Oecologia (1998) 117:279–285

John J. Obrycki · Kristopher L. Giles
Andrew M. Ormord

Interactions between an introduced and indigenous coccinellid species at different prey densities

Received: 15 September 1997 / Accepted: 20 May 1998

Abstract *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), a Palearctic coccinellid, has established and rapidly spread throughout the United States. This quantitative examination of larval interactions between *C. septempunctata* and *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), a Nearctic coccinellid, was conducted under controlled prey densities. Larvae of both coccinellid species are affected by a limited diet [one pea aphid per day *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae)] compared with an excess diet (>20 aphids per day). Larval survival decreased from 86 to 63% in *C. maculata* and from 84 to 33% in *C. septempunctata*; mean preimaginal developmental time increased from 20.6 to 26.7 days in *C. maculata*, and from 18.1 to 32.0 days in *C. septempunctata*. Additionally, on one aphid per day, mean adult weight was reduced from 12.39 to 9.79 mg in *C. maculata,* and from 39.57 to 14.44 mg in *C. septempunctata*. Interspecific interactions, favoring *C. septempunctata* over *C. maculata* at a low prey density (one aphid per day), take the form of reduced survival of *C. maculata* compared with *C. septempunctata* (14 versus 66%). Reduced survival of *C. maculata* may be the result of competition for aphids or intraguild predation by *C. septempunctata* on *C. maculata*. No interspecific interactions (measured as effects on larval survival, preimaginal developmental time, and adult weight) were observed between larvae of these two species at a high prey density (>20 aphids per predator per day).

J.J. Obrycki (✉)
Department of Entomology,
Iowa State University,
Ames, IA 50011, USA
e-mail: jobrycki@iastate.edu, Fax: +1-515-2944431

K.L. Giles
Oklahoma State University,
127 Noble Research Center,
Stillwater, OK 97331, USA

A.M. Ormord
2121 Walnut Street,
Cedar Falls, IA 50613, USA

Key words Interspecific interactions · Competition · Coccinellidae · Biological control · Intraguild predation

Introduction

Twenty-six of the over 470 described species of Coccinellidae in North America north of Mexico are exotic (Gordon 1985). Sixteen of these species were intentionally imported for biological control purposes; one such species is *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), an aphid-feeding species widely distributed in Eurasia (Gordon 1985; Hodek and Honek 1996). It is not known if North American populations of *C. septempunctata* are a result of intentional release or if establishment was accidental (Angalet et al. 1979; Schaefer et al. 1987). Recent intraspecific comparisons and electrophorectic analyses of selected Palearctic and Nearctic *C. septempunctata* populations failed to resolve the question of origins of Nearctic populations (Krafsur et al. 1992; Phoofolo and Obrycki 1995).

Because *C. septempunctata* has invaded many of the same habitats occupied by a complex of Nearctic coccinellids (Obrycki and Tauber 1985; Coderre et al. 1987; Giles et al. 1994), questions have been raised about the effects of *C. septempunctata* on these Nearctic coccinellid species (Schaefer et al. 1987; Kieckhefer and Elliott 1990). In South Dakota, densities of two coccinellid species, *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) and *C. transversoguttata*, were reduced following the establishment of *C. septempunctata* (Elliott et al. 1996). Based upon trends in sampling data in North America, the introduction of *C. septempunctata* is correlated with a decline in the indigenous species *C. novemnotata* (Wheeler and Hoebeke 1995).

Agarwala and Dixon (1992) reported on intraguild predation under laboratory conditions among larvae and adults of *A. bipunctata* (L.) (Coleoptera: Coccinellidae) and *C. septempunctata* on the eggs of both of these species. Intraguild predation by *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) and *C. sept-*

empunctata larvae on the eggs, prepupae, and pupae of both of these species in the field has been described by Takahashi (1989).

The Nearctic coccinellid selected for our research is *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), a widely distributed species in the eastern United States (Hagen 1962; Gordon 1985). It is frequently one of the more abundant coccinellid species in the herbaceous stratum [e.g., agricultural crops including alfalfa (*Medicago sativa* L.), maize (*Zea mays* L.), and potato (*Solanum tuberosum* L.) (Obrycki and Tauber 1985; Kieckhefer and Elliott 1990; Giles et al. 1994).

In this paper, we focus on interactions between larvae of *C. maculata* and *C. septempunctata* because adult coccinellids are highly mobile in the field (Tamaki and Weeks 1973; Kieckhefer and Olson 1974; Ives 1981). Coccinellid larvae are more likely to remain in a field under conditions that might result in competition for food or intraguild predation. The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), was selected as prey in our research because it is highly suitable for complete larval development of *C. maculata* and *C. septempunctata* (Smith 1965a; Obrycki and Tauber 1978, Obrycki and Orr 1990; Hodek and Honek 1996).

The objectives of this research were to quantify and compare the effects of intraspecific and interspecific competition and intraguild predation between larvae of *C. maculata* and *C. septempunctata* when prey resources are limiting. These interactions were measured as effects on larval survival, preimaginal developmental time, and adult weight. Interspecific interactions were also examined when the density of aphid prey was not limiting to larval development of either species.

Materials and methods

Larvae were obtained from eggs laid by first-generation laboratory-reared females. Adults of both species were collected in Story County, Iowa, USA. Pairs were maintained in individual 1/2-pint paper cages (Neptune Paper Products, Jersey City, NJ) with water, on *A. pisum* and the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Cages were held at 22 ± 1°C/16:8 (L:D). First instars were put into their respective treatments one day after eclosion.

C. maculata and *C. septempunctata* larvae were reared on *A. pisum* that were reared on fava beans (*Vicia faba* L.) in a greenhouse. Mature apterous aphids (average weight 3.02 mg, SE 0.07 mg, $n = 100$) were selected as prey. Coccinellid larvae were fed daily with freshly collected aphids and checked for survival and molting. All rearing was done at 22 ± 1°C/16:8 (L:D) in 1/2 pint paper cages. Water was supplied from a cotton-plugged glass vial.

The six experimental treatments were: (1) one coccinellid larva per cage with 1 *A. pisum* per day; (2) two coccinellid larvae of the same species per cage with 2 *A. pisum* per day; (3) two coccinellid larvae of different species (one *C. maculata* and one *C. septempunctata*) per cage with 2 *A. pisum* per day; (4) one coccinellid larva per cage with 2 *A. pisum* per day; (5) one coccinellid larva per cage with more than 20 *A. pisum* per day; (6) two coccinellid larvae of different species (one *C. maculata* and one *C. septempunctata*) per cage with more than 40 *A. pisum* per day.

There were three replicates with 30 cages for each treatment; a total of 90 cages was established for each of the six treatments. Treatments 1 (one aphid per predator per day) and 4 (two aphids per predator per day) have no potential competitor and were designed as controls for comparison with the competitive treatments. Treatments 2 and 3 were designed to measure intraspecific and interspecific competition, respectively, at a prey density of one aphid per predator per day. Treatment 5 was designed to show the effect of unlimited prey availability on survival, developmental time, and adult size. Treatment 6 was included to examine interspecific interactions at high levels of prey availability.

Newly emerged adults were held for 24 h in their cages at 22 ± 1°C/16:8 (L:D) with water, but no prey. Adults were then weighed to the nearest 0.01 mg using an analytical balance. Total body length and width were measured using an Olympus SZH zoom stereomicroscope and sex was determined. Voucher specimens of *C. maculata*, *C. septempunctata*, *A. pisum*, and *M. persicae* were deposited in the Iowa State University Insect Collection, Department of Entomology, Iowa State University, Ames, Ia 50011, USA.

Analysis of variance (PROC GLM; SAS 1985) was used to compare the effects of prey density and the presence of another larva on developmental time from first instar to adult, percentage survival, and adult size for each coccinellid species. The survival data were transformed for the analysis of variance and the mean comparisons by calculating the arcsin of the square root of proportion that survived (Steel and Torrie 1980). A priori-determined comparisons among treatment means were made using Bonferroni's method, $P = 0.05$ (Milliken and Johnson 1984).

To test the effects of prey density on larval survival, preimaginal developmental time, and adult weight, treatments (1, 4, and 5) in which larvae were reared alone at densities of 1, 2, or more than 20 aphids per day were compared for each coccinellid species. To test the effects of the presence of another larva (conspecific or heterospecific) on larval survival, preimaginal developmental time, and adult weight, treatments 2 and 3 with potential competitors (conspecific and heterospecific, respectively) and a prey density of 1 aphid per predator per day were compared with each other and with the two treatments in which larvae were reared alone on either 1 aphid per day (1) or 2 aphids per day (4). The comparison with the treatment with no competitor and 2 aphids per day (4) was made because this would be the maximum number of prey that could be captured by a larva in either of the treatments (2 and 3) in which another larva was present.

Finally, treatment 6 in which larvae were reared with a competitor of the other species and more than 20 aphids per predator per day was compared to the treatment in which a larva was reared alone with more than 20 aphids per day (treatment 5). At these prey densities, surplus aphids were continually available to larvae. This comparison was made to examine larval interactions when prey is unlimited.

An estimated measurement of adult coccinellid body area was calculated using the equation for an ellipse [$\Pi * a * b$, where $a = 1/2$(body length) and $b = 1/2$(body width)]. This is the general shape of a coccinellid adult when viewed from a dorsal perspective. Adult weight was correlated with this adult body area measurement. Using this body size measurement, a comparison was made between adult *C. maculata* and *C. septempunctata* sampled from alfalfa fields in central Iowa, USA, over a 6-year period (1987–1992) (J.J. Obrycki, unpublished data) and adults reared with excess aphids in this study. In the field study, body length and width were measured for 5,739 *C. maculata* and 1,866 *C. septempunctata*. Body area was calculated as above. Each individual from the field collections was tested using Z scores to determine if its body area was significantly less ($P < 0.05$) than those of adults reared in the laboratory with unlimited prey (Steel and Torrie 1980). Tests were performed separately for males and females of each species.

Results

Significant differences were observed for the effects of diet, presence of another larvae, and the interaction between the level of aphid prey and larval presence on developmental time from first instar to adult, adult weight, and transformed survival from first instar to adult for *C. maculata* and *C. septempunctata* (Table 1). Comparisons of main effects will be presented; however, it should be noted that significant interactions between prey density and presence of a competitor were observed (Table 1).

Comparisons of immature survival, preimaginal developmental time, and adult weight among different prey levels (1, 2, or >20 aphids per day: treatments 1, 4, and 5, respectively) showed that larval survival from first instar to adult was lower for *C. maculata* at 1 aphid per day than for those fed >20 aphids per day (63.3 versus 85.6% Table 2). Survival at 2 aphids per day (78.9%) was similar to that at >20 aphids per day for *C. maculata* (Table 2). Similar comparisons for *C. septempunctata* show a reduction in survival at 1 aphid per day (33.3%) compared to either 2 (83.3%) or >20 (84.4%) aphids per day (Table 2). The percentage reduction in larval survival at 1 aphid per day compared with 20 aphids per day was greater for *C. septempunctata* [(84.4–33.3)/84.4 = 60%] than for *C. maculata*. [(85.6–63.3)/85.6 = 26%] (Table 2).

Developmental time increased for *C. maculata* on a diet of 1 aphid (26.7 days) or 2 (27.0 days) aphids per day compared with a diet of >20 aphids per day (20.6 days; Table 2). Developmental time of *C. septempunctata* from first instar to adult was different at all diet levels (1, 2, or >20 aphids per day: 32.0, 25.8, and 18.1 days, respectively (Table 2).

The weight of adult *C. maculata* was reduced when fed 1 aphid per day (9.79 mg) compared to 2 aphids (12.56 mg) or >20 aphids (12.39 mg) per day (Table 2). Adult weights were different among diet levels (1, 2, or >20 aphids per day: 14.44, 18.26, and 39.57 mg, respectively) for *C. septempunctata* (Table 2).

C. maculata larval survival from first instar to adult was not affected by the presence of a conspecific larva (58.9%) compared with survival of *C. maculata* fed 1 aphid per day (63.3% Fig. 1). However, the presence of a *C. septempunctata* larva significantly reduced survival of *C. maculata* larvae to 14.4% (Fig. 1).

The presence of a conspecific larva did not significantly affect larval survival of *C. septempunctata* compared with that of *C. septempunctata* on 1 aphid per day (27.8 versus 33.3%; Fig. 1). Larval survival of *C. septempunctata* increased significantly when a *C. maculata* larva was present (65.5%) compared with *C. septempunctata* alone (33.3%) or with a conspecific larva (27.8%). However, *C. septempunctata* larval survival was significantly lower than that of *C. septempunctata* alone with 2 aphids per day (83.3%; Fig. 1).

Developmental time of *C. maculata* reared with a second *C. maculata* (26.0 days) did not differ with that of *C. maculata* alone with one aphid per day (26.7 days; Table 2). When *C. maculata* was reared with a larva of *C. septempunctata,* preimaginal developmental time decreased (23.8 days). In 7 of 11 instances, when a *C. maculata* larva survived in this treatment it did so because the *C. septempunctata* larva died as a first or second instar in the experiment. The presence of a second larva (*C. septempunctata* or *C. maculata*) did not affect preimaginal developmental time of *C. septempunctata* (25.3 and 25.1 days, respectively) compared to those reared alone with 2 aphids per day (25.8 days; Table 2). Preimaginal developmental times of *C. septempunctata* for these treatments (presence of a second larva or 2 aphids per day) was shorter than that of

Table 1 ANOVA table for arcsin [square root(proportion survival from first instar to adult)], preimaginal developmental time (from first instar to adult in days), and adult weight (mg) for *Coleomegilla maculata* and *Coccinella septempunctata*

Species	Variable	Source	*df*	MS	*P*
C. maculata	Survival	Prey density	2	0.429	0.0001
		Competitor	2	0.152	0.0001
		Prey density * competitor	1	0.217	0.0001
		Error	12	0.007	
	Developmental time	Prey density	2	624.830	0.0001
		Competitor	2	14.660	0.0292
		Prey density * competitor	1	56.491	0.0002
		Error	389	4.112	
	Adult weight	Prey density	2	66.249	0.0001
		Competitor	2	24.621	0.0008
		Prey density * competitor	1	51.894	0.0001
		Error	389	3.381	
C. septempunctata					
	Survival	Prey density	2	0.304	0.0001
		Competitor	2	0.095	0.0001
		Prey density * competitor	1	0.073	0.0002
		Error	12	0.003	
	Developmental time	Prey density	2	2,897.257	0.0001
		Competitor	2	376.303	0.0001
		Prey density * competitor	1	759.826	0.0001
		Error	355	2.272	
	Adult weight	Prey density	2	17,502.978	0.0001
		Competitor	2	33.105	0.0018
		Prey density * competitor	1	472.479	0.0001
		Error	355	5.137	

Table 2 Mean percentage survival from first instar to adult, preimaginal developmental time, and adult weight (±SE) of *C. maculata* and *C. septempunctata* reared at different competitive conditions and prey densities, 22°C ± 1°C/16:8 (L:D) [*Competitor*: *None* = no competitor, *Same* = competitor of the same species, *mixed* = competitor of different species; *Diet*: *1* = 1 aphid per predator per day, *2* = 2 aphids per predator per day, *>20* = more than 20 aphids per predator per day; *% Survival*: mean percent survival from first instar to adult based on three replicates; *Developmental time*: days from first instar to adult (*n* is the same as that for adult weight); *Weight*: adult weight (mg) (*n* from each of three replicates)]

Competitor (treatment number)	Diet		*C. maculata*			*C. septempunctata*		
			% Survival	Developmental time	Weight	% Survival	Developmental time	Weight
None	1	Mean	63.3	26.7	9.79	33.3	32.0	14.44
(1)		SE	(1.9)	(0.20)	(0.21)	(1.9)	(0.53)	(0.37)
		n			18, 19, 20			10, 11, 9
Same	1	Mean	58.9	26.0	11.17	27.8	25.3	16.96
(2)		SE	(0.6)	(0.25)	(0.22)	(1.4)	(0.29)	(0.29)
		n			35, 35, 36			18, 17, 15
Mixed	1	Mean	14.4	23.8	12.78	65.5	25.1	17.03
(3)		SE	(1.1)	(0.67)	(0.56)	(2.2)	(0.20)	(0.28)
		n			4, 4, 5			19, 21, 19
None	2	Mean	78.9	27.0	12.56	83.3	25.8	18.26
(4)		SE	(5.9)	(0.24)	(0.24)	(1.9)	(0.19)	(0.30)
		n			23, 27, 21			24, 26, 25
None	>20	Mean	85.6	20.6	12.39	84.4	18.1	39.57
(5)		SE	(2.9)	(0.23)	(0.30)	(2.9)	(0.10)	(0.41)
		n			27, 24, 26			27, 24, 25
Mixed	>20	Mean	85.6	21.0	12.26	85.6	18.8	36.24
(6)		SE	(4.8)	(0.19)	(0.23)	(2.9)	(0.10)	(0.52)
		n			28, 26, 23			27, 24, 26

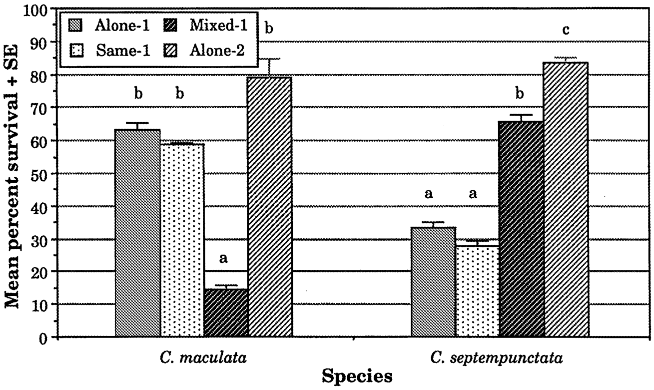

Fig. 1 Mean percentage survival of *Coleomegilla maculata* and *Coccinella septempunctata* from first instar to adult when reared in different competitive conditions (*Alone-1* one larva with one aphid per day, *Same-1* two individuals of the same species with one aphid per larva per day, *Mixed-1* two individuals of different species with one aphid per larva per day, *Alone-2* one larva with two aphids per day). *Letters* indicate significant differences among treatments within a species, Bonferroni test ($P < 0.05$)

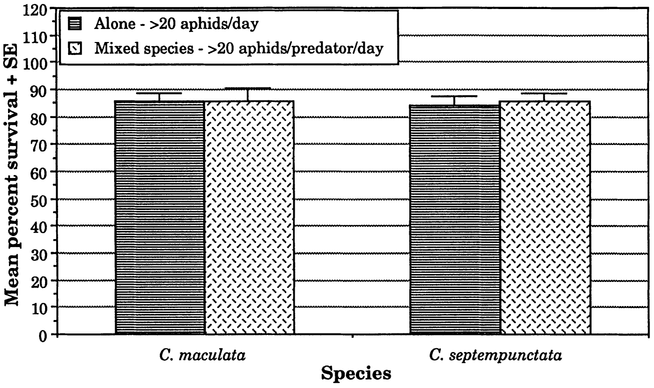

Fig. 2 Mean percentage survival of *C. maculata* and *C. septempunctata* from first instar to adult when reared alone or with an individual of the other species on unlimited prey. There are no significant differences

C. septempunctata reared singly on 1 aphid per day (32.0 days; Table 2).

Adult weight of *C. maculata* reared with a conspecific larva (11.17 mg) was between the weights of those alone with 1 aphid per day (9.79 mg) and those alone with 2 aphids per day (12.56 mg; Table 2). The adult weight of *C. maculata* reared with *C. septempunctata* (12.78 mg) was not different from weights of those alone with 2 aphids per day (12.56 mg; Table 2). The adult weight of *C. septempunctata* reared with another larva (*C. septempunctata* or *C. maculata*; 16.96 mg and 17.03 mg, respectively) was similar to the adult weight of *C. septempunctata* reared alone with 2 aphids per day (18.26 mg), but was greater than the adult weight of *C. septempunctata* reared alone with 1 aphid per day (14.44 mg; Table 2).

At high prey levels (>20 aphids per predator per day, treatments 5 and 6), *C. maculata* survival was not affected by the presence of a larva of the other species when compared with survival of those reared alone (both 85.6%). A similar pattern was observed for *C. septempunctata* (85.6 versus 84.4%; Table 2; Fig. 2). The developmental time of *C. maculata* reared with a

C. septempunctata larva at > 20 aphids per predator per day (21.0 days) was not different from that of those reared alone with > 20 aphids per day (20.6 days; Table 2). At this prey density; the preimaginal developmental time of *C. septempunctata* was not affected by the presence of a *C. maculata* larva (18.8 days) compared with that of those alone with > 20 aphids per day (18.1 days; Table 2).

The adult weight of *C. maculata* at > 20 aphids per predator per day when reared with a *C. septempunctata* larva (12.26 mg) was similar to the adult weight of *C. maculata* reared alone (12.39 mg; Table 2). The adult weight of *C. septempunctata* was also not affected by the presence of a *C. maculata* larva (36.24 mg) compared with weights of *C. septempunctata* reared alone (39.57 mg) at this prey density (Table 2).

Adult weight was highly correlated with the coccinellid body area calculation for female and male *C. maculata*. This correlation was higher for females ($P = 0.80$, $n = 215$) than for males ($P = 0.66$; $n = 186$). This relationship was used to compare the size of adults collected from the field with the size of those reared in the laboratory on a diet of > 20 aphids per day. In all 6 years, > 79% of female *C. maculata* from the field were significantly smaller than those reared in the laboratory > 20 aphids per day (Table 3). In half of the years, > 50% of *C. maculata* males collected from the field were significantly smaller than those reared in the laboratory on > 20 aphids per day (Table 3).

For *C. septempunctata*, adult weight was also highly correlated to coccinellid body area for females ($P = 0.97$, $n = 189$) and males ($P = 0.97$, $n = 178$). Comparison between field-collected adults and those reared in the laboratory at > 20 aphids per day showed that in all 6 years, > 79% of *C. septempunctata* females and > 68% of males from the field were significantly smaller than those reared in the laboratory at > 20 aphids per day (Table 3).

Table 3 Percentage of field collected *C. maculata* and *C. septempunctata* adult females and males significantly ($P < 0.05$) smaller than adults reared from larvae on unlimited prey in the laboratory (> 20 pea aphids per day). Collections from alfalfa fields in central Iowa

Year	Sex	*C. maculata*	*C. septempunctata*
1987	Female	86.2%, n = 1,080	79.5%, n = 39
	Male	55.3%, n = 293	79.3%, n = 29
1988	Female	97.0%, n = 263	92.0%, n = 87
	Male	81.6%, n = 87	78.4%, n = 102
1989	Female	90.5%, n = 359	84.3%, n = 562
	Male	64.2%, n = 173	80.8%, n = 484
1990	Female	79.1%, n = 129	89.9%, n = 69
	Male	41.7%, n = 84	87.5%, n = 56
1991	Female	85.8%, n = 1,123	82.2%, n = 90
	Male	36.6%, n = 659	68.5%, n = 89
1992	Female	85.4%, n = 907	84.5%, n = 129
	Male	33.0%, n = 582	76.2%, n = 130
Six-year total			
	Female	86.8%, n = 3,861	85.0%, n = 976
	Male	43.2%, n = 1,878	79.0%, n = 890

Discussion

Reduced food intake by preimaginal stages of predatory arthropods generally has been shown to result in reduced survival, increased developmental time, and reduced adult weight and reproduction (Smith 1965b; Turnbull 1965; Canard et al. 1984; Sengonca and Frings 1985; Valicente and O'Neil 1995; Hodek and Honek 1996). For example, Legaspi and O'Neil (1994) demonstrated that nymphs of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) fed a minimal diet had lower survival, longer developmental time, and developed into smaller adults than well-fed nymphs. Smaller female *P. maculiventris* produce fewer eggs than larger females (Evans 1982). Similarly, smaller females of *C. septempunctata* are less fecund than larger females (Sundby 1968). Larvae of *C. maculata* required at least 5 mg of dried *A. pisum* to complete development to the adult stage (Smith 1965a). The weight of the resulting adults was lowest at 5 mg and increased as the amount of dried *A. pisum* increased to 10 mg.

Interspecific competition between insect predators is based on a shared limited resource (Lawton and Hassell 1984; Keddy 1989). A reduction in the survival, growth, or fecundity of both species involved is the result of interspecific competition, but the effect may be one-sided, appearing to be amensalistic (Begon and Mortimer 1986). In this study, aphid prey was the resource for which the coccinellid larvae completed. Our data show that a prey intake rate of one mature *A. pisum* (3.02 mg live weight) per day is limiting to the development of *C. maculata* and *C. septempunctata* larvae compared with those to which excess aphids are available. Competition for food would manifest itself in the same way that reduced food availability would. Our study and the others discussed above show that competition between larvae of two coccinellids that share common prey can be assessed by measuring effects on larval survival, preimaginal developmental time, and adult weight.

The presence of a conspecific larva did not significantly affect survival of either *C. maculata* or *C. septempunctata* larvae on a diet of one pea aphid per predator per day. The survival of both *C. maculata* and *C. septempunctata* larvae was significantly affected by the presence of a heterospecific larva at a prey level of one pea aphid per predator per day. Survival of *C. maculata* larvae was significantly reduced when reared with a *C. septempunctata* larva. In contrast, survival of *C. septempunctata* larvae significantly increased when reared with a *C. maculata* larva. This asymmetry may be caused by the *C. septempunctata* larva capturing more prey, resulting in starvation of the *C. maculata* larva, or it could be caused by the *C. septempunctata* larva preying on the *C. maculata* larva, or a combination of the two. Larvae of both species were observed feeding on dead coccinellid larvae, but no attacks on a living larva were observed. This interspecific interaction between larval *C. maculata* and *C. septempunctata* favors survival of the larger *C. septempunctata* larvae. Agarwala and Dixon (1992) found that starvation increased the vulnerability of *A. bipunctata* larvae to predation by other coccinellid larvae. This may have been a contributing factor in our study; *C. maculata* larvae may have been stressed by low prey availability and became more vulnerable to predation by *C. septempunctata* larvae.

Asymmetry in interspecific competition in insects occurs more frequently than symmetric competition (Lawton and Hassell 1981; Ridsdill-Smith 1993). Persson (1985) argues that larger animals are competitively superior to smaller animals in interference competition. This may be the basis for the results of our study because adult *C. septempunctata* can be up to three times heavier than *C. maculata* (Table 2).

No previous studies have demonstrated asymmetric competitive interactions between an introduced coccinellid and an indigenous coccinellid. Evans (1991) studied competitive interactions between third-instar *Hippodamia convergens* Guerin (Coleoptera: Coccinellidae) and *C. septempunctata.* Larvae were placed together on living plants at an initial pea aphid density of eight aphids per predator; larval weight gain was measured over a 2-day period. No difference was found when an *H. convergens* larva was paired with conspecific or heterospecific larva. The pea aphids reproduced during the experiment, thus aphid densities were not limiting for either coccinellid species.

When prey is not limiting (i.e., surplus aphids are available, >20 aphids per day), no negative interactions were measured between larval *C. maculata* and *C. septempunctata*. At this prey density, larvae would not be starved and would be less vulnerable to predation by other larvae. Our results at these high prey levels are similar to the results of Evans (1991).

Our laboratory study documented competitive interactions between larvae of *C. maculata* and *C. septempunctata* only when prey levels were low. Aphid prey levels vary in the field, and when prey levels are limiting in the field, our laboratory results may be used as a basis to explain interactions under field conditions. The majority of *C. maculata* and *C. septempunctata* adults collected from alfalfa fields from 1987 to 1992 were smaller than those reared in the laboratory on >20 aphids per day. One possible factor causing reduced adult size would be low food intake during the larval stage. Thus, at low prey densities, asymmetric competitive interactions similar to those observed in our laboratory study could occur in the field.

Interspecific competition and intraguild predation among arthropod predators have been previously studied (Spiller 1986; Niemala 1993; Wissinger and McGrady 1993). Because coccinellids are predatory, intraguild predation is likely to occur among these species (Polis et al. 1989; Polis and Holt 1992; Rosenheim et al. 1995). Understanding these interactions is important when several natural enemies are used for biological control of pest species (Rosenheim et al. 1993, 1995). Intraguild predation by predatory bugs in the genera *Geocoris, Nabis,* and *Zelus* (Heteroptera) on the larvae of *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) results in higher aphid densities than those resulting from *C. carnea* predation alone (Rosenheim et al. 1993).

Our study provides a first step in identifying the effects that *C. septempunctata* might have on Nearctic coccinellid species in the United States. We documented two possible mechanisms (competition and intraguild predation between coccinellid larvae) that could be involved. Cage studies conducted to determine if these interactions occur in the field have shown that interspecific interactions between *C. septempunctata* and *C. maculata* larvae did not significantly affect aphid densities (Ormord 1994; Obrycki and Ormord 1998).

Acknowledgments We thank C. Cook, T. Cortilet, and K. Price of Iowa State University for technical assistance, and P.N. Hinz of Iowa State University for statistical assistance. We thank L.P. Pedigo, Department of Entomology and W.R. Clark, Department of Animal Ecology, Iowa State University for their critical review of an early version of this manuscript. This research was supported by USDA NRI Grant 90-37250-5357 and the Leopold Center for Sustainable Agriculture. This is Journal Paper no. J-16543 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project no. 2755.

References

Agarwala BK, Dixon AFG (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. Ecol Entomol 17: 303–309

Angalet GW, Tropp JM, Eggert AN (1979) *Coccinella septempunctata* in the United States: recolonization and notes on its ecology. Environ Entomol 8: 896–901

Begon M, Mortimer M (1986) Population ecology: a unified study of animals and plants, 2nd edn. Blackwell, Oxford

Canard M, Semeria Y, New TR (1984) Biology of Chrysopidae. Junk, The Hague

Coderre D, Provencher L, Tourneur JC (1987) Oviposition and niche partitioning in aphidophagous insects on maize. Can Entomol 119: 196–203

Elliott NC, Kieckhefer RW, Kauffman WC (1996). Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia 105: 537–544

Evans EW (1982) Consequences of body size for fecundity in the predatory stinkbug, *Podisus maculiventris* (Hemiptera: Pentatomidae). Ann Entomol Soc Am 75: 418–420

Evans EW (1991) Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. Oecologia 87: 401–408

Giles KL, Obrycki JJ, DeGooyer TA (1994) Prevalence of predators associated with *Acyrthosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. Biol Control 4: 170–177

Gordon RD (1985) The Coccinellidae (Coleoptera) of America north of Mexico. J N Y Entomol Soc 93: 1–912

Hagen KS (1962) Biology and ecology of predaceous Coccinellidae. Annu Rev Entomol 7: 289–326

Hodek I, Honek A (1996) Ecology of Coccinellidae. Kluwer, Dordrecht

Ives PM (1981) Estimation of coccinellid numbers and movement in the field. Can Entomol 113: 981–997

Keddy PA (1989) Competition. Chapman & Hall, London

Kieckhefer RW, Elliott NC (1990) A 13-year survey of the aphidophagous Coccinellidae in maize fields in eastern South Dakota. Can Entomol 122: 579–581

Kieckhefer RW, Olson GA (1974) Dispersal of marked adult coccinellids from crops in South Dakota. J Econ Entomol 67: 52–54

Krafsur ES, Obrycki JJ, Flanders RV (1992) Gene flow in populations of the seven-spotted lady beetle, *Coccinella septempunctata*. J Hered 83: 440–444

Lawton JH, Hassell MP (1981) Asymmetrical competition in insects. Nature 289: 793–795

Lawton JH, Hassell MJ (1984) Interspecific competition in insects. In: Huffaker CB, Rabb RL (eds) Ecological entomology Wiley, New York pp 451–495

Legaspi JC, O'Neil RJ (1994) Developmental response of nymphs of *Podisus maculiventris* (Heteroptera: Pentatomidae) reared with low numbers of prey. Environ Entomol 23: 374–380

Milliken GA, Johnson DE (1984) Analysis of messy data, vol 1, designed experiments. Lifetime Learning. Belmont, Calif

Niemela J (1993) Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? Oikos 66: 325–335

Obrycki JJ, Ormord AM (1998) Experimental assessment of interactions between larval *Coleomegilla maculata* (DeGeer) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) in field cages. Environ Entomol 27

Obrycki JJ, Orr CJ (1990) Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). J Econ Entomol 83: 1292–1297

Obrycki JJ, Tauber MJ (1978) Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera: Braconidae). Can Entomol 110: 407–412

Obrycki JJ, Tauber MJ (1985) Seasonal occurrence and relative abundance of aphid predators and parasitoids on pubescent potato plants. Can Entomol 117: 1231–1237

Ormord AM (1994) Interactions between larval *Coccinella septempunctata* L. and *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae). MS thesis, Iowa State University

Persson L (1985) Asymmetrical competition: are larger animals competitively superior? Am Nat 126: 261–266

Phoofolo M, Obrycki JJ (1995) Comparative life-history studies of Nearctic and Palearctic populations of *Coccinella septempunctata* (Coleoptera: Coccinellidae). Environ Entomol 24: 581–587

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

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitiors that eat each other. Annu Rev Ecol Syst 20: 297–330

Ridsdill-Smith TJ (1993) Asymmetic competition in cattle dung between two species of *Onthophagous* dung beetle and the bush fly, *Musca vetustissima*. Ecol Entomol 18: 241–246

Rosenheim JA, Wilhoit LR, Armer CA (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96: 439–449

Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological control agents: theory and evidence. Biol Cont 5: 303–335

SAS (1985) SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, NC

Schaefer PW, Dysart RJ, Specht HB (1987) North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. Environ Entomol 16: 368–373

Sengonca C, Frings B (1985) Interference and competitive behaviour of the aphid predators, *Chrysoperla carnea* and *Coccinella septempunctata* in the laboratory. Entomophaga 30: 245–251

Smith BC (1965a) Differences in *Anatis mali* Auct. and *Coleomegilla maculata lengi* Timberlake to changes in the quality and quantity of the larval food (Coleoptera: Coccinellidae). Can Entomol 97: 1159–1166

Smith BC (1965b) Effects of food on the longevity, fecundity, and development of adult coccinellids (Coleoptera: Coccinellidae). Can Entomol 97: 910–919

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

Steel RGD, Torrie JH (1980) Principles and procedures of statistics: a biometrical approach, 2nd edn. McGraw-Hill, New York

Sundby RA (1968) Some factors influencing the reproduction and longevity of *Coccinella septempunctata* Linnaeus [(Coleoptera: Coccinellidae)]. Entomophaga 13: 197–202

Takahashi K (1989) Intra- and inter-specific predations of lady beetles in spring alfalfa fields. Jpn J Entomol 57: 199–203

Tamaki G, Weeks RE (1973) The impact of predators on populations of green peach aphids on field-grown sugarbeets. Environ Entomol 2: 345–349

Turnbull AL (1965) Effects of prey abundance on the development of the spider *Agelenopsis potteri* (Blackwall) (Araneae: Agelenidae). Can Entomol 97: 141–147

Valicente FH, O'Neil RJ (1995) Effects of host plants and feeding responses on selected life history characteristics of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). Biol Control 5: 449–461

Wheeler AG, Hoebeke ER (1995) *Coccinella novemnotata* in northeastern North America: historical occur rence and current status (Coleoptera: Coccinellidae). Proc Entomol Soc Wash 97: 701–716

Wissinger S, McGrady J (1993) Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. Ecology 74: 207–218