate lacewing larvae, we first chose a plant at random in the field and searched the upper half of the plant's canopy to locate all unhatched lacewing eggs, whose location we marked with flagging tape. (Lacewing eggs are concentrated in the upper plant canopy [J. A. Rosenheim, D. D. Limburg, and R. G. Colfer, *unpublished data*], and observations are very difficult on foliage close to the ground.) Hours or days later we returned and randomly selected one of the locations that still bore an unhatched egg as a site for neonate lacewing release. We removed the original egg and used a fine brush to release the neonate lacewing near the base of the egg stalk.

Working in teams of two, we attempted to record continuous observations of lacewing behavior for 4 h using a hand-held computer (Psion Organiser II [Psion PLC, London, UK]) running behavioral-event recording software (The Observer 3.0 [Noldus Information Technology b.v., Wageningen, The Netherlands]). We recorded lacewing behavior (rest, walk, feed), the identity of all arthropod prey, whether the lacewing remained on the release leaf or moved to other plant structures, and all contacts with other predators and instances of predation. We estimated the developmental instar of hemipteran predators making contacts with the focal lacewing from their body size. We also recorded instances of the lacewing falling from the plant, in which case we carefully searched foliage beneath the drop point to see if the lacewing remained on the plant (we were never able to locate larvae that fell to the soil). Throughout the process of lacewing release and subsequent observations we attempted to minimize our movements to reduce disturbances to other predators on the plant. Observations were conducted during daylight hours only (0730 to 2000).

Because the presence of alternate prey may modulate the intensity of predator–predator interactions, we chose field sites with a wide range of *Aphis gossypii* densities, and we sampled each cotton field to characterize the resident arthropod communities. Immediately after the completion of a focal observation, we counted all insects on the release leaf and estimated the percentage of the lower leaf surface that was covered by active colonies of spider mites (*Tetranychus* spp.); insects eaten by the observed lacewing larva on the release leaf were added to these counts to estimate initial prey availability. These release-leaf samples document the community of potential prey most immediately available to the released lacewings, which spent an average of 71.1% of their time within the 4-h observation period on the release leaf. An additional

TABLE 1. Summary statistics for focal observations of neonate *Chrysoperla carnea* foraging freely in insecticide-free cotton at each of ten field sites in the Central Valley of California, USA.

Site (County)	Date of observations	Number of <i>C. carnea</i> observed	Total duration of observations (h)	Total number of drops where the larva could not be relocated on the plant
1) Shafter S40 (Kern)	10–13 July 1995	14	53.97	0
2) Westside (Fresno)	17–20 July 1995	17	52.03	2
3) Sheppard M2 (Merced)	7–25 Aug. 1995	17	57.91	0
4) Sheppard 17-2S (Madera)	6–8 Sept. 1995	14	39.84	0
5) Davis W (Yolo)	12–15 Sept. 1995	14	46.21	1
6) Davis E (Yolo)	18–22 Sept. 1995	10	38.71	1
7) Sheppard 17-2N (Madera)	25–27 Sept. 1995	13	41.66	0
8) Shafter S40 (Kern)	30 July–1 Aug. 1996	13	34.23	2
9) Westside (Fresno)	21–23 Aug. 1996	12	40.84	0
10) Davis Armstrong (Yolo)	17–19 Sept. 1996	12	43.15	0
Totals		136	448.55	6

† Mean \pm 1 SE.

sample of 50 mainstem leaves, collected from the fifth node from the growing terminal from plants randomly selected within each study plot, was collected into 70% ethanol and hand-washed in the laboratory over a fine sieve (openings 75 μ m square) to collect all foliar arthropods. We also conducted whole-plant searches of 20 randomly selected plants, carefully inspecting all foliage, fruits, and stems to quantify the abundance of all predatory taxa. Plants were clipped below the cotyledonary scars on the main stem and carried to the edge of the field before being inspected. Predator densities per plant were multiplied by the density of cotton plants (estimated by counting the number of plants per 2-m of row at each of 10 locations per site) to estimate predator densities per hectare of cotton. These whole-plant searches provide good density estimates for most predatory arthropods, including lacewing larvae, which cling to plants being handled, but underestimate the densities of some mobile adult predators, which tend to fly off of handled plants (including primarily adult lacewings, *Nabis* spp., and *Zelus renardii*). Densities of these mobile predators were estimated with sweep-net samples, each comprised of 10 sweeps of a standard 38.1-cm-diameter insect net through the upper canopy of the cotton plants (1995: $n = 15$ and 1996: $n = 10$ samples per site). Adult predators collected in the sweep net were returned to the laboratory for identification to the species level. With one exception, all arthropod sampling was conducted on the same days that the neonates were observed (Table 1; the exception was the 50-leaf sample at site 6, which was taken two days later).

Bootstrapped standard errors for observed rates of neonate dislodgment from the plant, encounter with predators, and predation were obtained by resampling the original data set 1000 times.

RESULTS

As observed in previous studies, whole-plant searches indicated that densities of lacewing larvae and pupae

were relatively low in comparison with densities of lacewing eggs (Table 2), suggesting that an important mortality factor was operating on the early developmental stages.

We observed a total of 136 neonate *Chrysoperla carnea* larvae foraging freely in the field for a cumulative observation period of 448.6 h. Only three instances of contact between the focal neonate *C. carnea* and other lacewing larvae were observed (Table 1; 0.00669 ± 0.00373 encounters/h [mean \pm 1 SE]), and none of these contacts led to an attack. Thus, this study provides no evidence that cannibalism or interspecific predation within the family Chrysopidae are important sources of mortality for *C. carnea* larvae.

Contacts between neonate lacewing larvae and non-chrysopid predators occurred far more frequently. Twenty-six encounters were observed between lacewings and arthropods that might act as their predators (Table 1; 0.0580 ± 0.0164 encounters/h; 16 lacewings had a single encounter, 1 had two encounters, and 2 had four encounters); only first-instar *Orius tristicolor* were excluded from consideration as lacewing predators because of their small size and our observations that they may be preyed upon by neonate *C. carnea* (J. A. Rosenheim, unpublished data). Of the 26 encounters, 9 resulted in predation of the focal neonate *C. carnea* (0.0202 ± 0.0068 predatory encounters/h). We observed neonate *C. carnea* being preyed upon by five species of hemipteran predators: *Orius tristicolor*, 4th-instar nymph (1) and adults (2); *Geocoris pallens*, adults (2); *Geocoris punctipes*, adult (1); *Geocoris* sp., 4th-instar nymph (1); *Nabis* sp., 3rd-instar nymph (1); and *Zelus renardii*, adult (1).

Neonate lacewing larvae were more likely to encounter potential predators (other lacewings and non-chrysopid predators) while foraging (19 encounters observed, 11.2 expected based upon 38.6% of total time spent foraging) than while stationary (resting or feeding; $G = 4.3$, $P < 0.05$). Lacewings were not, however,

TABLE 1. Extended

Total number of contacts with larval Chrysopidae	Total number of contacts with nonchrysopid predators of larval <i>C. carnea</i>	Total number of predation events	Predation rate (per hour)
1	1	1	0.019
1	3	1	0.019
0	2	0	0
0	1	1	0.025
0	3	0	0
0	4	1	0.026
0	2	2	0.048
1	2	1	0.029
0	6	1	0.024
0	2	1	0.023
3	26	9	0.0202 ± 0.0068†

more likely to suffer predation while foraging (3.47 predation events expected, 4 observed; $G = 0.1$, NS).

We can use the natural variation in densities of herbivorous and predatory arthropods across the 10 field sites to examine whether correlations exist between these variables and lacewing encounters with predators or risk of predation. The arthropod communities at the 10 study sites were highly variable; mean densities of *Aphis gossypii*, the dominant herbivore, varied over >2 orders of magnitude, and densities of lacewings and other predators varied by >1 order of magnitude (Table 2). The small number of study sites and the rarity of lacewing–predator encounters and predation events (Table 1) provide little statistical power, however, so these correlational analyses should be viewed only as sources of hypotheses for future investigation. Observed encounter and predation rates were not significantly correlated with herbivore densities (herbivore densities on release leaves measured as $\ln[\text{aphids} + \text{thrips} + \text{whiteflies}]$, $r = 0.15$, NS, and $r = -0.09$, NS, respectively; herbivore densities on the fifth mainstem node leaves measured as $\ln[\text{aphids} + \text{mites} + \text{thrips} + \text{whiteflies}]$, $r = -0.25$, NS and $r = -0.31$, NS, respectively). Furthermore, neither encounter nor predation rates were significantly positively associated with the density of predators (predator densities measured using either the whole-plant searches multiplied by plant density or using the sweep-net samples; all correlations NS except predation rate vs. predator density per hectare from whole-plant searches, which showed a negative association, $r = -0.65$, $P < 0.05$).

What might explain the absence of a strong positive relationship between predator densities and rates of predation experienced by neonate lacewing larvae? Predator densities as measured in the whole-plant searches were positively correlated with herbivore densities on the fifth mainstem node leaves ($r = 0.79$, $P = 0.006$), although the positive trend was nonsignificant for predators sampled with sweep nets ($r = 0.33$, NS). If predator densities are higher in fields with more

abundant herbivore prey, then it may be that two opposing effects on lacewing mortality are offsetting one another: increasing availability of alternate prey may decrease the impact of any given predator individual, but increased total density of predators may increase the collective impact of the predator population. We can examine the per individual impact of predators on lacewings by dividing rates of encounter or predation by observed predator densities. Correlation coefficients between herbivore densities and per predator rates of encounter or predation on lacewings were consistently negative (eight of eight correlations); in only one case, however, was the negative correlation significant (contact rate per predator found in whole-plant searches vs. herbivore densities on the fifth mainstem node leaves, $r = -0.80$, $P = 0.005$). Thus, when herbivores are more abundant, each individual predator appears to have a reduced likelihood of contacting or preying on a lacewing larva. However, when herbivores are more abundant, predators are also more abundant, and these potentially offsetting effects may explain the relatively modest variation in predation rates observed across sites with widely varying densities of herbivores and predators (Table 1).

The only other possible source of mortality directly observed was dislodgment of the *C. carnea* from the cotton plant. Drops were observed 8 times, in all cases when the lacewings were actively foraging (probability of dislodgment was greater for foraging than for stationary lacewings; exact binomial probability = 0.00049). In two cases the lacewing fell to a lower leaf and resumed foraging, whereas in the remaining six cases the lacewing was not found lower on the plant and was presumed to have fallen to the ground, where we could not re-locate them because their color matched that of the soil (Table 1; 0.0134 ± 0.00553 drops/h [mean ± 1 SE]). Four drops occurred while the lacewing was foraging on the underside of the leaf. One of these cases occurred when an aphid dropped from the leaf in response to a lacewing that had walked

TABLE 2. Densities of dominant herbivorous arthropods (nymphs and adults) per leaf and possible predators of lacewing larvae (motile stages) per plant at California field sites.

Site no.	Density of dominant herbivores per release leaf				Density of predators per plant (whole-plant searches)	
	<i>Aphis gossypii</i>	<i>Tetranychus</i> spp.†	Thysanoptera	Aleyrodidae	Lacewing eggs	Lacewing larvae
1	11.9 ± 3.1	4.6 ± 1.5	1.6 ± 0.4	0.0 ± 0.0	1.60 ± 0.37	0.30 ± 0.13
2	1.2 ± 0.7	1.0 ± 0.4	1.6 ± 0.4	0.0 ± 0.0	0.55 ± 0.28	0.05 ± 0.05
3	168.8 ± 49.6	13.2 ± 5.4	4.1 ± 1.0	0.0 ± 0.0	8.15 ± 2.35	1.85 ± 0.57
4	3.9 ± 1.3	0.9 ± 0.5	0.2 ± 0.1	0.0 ± 0.0	1.25 ± 0.38	0.00 ± 0.00
5	1.1 ± 0.7	0.0 ± 0.0	0.3 ± 0.1	0.4 ± 0.2	0.95 ± 0.20	0.05 ± 0.05
6	0.8 ± 0.5	0.6 ± 0.5	0.2 ± 0.1	2.9 ± 1.1	1.55 ± 0.34	0.00 ± 0.00
7	9.8 ± 3.0	0.4 ± 0.4	0.1 ± 0.1	0.0 ± 0.0	0.85 ± 0.29	0.00 ± 0.00
8	43.5 ± 26.0	0.2 ± 0.1	0.4 ± 0.2	0.0 ± 0.0	3.15 ± 0.60	1.45 ± 0.29
9	41.4 ± 30.6	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	1.35 ± 0.28	0.20 ± 0.12
10	0.5 ± 0.4	0.0 ± 0.0	0.3 ± 0.2	0.6 ± 0.3	0.20 ± 0.09	0.05 ± 0.05

Notes: Herbivore densities were derived from counts of leaves where neonates were released for focal observations; predator densities were derived from whole-plant searches and sweep-net samples. Data are means ± 1 SE.

† Percentage lower leaf area with colonies.

‡ *Orius*, *Geocoris*, *Nabis*, *Zelus*, and spiders.

partially onto its back, thereby dislodging the lacewing as well. The remaining four drops occurred while lacewings foraged on leaf petioles or fruit peduncles, structures that bear dense trichomes. We consistently observed that lacewings encountered great difficulties locomoting on these trichome-rich surfaces (probability of dislodgment was greater for lacewings foraging on stems or fruits vs. leaves; exact binomial probability = 0.032). The risk of mortality associated with dropping to the soil surface is, however, not known. Although lacewings occasionally descended the main stem of the plant to near the soil surface, we never observed them to walk off the plant and onto the soil.

Neonate lacewings consumed a wide array of soft-bodied arthropod prey and plant-derived food during our observations. Based upon the time spent consuming different prey, the aphid *Aphis gossypii* was the predominant prey resource; aphid consumption reached high and apparently nearly saturated levels at relatively low aphid densities (site 4, mean of 3.9 aphids/release leaf; Table 2). At 4 of our 10 field sites, aphid densities were low (0.5–1.2 aphids/leaf). At these sites, the rate of aphid predation and the time spent consuming aphids were significantly lower than at the remaining six sites (Wilcoxon rank sum tests, $\chi^2 = 36.3$, $P < 0.0001$, and $\chi^2 = 43.0$, $P < 0.0001$, respectively; Table 2). Time spent consuming non-aphid arthropods (including *Tetranychus* spp. eggs and motile stages, *Frankliniella occidentalis* motile stages, *Bemisia argentifolia* nymphs and adults, *Orius tristicolor* nymphs, *Geocoris* sp. eggs, and *Chrysoperla* sp. eggs) showed a nonsignificant increase at the low-aphid-density sites (0.86 ± 0.29 min/h observation at low-aphid-density sites, 0.52 ± 0.22 min/h at high-density sites [mean ± 1 SE]; $\chi^2 = 1.7$, $P = 0.2$). Neonate lacewings spent significantly more time feeding on extrafloral nectar at sites where aphid prey were scarce ($\chi^2 = 4.2$, $P = 0.04$; Table 2).

DISCUSSION

Of 136 neonate lacewing larvae observed foraging freely in the field for a total of 448.6 h, 9 were observed to be killed by generalist hemipteran predators. How should this central result be interpreted? At first, predation may seem to be a rare event. However, because we observed lacewings for only a tiny fraction of their total immature developmental period (4 h out of 12 d = 1.4%), the fact that we observed 9/136 = 6.6% killed by predators indicates that predation is a major source of mortality. The task of projecting the total risk of predation during the three larval instars from the observed predation risk experienced by neonates is made difficult by two important lacunae in our knowledge: we do not have an estimate of predation rates during the night, and we do not have an estimate of predation rates for older-lacewing developmental stages. In Fig. 2 we have plotted the simplest case, in which we assume that the risk of predation is constant at the value observed in this study (0.0202 predatory encounters/h) across the entire period of lacewing larval development. Assuming a 12-d larval developmental period, only 0.3% of neonate lacewing larvae are expected to survive to the pupal stage (95% CI: 0.006–14.3%). Predation risk may decrease at night; if we assume zero predation during the 10-h scotophase that is typical for mid- and late-season conditions in California, our estimate of larval survivorship is 3.4% (95% CI: 0.4–32.1%). Predation risk may also decrease as lacewings grow. However, we suspect that while some small-bodied predators, such as *Orius tristicolor*, may impose less mortality on larger lacewing larvae, larger predators, such as the *Nabis* spp. and *Zelus renardii* may become more important. *Zelus renardii* appears to respond strongly to moving prey (Cisneros and Rosenheim 1997), and larger lacewings, which cover more substrate while foraging, may be at a much higher risk

TABLE 2. Extended.

Density of predators per plant (whole-plant searches)		Density in sweep-net samples	Number of aphids preyed upon per hour	Time spent consuming food (minutes per hour of observation)		
Lacewing cocoons	Other‡	Other‡		Aphid prey	Other arthropod prey	Extrafloral nectar
0.05 ± 0.05	3.05 ± 0.48	6.20 ± 0.79	0.34 ± 0.10	6.29 ± 1.88	0.23 ± 0.14	0.01 ± 0.01
0.00 ± 0.00	3.45 ± 0.49	7.73 ± 0.95	0.18 ± 0.08	2.01 ± 1.18	0.73 ± 0.57	0.16 ± 0.06
0.90 ± 0.37	37.30 ± 8.80	14.70 ± 1.69	0.86 ± 0.22	9.10 ± 1.83	0.84 ± 0.36	0.02 ± 0.02
0.00 ± 0.00	2.20 ± 0.46	9.87 ± 0.98	0.45 ± 0.11	7.87 ± 2.19	0.66 ± 0.45	0.14 ± 0.08
0.00 ± 0.00	7.65 ± 1.17	2.00 ± 0.49	0.00 ± 0.00	0.00 ± 0.00	1.04 ± 0.78	0.32 ± 0.24
0.00 ± 0.00	5.40 ± 1.15	1.67 ± 0.33	0.05 ± 0.03	0.42 ± 0.34	0.99 ± 0.43	0.00 ± 0.00
0.00 ± 0.00	4.55 ± 1.19	2.20 ± 0.37	0.30 ± 0.09	6.57 ± 2.21	1.23 ± 1.23	0.03 ± 0.03
0.00 ± 0.00	6.35 ± 0.73	13.10 ± 1.36	0.62 ± 0.19	7.62 ± 2.91	0.00 ± 0.00	0.06 ± 0.06
0.05 ± 0.05	6.75 ± 0.87	14.20 ± 2.06	0.34 ± 0.11	8.25 ± 2.97	0.00 ± 0.00	0.13 ± 0.09
0.00 ± 0.00	3.50 ± 0.72	6.70 ± 1.17	0.17 ± 0.17	0.83 ± 0.83	0.70 ± 0.39	0.11 ± 0.06

of being detected and attacked. We have observed adult *Z. renardii* consuming second- and third-instar lacewing larvae in the field (J. A. Rosenheim, unpublished data). Previous field-cage experiments initiated with older first-instar and second-instar lacewings and running long enough for the lacewings to complete most of their third instar suggested that *Geocoris* spp., *Nabis* spp., and *Z. renardii* were more important predators per capita than *Orius tristicolor*, whose impact was not measurable (Rosenheim et al. 1993, Cisneros and Rosenheim 1997). Finally, despite our efforts to minimize the disturbances that we generated in the field during the focal observations, we suspect that our presence may have decreased the observed impact of the more visually responsive predators, and in particular *Nabis* spp. and *Z. renardii*, on the neonate lacewings. We conclude, therefore, that we have documented an intense risk of predation for lacewing larvae, one that is fully consistent with the dramatic reductions of lacewing survivorship observed in our earlier experiments employing field cages.

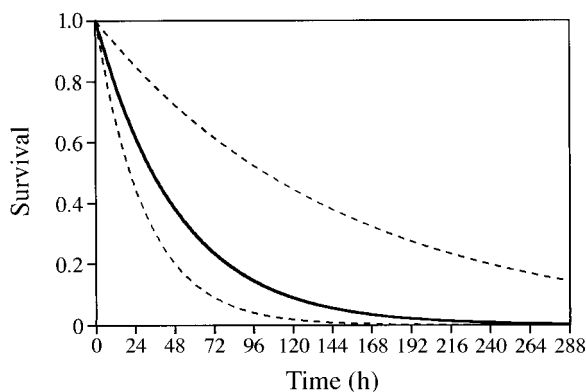


FIG. 2. Impact of generalist predators on the survivorship of larvae of the predatory lacewing, *Chrysoperla carnea*. Shown is the expected survival (solid line) and the 95% confidence interval (dashed lines) under the assumption that the risk of predation is constant (throughout a 12-d larval development) at the rate observed for neonate larvae foraging freely in the field.

Although our data set is still too small to rule out the possibility that cannibalism contributes to the mortality experienced by young lacewing larvae, it is clear that non-chrysopid predators, and in particular predatory bugs in the order Hemiptera, are the primary predators of neonate *C. carnea*. Cannibalism has been observed frequently in laboratory settings under conditions of food limitation (Canard and Duelli 1984). However, our study with *C. carnea*, a species that lays its eggs singly, suggests that larval-larval interactions are rare even in fields with high densities of lacewing eggs. Predation exerted by predatory Hemiptera may often prevent lacewing larvae from reaching densities where cannibalism could become a dominant interaction.

We observed a direct effect of the cotton plant on the ability of neonate *C. carnea* larvae to locomote. Trichomes of *Gossypium hirsutum*, which have been shown to decrease the efficacy of another larval lacewing, *Chrysopa rufilabris*, as a predator of moth eggs (Schuster and Calderon 1986), were found to dislodge neonate *C. carnea*. Lacewing larvae produce an adhesive substance in their malpighian tubules that passes through the hindgut and is applied by the tip of the abdomen to the substrate as the lacewing forages (Spiegler 1962). Lacewings struggling to move across trichome-rich plant substrates were often observed to lose grip with their legs and hang momentarily by the tip of their abdomens from the plant. This adaptation for decreasing the risk of dropping off the plant suggests that dropping is dangerous for lacewing larvae. While we have observed that neonate *C. carnea* die almost immediately if we drop them onto sunlit soil where surface temperatures are extreme (J. A. Rosenheim, D. D. Limburg, and R. G. Colfer, personal observation), most drops from the cotton canopy during the middle and late season when lacewings are abundant will be onto shaded soil. We have no knowledge of the ability of neonates to survive on the soil long enough to re-ascend plants; further work on this subject will be needed to assess the significance of dislodgment from the plant.

Our previous field experiments, initiated with plants harboring ~5–10 aphids per leaf, demonstrated that lacewing developmental success through the larval instars was high, often near 50%, and insensitive to further increases in aphid densities when other predators were experimentally excluded (Rosenheim et al. 1993, Cisneros and Rosenheim 1997, J. A. Rosenheim, *unpublished data*), suggesting that food was not limiting. This inference is consistent with our current observation that neonate larvae achieve high and perhaps saturated rates of aphid consumption at relatively low aphid densities (3.9 aphids/leaf; Table 2). Because our directly observed rates of predation on neonate lacewing larvae did not decline at sites with low aphid densities (Tables 1 and 2), it appears that the impact of higher-order predators is sufficient to produce substantial lacewing mortality under the full range of aphid densities. However, as the availability of aphid prey declines, it seems likely that food limitation will eventually become an important reinforcing or competing source of mortality. Only experimentation will provide a definitive means of assessing at what prey density neonate lacewings become food limited. Our observations suggest, however, that assessments of resource limitation for lacewings will need to consider not only aphids, but also an array of alternate arthropod prey (including herbivores, omnivores, and other predators) and plant-based resources (extrafloral nectar). We have demonstrated with a field experiment that neonate lacewing larvae live for only 1–2 d on cotton leaves without prey, but that access to extrafloral nectar extends longevity to ~14 d, although larvae never reached the second instar (J. A. Rosenheim and D. L. Limburg, *unpublished data*). The developmental schedule of lacewing larvae appears, therefore, to be highly plastic, given that the first larval instar lasts only 3–4 d when larvae are fed ad libitum (Zheng et al. 1993a, b). Because neonate lacewings captured prey at all of our sites, including those with extremely low aphid and other arthropod densities, and because lacewings require only a small number of aphid or other prey to complete their first instar (e.g., as few as 1–2 aphids/d; Baumgaertner et al. 1981, Principi and Canard 1984), it may be that extrafloral nectar and alternate prey allow neonate lacewings to sustain foraging activity during periods of aphid scarcity, decreasing the likelihood of starvation. Food limitation may, however, interact with predation if prey scarcity prolongs lacewing larval development, extending the period of lacewing vulnerability to hemipteran predators.

This study documents in a direct way an important influence of higher-order predators in a community of terrestrial arthropods, one with important ramifications for the success of biological control. Hairston and Hairston (1997), in marshaling support for the three-trophic-level model of terrestrial arthropod communities, have recently addressed the distinction between biol-

ogists who search for rules and those who search for exceptions. While additional community-level experimental work with terrestrial systems is clearly needed, it may be that the simplest-case three-discrete-trophic-level model is more the exception than the rule. A model incorporating higher-order predators and a greater diversity of trophic interactions may prove to be a more fruitful starting point in our search for general rules of pattern and process in the regulation of herbivore populations.

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