Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae

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Abstract

In a laboratory study two coccinellid species, *Coleomegilla maculata* (DeGeer) and *Harmonia axyridis* Pallas, completed preimaginal development on lacewing eggs, *Chrysoperla carnea* Stephens or pea aphids, *Acyrthosiphon pisum* (Harris) in similar times. Preimaginal survival on *C. carnea* eggs was similar to survival on *A. pisum* for all stages of *C. maculata* and *H. axyridis*. Coccinellid adults that developed on *C. carnea* eggs were smaller than adults reared on *A. pisum*. *Coccinella septempunctata* L. did not complete preimaginal development on *C. carnea* eggs. *Chrysoperla carnea* preimaginal developmental time was approximately 20 days when fed either *C. maculata* eggs or *A. pisum*. *Chrysoperla carnea* fed *C. maculata* eggs developed into smaller adults, compared to adults reared as larvae on *A. pisum*, *Ostrinia nubilalis* (Hübner) eggs, or *A. pisum* alternated daily with *O. nubilalis* eggs. *C. carnea* did not complete preimaginal development on *H. axyridis* eggs. Cannibalism occurred more frequently between *C. carnea* third instars than between *C. maculata* fourth instars. When a *C. carnea* third instar was paired with a *C. maculata* fourth instar, more *C. maculata* were preyed upon by *C. carnea*, regardless of the herbivorous prey density. In the field these two predator species may negatively affect each other and reduce their suppression of pest densities.

Introduction

Predation (and parasitism), competition, and mutualism are three types of species interactions that structure biotic populations and communities (Pianka, 1994). Predation and parasitism are the cornerstones of biological control (DeBach, 1964), but there is no consensus on the role of competition in biological control. Some researchers contend that species interactions through (within-guild) interspecific competition may reduce pest suppression (Ehler, 1985; Force, 1974; Watt, 1965); whereas others have demonstrated species interactions that led to better pest density suppression, as a result of complementary actions (Huffaker & Kennett, 1966; Huffaker, 1986). The importance of mutualism in biological control is observed primarily when predation and/or parasitism of homopterans are reduced when homopterans are tended by ants (Hölldobler & Wilson, 1990).

A fourth species interaction that may influence the structure of communities is the combination of predation and competition called intraguild predation (Polis et al., 1989; Polis & Holt, 1992). Polis et al. (1989) defined intraguild predation as 'the killing and eating of species that use similar, often limiting, resources and are thus potential competitors'. Such predator–predator interactions are thought to contribute to reductions in biological control (Rosenheim et al., 1993, 1995).

Several species of predatory Coccinellidae and Chrysopidae are commonly found in corn and alfalfa agroecosystems in the midwestern United States. *Chrysoperla carnea* Stephens is one of the most prevalent chrysopid species, whereas *Coleomegilla maculata* (DeGeer) is one of the most common coccinellid

species. Both *C. carnea* and *C. maculata* feed on a range of prey species including *Ostrinia nubilalis* eggs and *Acyrthosiphon pisum* (Principi & Canard, 1984; Obrycki et al., 1989; Hodek & Honek, 1996, Phoofolo & Obrycki, 1997). Because of spatial and temporal co-occurrence and polyphagous habits of these predators there is potential for intraguild predation.

We investigated this potential by determining the suitability of interspecific eggs as prey for the larval stages of each predatory species. Prey suitability may be an indicator of the likelihood that the prey would be attacked in the field. We also determined the suitability of *C. carnea* eggs as prey for larvae of two additional lady beetle species (*Coccinella septempunctata* L., and *Harmonia axyridis* Pallas), which co-occur seasonally with *C. carnea*, and the suitability of *H. axyridis* eggs as prey for *C. carnea* larvae. Additonally, we examined cannibalism and intraguild predation between the last larval stages of *C. carnea* (3rd instar) and *C. maculata* (4th instar).

Materials and methods

Insects. All experiments were carried out in table-top growth chambers (Percival, Boone, IA, USA), set at $26 \pm 1\,°C$, a photoperiod of L16:D8 h, and a relative humidity of 40–60%. Coccinellid and *C. carnea* adults were collected from corn fields in Story County, IA, in 1996. We maintained individual pairs of coccinellids and *C. carnea* in half-pint paper cartons (0.24 l) covered with a piece of white organdy. Pairs were provided with water, a 1:1 mixture of honey and Wheast® (Qualcepts, Minneapolis, MN, USA), and an ad libitum daily supply of *Acyrthosiphon pisum*, which was prey for adult beetles and supplied honeydew for adult *C. carnea*. These pairs provided one source of eggs used in the experiment. Additional *C. carnea* eggs were obtained from commercial insectaries (Gardens Alive, Lawrenceburg, IN, USA, and Rincon-Vitova Insectaries, Inc., Ventura, CA, USA). Both *A. pisum* and *O. nubilalis* eggs were supplied from laboratory colonies.

Preimaginal development and survival of coccinellids on C. carnea *eggs.* Eggs were collected from *C. maculata*, *H. axyridis*, and *C. septempunctata* and placed in glass vials; upon hatching, first-instars (<24 h old) were placed individually in glass vials. The larvae were provided with an ad libitum daily supply of *C. carnea* eggs (<3 d old) from Rincon-Vitova In-

sectaries. To avoid predation between coccinellid and *C. carnea* larvae, *C. carnea* eggs that were not eaten within 24 h were removed. Each day larvae were examined to determine survival, and larval and pupal stadia. Weight and sex were determined within 24 h of adult eclosion. To compare developmental time and survival of *H. axyridis* reared on *C. carnea* eggs to *A. pisum*, we reared 40 first instars on an ad libitum daily supply of *A. pisum*. Developmental time and survival of *C. maculata* and *C. septempunctata* fed *C. carnea* eggs were compared to previous studies in which these predators were reared on *A. pisum* (Phoofolo & Obrycki, 1995, 1997; Bogran, 1996).

For *C. maculata* and *H. axyridis*, differences in larval stadia, duration of pupal stage, total developmental time, and adult weight between larvae fed *A. pisum* and *C. carnea* eggs were analyzed using the Student *t*-test (SAS Institute, 1985). Percentage survival data were arc-sine transformed before statistical analysis.

Preimaginal development and survival of C. carnea *on coccinellid eggs.* Eggs were collected from *C. carnea* and placed in glass vials; upon hatching, first-instars (<24 h old) were placed individually in glass vials. Larvae were fed five diets: (1) *A. pisum* (nymphs and adults), (2) *O. nubilalis* eggs (<2 d old), (3) *A. pisum* alternated daily with *O. nubilalis* eggs, (4) *C. maculata* eggs (<3 d old), and (5) *H. axyridis* eggs (<3 d old). Prey were supplied daily to larvae ad libitum; uneaten prey items were removed from the vials after 24 h. Larvae were examined each day to determine survival and larval and pupal stadia. Weight and sex were determined within 24 h of adult eclosion. Diet groups were compared by ANOVA and Student-Newman-Keuls multi-range test (SAS Institute, 1985). Percentage survival data were arc-sine transformed before statistical analysis.

Intra- and inter-specific interactions between third-instar C. carnea *and fourth-instar* C. maculata. *Chrysoperla carnea* and *C. maculata* first instars were reared individually in glass vials and fed *A. pisum* ad libitum. Within 48 h after *C. carnea* and *C. maculata* larvae became 3rd instars and 4th instars, respectively, they were set up as conspecific pairs in 3-by-10 cm glass vials. For each species, the pairs were divided into six groups (each group= 10 pairs): (1) no prey supplied, (2) four adult *A. pisum* per day, (3) 10–20 adult *A. pisum* per day, (4) one *O. nubilalis* egg mass (<24 h old) per day, (5) three *O. nubilalis* egg masses per day, and (6) five *O. nubilalis* egg masses

per day. The larvae were examined each day, and if mortality occurred, it was qualitatively ascribed to either cannibalism (if feeding was observed or the remains were small or nonexistent) or starvation (if the remains were intact, i.e., no evidence of predation). We stopped recording data on pairs without mortality when either one or both *C. carnea* larvae spun a cocoon or one or both *C. maculata* larvae pupated. Interspecific interactions between third-instar *C. carnea* and fourth-instar *C. maculata* were examined in the same way, except one *C. carnea* larva was paired with one *C. maculata* larva in each vial. Mortality was ascribed to intraguild predation or starvation.

Voucher specimens of each predatory species are in the Iowa State University Insect Collection, Department of Entomology, Iowa State University, Ames.

Results

Preimaginal development of coccinellids on C. carnea *eggs.* Developmental times of *C. maculata* first, second, and fourth instars, and pupae, were significantly different on *C. carnea* eggs compared with *A. pisum* (Table 1). However, these differences were less than one day; we cannot attribute any biological meaning to these differences. Furthermore, total developmental period from hatching to adult eclosion was not significantly different for *C. maculata* feeding on these two prey (Table 1). The developmental time for females was similar to that for males (for larvae on *A. pisum*: *t*-test, $t = 1.15$; df$= 60$; P$= 0.25$ and for larvae on *C. carnea* eggs: $t = 0.0001$; df$= 26$; P$= 1.0$). *Coleomegilla maculata* larvae fed *C. carnea* eggs developed into lighter adults, compared to larvae fed *A. pisum* (Table 1). Females were heavier than males in both prey treatments (*t*-test, *A. pisum*: $t = 3.6$; df$= 60$; P$= 0.0006$ and *C. carnea* eggs: $t = 2.6$; df$= 26$; P$= 0.02$).

Second and third instar, pupal, and total developmental time of *H. axyridis* were significantly different between *A. pisum* and *C. carnea* eggs, but differences were less than a day, indicating that they were not biologically significant (Table 2). *Harmonia axyridis* larvae fed *A. pisum* developed into larger adults than larvae fed *C. carnea* eggs (Table 2).

Preimaginal survival of coccinellids on C. carnea *eggs.* Preimaginal survival of *C. maculata* fed *A. pisum* (data from Phoofolo & Obrycki, 1997) was similar to survival of individuals fed *C. carnea*

eggs (Table 3). Survival of *H. axyridis* varied between *A. pisum* and *C. carnea* eggs during the pupal stage (Table 3). *C. carnea* eggs were not suitable for *C. septempunctata* preimaginal survival; no fourth instars survived (Table 3).

Preimaginal development and survival of Chrysoperla carnea. Development of first and second instar *C. carnea* was slowest on *C. maculata* eggs, whereas feeding on either *A. pisum* or *C. maculata* eggs resulted in longer stadia of third instars (Table 4). Individuals reared on *A. pisum* spent the longest time as pupae (Table 4).

Developmental time of females was not significantly longer than that of males (for larvae on *A. pisum*: *t*-test, $t = 0.40$; df$= 27$; P$= 0.70$; for larvae on *O. nubilalis* eggs: $t = 1.42$; df$= 33$; P$= 0.16$; for larvae on *A. pisum* alternated daily with *O. nubilalis* eggs: $t = 1.54$; df$= 19$; P$= 0.06$; and for larvae on *C. maculata* eggs: $t = 1.26$; df$= 11$; P$= 0.23$). Therefore, total developmental times for both sexes were combined into a single analysis of variance. Total developmental time from hatching to adult eclosion was influenced by larval diet; individuals feeding either on *A. pisum* or *C. maculata* eggs required approximately 20 d from hatching to adult eclosion, whereas individuals feeding either on *O. nubilalis* eggs or *A. pisum* alternated with *O. nubilalis* eggs required approximately 16.5 d (Table 4).

Weight of females was significantly greater than that of males (*A. pisum* prey: *t*-test, $t = 3.68$; df$= 27$; P$= 0.001$; *O. nubilalis* eggs prey: $t = 4.67$; df$= 33$; P< 0.0001; *A. pisum* alternated daily with *O. nubilalis* eggs prey: $t = 3.64$; df$= 19$; P$= 0.002$; and *C. maculata* eggs prey: $t = 2.62$; df$= 11$; P$= 0.02$). Therefore, a separate ANOVA was performed on females and males. Both female and male weights were influenced by the larval prey (Table 4).

The percentage of *C. carnea* first instars that survived when fed *H. axyridis* eggs was significantly lower than the percentage of first instars that survived when fed either *A. pisum*, *O. nubilalis* eggs, *A. pisum* alternated with *O. nubilalis* eggs or *C. maculata* eggs (Table 5). None of the *C. carnea* larvae reared on *H. axyridis* eggs successfully developed to the adult stage; however, 65% of *C. carnea* larvae reared on *C. maculata* eggs successfully developed to the adult stage (Table 5).

Intraspecific interactions between C. carnea *third instars and* C. maculata *fourth instars.* When *C. mac-*

Table 1. Comparison of developmental times and adult weights of *Coleomegilla maculata* larvae fed *Acyrthosiphon pisum* or *Chrysoperla carnea* eggs, at 26 °C and a photoperiod of L16:D8 h

Prey	Larval stadia, days				Pupa	1st instar to	Adult weight, mg	
	I	II	III	IV	days	adult, days	Female	Male
A. pisum								
Mean	2.8	1.6	1.9	3.5	3.6	13.4	11.3	9.9
SD	0.5	0.7	0.4	0.5	0.5	1.0	1.7	1.3
n^a	62	62	62	62	62	62	36	26
C. carnea eggs								
Mean	2.5	2.0	2.0	4.0	3.1	13.5	9.4	7.9
SD	0.5	0.3	0.6	0.9	0.9	0.7	1.3	0.9
n^a	28	28	28	28	28	28	22	6
t value	2.8	2.8	0.6	3.3	3.6	0.3	4.4	3.4
df	88	88	88	88	88	88	56	32
P	0.006	0.007	0.6	0.01	0.006	0.8	0.0001	0.002

^{a} Number of individuals analyzed (*n*) are those that survived to the adult stage.

ulata fourth instars were paired without prey, cannibalism occurred in six of 10 pairs during the second day. By the third day, cannibalism had occurred in the remaining four pairs (Figure 1A). When supplied with four adult *A. pisum* per day, cannibalism occurred in one of 10 pairs during the first day; the cause of mortality in the other three pairs was starvation (bodies were not consumed but they were smaller than their living partners. Mortality occurred in only one of 10 pairs of *C. maculata* fourth instars when fed 10 to 20 *A. pisum* per day per pair, and that individual died on the day that its partner pupated; the cause of its mortality was unknown because the body was neither consumed nor relatively smaller. In the presence of one *O. nubilalis* egg mass, no cannibalism was observed one day after pairing, but cannibalism occurred in four pairs on day 2, in two pairs on day 3, in one pair on both days 5 and 6 (Figure 1A). When the pairs were fed three *O. nubilalis* egg masses per day only one larva died (due to cannibalism). Similarly for pairs fed five *O. nubilalis* egg masses per day, only one larva died (cause unknown) (Figure 1A).

When *C. carnea* third instars were paired in the absence of prey, cannibalism occurred in seven of 10 pairs during the first day and in the remaining pairs by the second day (Figure 1B). When fed four *A. pisum* per day, cannibalism occurred in four of 10 pairs during the first day, followed by five more pairs the next day, and by the third day cannibalism had occurred in all the pairs (Figure 1B). In the presence of 10–20 *A. pisum* per pair, cannibalism occurred

in half of the pairs by the first day, followed by one pair the second day, and three more pairs by day 3. Only one pair developed to the cocoon-spinning stage without cannibalism (Figure 1B). In the presence of one *O. nubilalis* egg mass per day, cannibalism occurred in all pairs (Figure 1B). When fed three egg masses, cannibalism occurred in seven of 10 pairs, whereas among pairs fed five egg masses per day, cannibalism occurred in two pairs (Figure 1B).

Interspecific interactions between paired C. carnea *third-instar and* C. maculata *fourth-instar.* In the absence of prey, *C. carnea* third instars killed and preyed on *C. maculata* fourth instars during the first day after pairing (Table 6). When fed four or 10–20 *A. pisum* per day, predation of *C. maculata* larvae by *C. carnea* larvae occurred in nine of 10 pairs, whereas predation of *C. carnea* by *C. maculata* occurred once (Table 6). *C. carnea* killed *C. maculata* in eight of 10 pairs when fed one *O. nubilalis* egg mass per day, whereas *C. maculata* killed *C. carnea* in one pair (Table 7). All *C. maculata* died when pairs were fed three *O. nubilalis* egg masses, whereas eight *C. maculata* died when pairs were fed five *O. nubilalis* egg masses (Table 6).

Discussion

Several coccinellid and chrysopid species have common prey, such as aphids and lepidopteran eggs, resulting in their co-occurrence in the same macro- and micro-habitats (Hagen, 1986; Coderre et al., 1987;

Table 2. Comparison of developmental times and adult weights of *Harmonia axyridis* larvae fed *Acyrthosiphon pisum* or *Chrysoperla carnea* eggs, at 26 °C and a photoperiod of L16:D8 h

Prey	Larval stadia, days				Pupa	1st instar to	Adult weight, mg	
	I	II	III	IV	days	adult, days	Female	Male
A. pisum								
Mean	2.5	1.6	1.5	4.6	4.3	14.6	34.2	30.7
SD	0.5	0.5	0.6	0.6	0.5	0.8	2.5	2.4
n^a	38	38	38	38	38	38	21	17
C. carnea eggs								
Mean	2.3	1.3	1.9	4.5	4.0	14.0	24.9	21.2
SD	0.6	0.5	0.3	0.6	0.4	0.8	4.1	3.4
n^a	24	24	24	24	24	24	11	13
t-value	1.9	2.2	3.2	0.8	2.5	3.1	8.1	8.9
df	60	60	60	60	60	60	30	28
P	0.06	0.03	0.002	0.42	0.02	0.003	0.0001	0.0001

[a] Number of individuals analyzed (*n*) are those that survived to the adult stage.

Majerus, 1994). Because of their polyphagous behavior, these predators not only feed on prey but may feed on each other (i.e., intraguild predation) to varying degrees, depending on predator and prey densities.

Chrysoperla carnea eggs are suitable prey for development of *C. maculata* and *H. axyridis*. Feeding exclusively on *C. carnea* eggs may have some negative effects, particularly on reproduction, as fecundity has been shown to be related to female body size (Stewart et al., 1991). *Coccinella septempunctata* did not complete preimaginal development on *C. carnea* eggs.

C. carnea completed preimaginal development when fed *C. maculata* eggs, and developmental time was not different from *C. carnea* larvae fed *A. pisum*. Feeding exclusively on *C. maculata* eggs by *C. carnea* larvae resulted in smaller adults, which might affect fecundity (Zheng et al., 1993). Furthermore, smaller females have longer preoviposition periods because of delayed ovarian development (Rousset, 1984). *Chrysoperla carnea* did not complete preimaginal development on *H. axyridis* eggs.

Levels of intraguild predation for *C. carnea* and coccinellids that we determined in these laboratory studies may not reflect those found under natural field conditions. This is because predators were confined with prey, thus magnifying co-occurrence, and presented with high prey densities, which may not occur in the field. However, these studies of prey suitability of other predatory species represent a first step to understand possible predator-predator interactions. Feeding behaviors of some predator species are in-

fluenced by relative prey abundance (Sharrett, 1993). Because *Chrysoperla carnea* and *C. maculata* females generally do not lay eggs in close proximity to prey such as aphids (Duelli, 1984; Coderre et al., 1987; Coderre & Tourneur, 1986), larval interactions while searching for prey may increase the probability of intraguild predation.

Cannibalism and intraguild predation are observed within larval stages, where they are regarded as extreme forms of (interference) competition (Fox, 1975; Wilbur, 1988; Polis, 1988). Predator life stage and size influence the degree of cannibalism and intraguild predation (Sengonca & Frings, 1985; Wilbur, 1988; Polis, 1988). For example, Sengonca & Frings (1985) found that when larvae of *C. septempunctata* and *C. carnea* were paired, the larger individual always preyed on the smaller individual. We observed that cannibalism occurred more frequently between *C. carnea* third instars than between *C. maculata* fourth instars. We also found that when a *C. carnea* third instar was paired with a *C. maculata* fourth instar, more *C. maculata* became prey for *C. carnea*.

Intraguild predation may have a negative impact on the degree of pest suppression through its effects on the population dynamics of the predatory species (Rosenheim et al., 1995). We have demonstrated that there is potential for *C. carnea* and *C. maculata* to negatively affect each other. *Chrysoperla carnea* is used in augmentative biological control projects (e.g., Daane et al., 1996). Such mass releases of *C. carnea*

Table 3. Comparison of stage-specific survival of *Coleomegilla maculata*, *Harmonia axyridis*, and *Coccinella septempunctata* fed *Acyrthosiphon pisum* or *Chrysoperla carnea* eggs; 26 °C and a photoperiod of L16:D8 h

Predator/prey	Percent survival				
	1st instars	2nd instars	3rd instars	4th instar	Pupa
Coleomegilla maculata					
A. pisum[a]	94.0 ± 7.3	89.1 ± 9.1	83.5 ± 10.4	83.5 ± 10.4	81.8 ± 9.7
C. carnea eggs	95.0 ± 6.8	92.5 ± 6.8	92.5 ± 6.8	90.0 ± 10.5	87.5 ± 8.8
Harmonia axyridis					
A. pisum	100 ± 0.0	100 ± 0.0	100 ± 0.0	97.5 ± 5.6	97.5 ± 5.6
C. carnea eggs	96.9 ± 6.3	96.9 ± 6.3	96.9 ± 6.3	90.6 ± 6.3	78.1 ± 18.8
P	0.29	0.29	0.29	0.13	0.02
Coccinella septempunctata					
A. pisum[b]	99.8 ± 0.9	99.8 ± 0.9	99.8 ± 0.9	98.5 ± 3.2	97.7 ± 5.2
C. carnea eggs	41.7 ± 29.2	14.6 ± 12.3	8.3 ± 6.5	0.0 ± 0.0	0.0 ± 0.0

[a] Data from Phoofolo & Obrycki (1997).
[b] Data from Phoofolo & Obrycki (1995).

Table 4. Developmental times and adult weights of *Chrysoperla carnea* larvae fed *Acyrthosiphon pisum*, *Ostrinia nubilalis* eggs, *A. pisum* alternated daily with *O. nubilalis* eggs, or *Coleomegilla maculata* eggs, at 26 °C and a photoperiod of L16:D8 h

Prey	Larval stadia, days[a]			Pupa days[a]	1st instar to adult, days[a]	Adult weight, mg[a]	
	I	II	III			Female	Male
A. pisum							
Mean	3.1[b]	2.8[b]	5.3[a]	8.9[a]	20.0[a]	7.9[b]	6.2[b]
SD	0.6	0.7	1.3	1.1	2.3	1.3	1.1
n[b]	29	29	29	29	29	16	13
O. nubilalis eggs							
Mean	3.0[b]	2.5[b]	3.0[b]	7.9[b]	16.5[b]	10.5[a]	8.4[a]
SD	0.5	0.5	0.6	0.4	1.0	1.2	1.4
n[b]	35	35	35	35	35	15	20
A. pisum alternated with *O. nubilalis* eggs							
Mean	3.2[b]	2.4[b]	3.0[b]	7.9[b]	16.6[b]	10.1[a]	8.4[a]
SD	0.8	0.7	0.5	0.4	1.2	1.1	0.7
n[b]	21	21	21	21	21	15	6
C. maculata eggs							
Mean	4.0[a]	3.8[a]	4.6[a]	8.2[b]	20.7[a]	5.7[c]	4.7[c]
SD	1.1	0.9	1.4	0.7	1.6	0.9	0.5
n[b]	13	13	13	13	13	5	8
F-value[c]	6.6	14.4	34.2	13.3	44.4	18.1	25.9
P	0.0004	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

[a] Means followed by the same letter within a column are not significantly different (P= 0.05, Student-Newman-Keuls multi-range test).
[b] Number of individuals analyzed (*n*) are those that survived to the adult stage.
[c] Degrees of freedom: for larval, pupal, and total developmental time, 3 and 94; for female weight, 3 and 47; for male weight, 3 and 43.

Table 5. Comparison of cumulative stage survival of *Chrysoperla carnea* fed *Acyrthosiphon pisum, Ostrinia nubilalis* eggs, *A. pisum* alternated daily with *O. nubilalis* eggs, *Coleomegilla maculata* eggs, or *Harmonia axyridis* eggs at 26 °C and a photoperiod of L16:D8 h

| Prey $(n)^b$ | Percent survival^a | | | |
	1st instars	2nd instars	3rd instars	Pupa
A. pisum (10)				
Mean ± SD	92.5 ± 8.7^a	87.5 ± 11.8^a	81.3 ± 14.7^{ab}	36.3 ± 19.0^a
O. nubilalis eggs (10)				
Mean ± SD	85.0 ± 11.5^{ab}	83.8 ± 10.3^{ab}	78.8 ± 15.6^{ab}	43.8 ± 17.9^a
A. pisum alternated with *O. nubilalis* eggs (5)				
Mean ± SD	72.5 ± 16.3^b	65.0 ± 20.5^b	65.0 ± 20.5^a	52.5 ± 27.1^{ab}
C. maculata eggs (5)				
Mean ± SD	95.0 ± 11.1^a	85.0 ± 22.4^a	85.0 ± 22.4^b	65.0 ± 33.5^b
H. axyridis eggs (8)				
Mean ± SD	34.4 ± 33.9^c	20.3 ± 22.1^c	6.3 ± 13.4^c	0.0 ± 0.0^c
F-value^c	10.1	16.8	27.6	15.5
P	0.0001	0.0001	0.0001	0.0001

^{a} Means followed by the same letter are not significantly different (P= 0.05, Student-Newman-Keuls multi-range test).
^{b} n refers to number of females whose progeny contributed to the mean percent survival; 10 neonates per female were started.
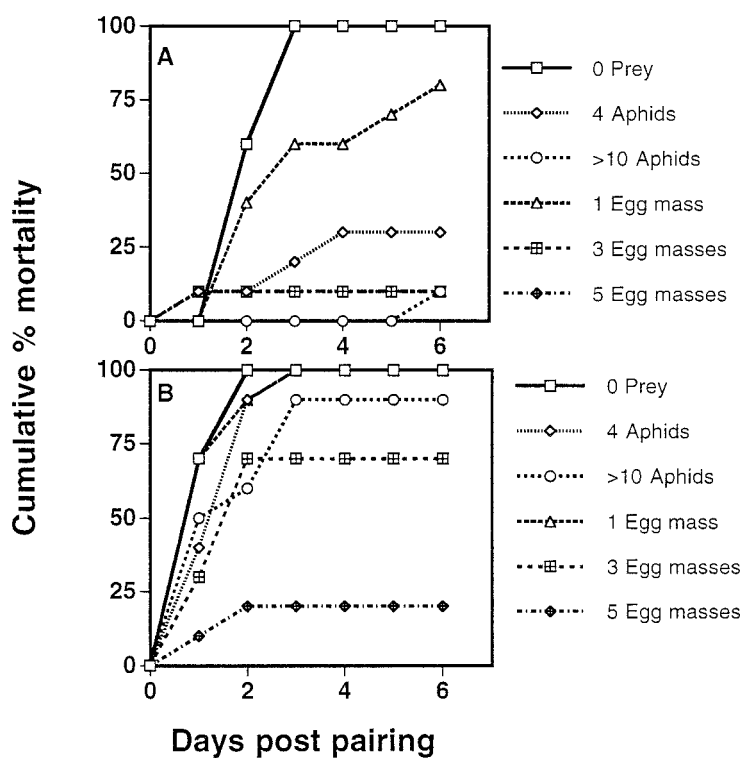^{c} Degrees of freedom= 4 and 33.

Figure 1. Cumulative mortality for 6 days after pairing larvae, as a result of competition and cannibalism between respectively (A) *Coleomegilla maculata* fourth instars and (B) *Chrysoperla carnea* third instars at 26 °C, L16:D8 h. The pairs were divided into six groups (each group= 10 pairs): (1) no prey, (2) four *Acyrthosiphon pisum* per day, (3) 10–20 *A. pisum* per day, (4) one *Ostrinia nubilalis* egg mass per day, (5) three *O. nubilalis* egg masses per day, and (6) five *O. nubilalis* egg masses per day.

Table 6. Competition and predation between a pair of third instar *Chrysoperla carnea* and fourth instar *Coleomegilla maculata*

Day[a]	Cumulative % incidence of mortality due to either starvation or predation											
	No prey		No. of *A. pisum* per day				No. of *O. nubilalis* egg masses per day					
			4		10–20		1		3		5	
	C. car[b]	C. mac[c]	C. car	C. mac	C. car	C. mac	C. car	C. mac	C. car	C. mac	C. car	C. mac
1	0	100	10	90	0	80	10	70	0	90	0	50
2	0	100	10	90	10	90	10	80	0	100	0	70
3	0	100	10	90	10	90	10	80	0	100	0	80

[a] Day is the number of days post pairing of *Chryoperla carnea* third instar and *Coleomegilla maculata* fourth instar.
[b] C. car = *Chrysoperla carnea* third instar.
[c] C. mac = *Coleomegilla maculata* fourth instar.

may magnify intraguild predation to levels which effect local densities of coccinellid larvae.

Acknowledgements

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