Experimental Assessment of Interactions Between Larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in Field Cages

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ABSTRACT This experimental field study examined the interactions between larvae of *Coccinella septempunctata* L., an introduced Palearctic species, and *Coleomegilla maculata* (Degeer), a Nearctic species. The interactions were examined in 5.8-m^3 field cages enclosing potatoes infested with *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Intra- and interspecific interactions were compared by using 4 measurements: developmental time and survival from 1st instar to adult, adult weight for each coccinellid species, and *M. persicae* density. No significant differences were found between intra- and interspecific treatments in *C. maculata* survival: 19.6 and 18.3%, in 1992 and 5.7 and 3.3%, in 1993, respectively; or developmental time: 24.6 and 25.4 d in 1992 and 20.4 and 20.6 d in 1993, respectively. In 1992, no significant differences were observed between the intra- and interspecific treatments in *C. septempunctata* survival (38.3 and 39.2%) or developmental time (20.0 and 20.5 d). In 1993, no *C. septempunctata* survived to adults at the relatively lower prey densities. Interspecific interactions between *C. septempunctata* and *C. maculata* larvae did not significantly affect *M. persicae* density, compared with densities in intraspecific cages.

KEY WORDS *Coccinella septempunctata, Coleomegilla maculata,* competition, intraguild predation, interspecific interactions, nontarget effects

Coccinella septempunctata L. is a Palearctic species that has established and spread in North America (Obrycki and Kring 1998). The establishment may have been fortuitous or resulted from intentional releases (Schaefer et al. 1987, Krafsur et al. 1992). In Iowa, *C. septempunctata* was first recorded in 1985 and is now one of the more abundant coccinellid species found in agricultural crops (Obrycki et al. 1987, Giles et al. 1994, Obrycki et al. 1997). The possible effects of *C. septempunctata* on indigenous coccinellids through competitive interactions has been raised by several researchers (Gordon 1985, Schaefer et al. 1987, Kieckhefer and Elliott 1990, Wheeler and Hoebeke 1995). In South Dakota, densities of 2 coccinellid species, *Adalia bipunctata* L. and *Coccinella transversoguttata* Brown, were reduced after the establishment of *C. septempunctata* (Elliott et al. 1996).

Coccinella septempunctata may affect native coccinellids through intraguild predation, which is defined as predation among predators of a common prey species (Polis et al. 1989, Rosenheim et al. 1995). However, no field studies have quantitatively evaluated the interactions between *C. septempunctata* and any indigenous Nearctic coccinellid species or assessed the interactive effects on aphid suppression. A laboratory experiment found no negative interactions at high prey densities between 3rd-instar *C. septempunctata* and 3rd instars of the Nearctic coccinellid species *Hippodamia convergens* Guerin (Evans 1991). No manipulative field studies have been done We have examined the interactions of *C. septempunctata* and *C. maculata* larvae in the laboratory under controlled low prey densities (Obrycki et al. 1998). We focused on interactions between the larvae of *C. maculata* (Degeer) and *C. septempunctata* because predaceous larvae are more likely than adults to remain in areas where prey is scarce, resulting in competition or intraguild predation (Ives 1981).

Coleomegilla maculata was used in this study because it is one of the more abundant coccinellid species in the herbaceous stratum in the eastern United States (e.g., potato (*Solanum tuberosum* L.), maize (*Zea mays* L.), and alfalfa (*Medicago sativa* L.) (Gordon 1985, Obrycki and Tauber 1985, Kieckhefer and Elliott 1990, Giles et al. 1994). *C. maculata* and *C. septempunctata* overlap spatially and temporally in Iowa alfalfa fields (Obrycki et al. 1997).

Several methods have been used to measure the effect of predators on aphid populations (Hagen and van den Bosch 1968, Hodek et al. 1972). One common technique is to use field cages to exclude naturally occurring predators from aphids in cages or to enclose known numbers of predatory species with aphids (see Luck et al. 1988). Chambers et al. (1983) used the former technique to exclude aphid predators in wheat and observed that predators reduced aphid popula-

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Table 1. ANOVA table for arcsine (square root) transformed survival, developmental time, and adult weight for *C. maculata* and *C. septempunctata* in field cages in 1992 and 1993

Year	Species	Variable	Source	df	MS	*P*
1992	*C. maculata*	Survival[a]	Treatment[b]	1	0.0084	0.8520
			Error	6	0.2205	
		Dev. time[c]	Treatment	1	7.8663	0.3123
			Sex	1	4.2882	0.4550
			Treatment * Sex	1	1.3401	0.6759
			Error	84	7.6126	
		Adult wt[d]	Treatment	1	10.9873	0.0421
			Sex	1	108.6301	0.0001
			Treatment * Sex	1	5.0931	0.1637
			Error	84	2.5799	
1992	*C. septempunctata*	Survival[a]	Treatment	1	0.0788	0.5833
			Error	6	0.2348	
		Dev. time[c]	Treatment	1	10.5557	0.0388
			Sex	1	1.4727	0.4370
			Treatment * Sex	1	6.9439	0.0928
			Error	135	2.4236	
		Adult wt[d]	Treatment	1	4.1919	0.6424
			Sex	1	1,249.5729	0.0001
			Treatment * Sex	1	30.0149	0.2151
			Error	135	28.4634	
1993	*C. maculata*	Survival[a]	Treatment	1	0.2594	0.0762
			Error	8	0.0626	
		Dev. time[c]	Treatment	1	0.1939	0.6288
			Sex	1	0.0570	0.7927
			Treatment * Sex	0		
			Error	19	0.8032	
		Adult wt.[d]	Treatment	1	16.8189	0.0492
			Sex	1	10.4574	0.1140
			Treatment * Sex	0		
			Error	19	3.8101	
1993	*C. septempunctata*	Survival[a]	Treatment	1	0.1697	0.1626
			Error	8	0.0717	

[a] Arcsine [square root (proportion that survived from first instar to adult)].
[b] Treatments are single species (all larvae of the same species) versus mixed (larvae of both species).
[c] Developmental time from 1st instar to adult (days).
[d] Adult weight (mg).

tions outside the cages below that found within cages. Shands et al. (1972) used the latter technique and found that introductions of larval *Chrysopa* spp. (Neuroptera: Chrysopidae), *C. septempunctata*, or *Coccinella transversoguttata* reduced populations of *Myzus persicae* Sulzer (Homoptera: Aphididae) on potatoes.

The objectives of this study were to compare intra- and interspecific interactions on immature survival, developmental time from 1st instar to adult, and adult weight for *C. maculata* and *C. septempunctata* when reared in field cages with *M. persicae*. Additionally, we examined the effects of intra- and interspecific larval interactions on *M. persicae* densities on potatoes.

Materials and Methods

Experimental Conditions. Adults of both coccinellid species were collected in Story County, IA, in 1992 and 1993. Pairs of both species were maintained in individual [½]-pint paper cages (Neptune Paper Products, Jersey City, NJ) at 22 ± 1°C and a photoperiod of 16:8 (L:D) h and on an aphid diet of *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae) and *M. persicae*. Larvae were reared from eggs laid by 1st-generation laboratory reared females. First instars were held at 14 ± 1°C and a photoperiod of 16:8 (L:D) h for 1 or 2 d with *M. persicae*, until released into field cages.

The field experiment was conducted in Lumite 52-mesh field cages (1.8 by 1.8 by 1.8 m). Black polyethylene film was placed over the soil in each cage to control weeds. Fifteen potatoes (*Solanum tuberosum* L. 'Norland') were planted in each cage through holes cut in the polyethylene film. Each cage had 3 rows of potatoes (0.62 m apart) with 5 plants in each row (0.31 m apart). Each cage was at least 4 m from adjacent cages. The aphid species used as prey in this research was *M. persicae*, a pest of potatoes (Radcliffe 1982) that is suitable for larval development of both *C. maculata* and *C. septempunctata* (Hodek and Honek 1996, Obrycki and Tauber 1978, Obrycki and Orr 1990). Potatoes were selected as the host plant because coccinellid larvae and aphids can be easily counted in situ.

When the potatoes were ≈0.15 m tall they were infested with ≈20 mature *M. persicae* per plant (≈300 *M. persicae* per cage). The populations of *M. persicae* were monitored every 48–72 h by counting the number of aphids in situ on a random sample of 3 leaves (upper, middle, and lower canopy) per plant (Obry-

Table 2. Mean percentage survival, developmental time, and adult weight (±SE) of *C. maculata* and *C. septempunctata* reared in field cages in 1992 and 1993

Year	Treatment[a]	*C. maculata*				*C. septempunctata*			
		% Survival[b]	Dev. time[c]	Weight[d] female	Weight[d] male	% Survival[b]	Dev. time[c]	Weight[d] female	Weight[d] male
1992	Same (Mean)	19.6	24.5	13.85	11.73	38.3	20.5	33.17	27.81
	(SE)	10.81	0.34	0.20	0.43	8.22	0.18	0.83	0.57
	(*n*)	4	66	47	19	4	92	41	51
1992	Mixed	18.3	25.4	13.58	10.28	39.2	20.0	34.53	27.19
		9.08	0.58	0.68	0.47	11.42	0.19	0.82	0.78
		4	22	8	14	4	47	23	24
1993	Same	5.7	20.4	11.63	9.99	0.0			
		3.38	0.21	0.31	1.42	0.00			
		5	17	11	6	5			
1993	Mixed	3.3	20.6		7.51	0.0			
		2.11	0.40		0.31	0.00			
		5	5		5	5			

[a] Same, all coccinellid larvae of the same species; mixed, coccinellid larvae of both species.
[b] Mean percentage survival from 1st instar to adult.
[c] Developmental time (days) from 1st instar to adult.
[d] Adult weight (female/male) (mg).

cki and Tauber 1985). In total, 45 leaf counts were made in each cage on each sampling day. The total number of potato leaves per cage was also counted on each sampling day.

When the average density of *M. persicae* reached ≈2,000 aphids per cage, 1st-instar coccinellids were released into their respective treatments. There were 4 treatments: 60 larvae of *C. maculata*, 60 larvae of *C. septempunctata*, 30 larvae of each coccinellid species, and a control with no coccinellid larvae. The larvae were released late in the day, 18:00–2000 hours. Four larvae were placed on each plant in the cages designated to receive coccinellid larvae (2 of each species in the treatment with both coccinellid species). Each treatment was replicated 4 times in 1992 and 5 times in 1993.

After release of coccinellid larvae, sampling of *M. persicae* densities continued as described above. Coccinellid larvae seen on the sampled leaves were noted. In addition, the number of coccinellid larvae was counted by using a 3-min count during which plants and cage walls were examined. Sampling was done 8 times over a 16-d period in 1992 and 7 times over a 14-d period in 1993 until the coccinellid larvae pupated. The number of *M. persicae* per cage was estimated on each sampling day by using the mean number of aphids per leaf and the total number of leaves present in a cage. The number of coccinellid larvae of each species per cage was also estimated on each sampling day by using the same technique as for *M. persicae*, but the number of larvae observed on the cage walls was added to the estimate. Newly eclosed adults were collected daily until all had emerged; this was determined by a 1-wk period in which no adults were found. The weight and sex of each adult was determined. Adult weight of *C. maculata* and *C. septempunctata* is highly correlated to adult size, which is directly influenced by larval prey consumption (Ormord 1994).

Voucher specimens of *C. maculata*, *C. septempunctata*, *M. persicae*, and *A. pisum* are deposited in the Iowa State University Insect Collection, Department of Entomology, Iowa State University, Ames, IA.

Statistical Analyses. Comparisons were based on the null hypothesis that the effects of the single species treatment were the same as those of the 2 species treatment. Rejection of this null hypothesis indicates that interspecific interactions are different than intraspecific interactions in their effect on survival, developmental time, and adult weight of each coccinellid species and on *M. persicae* density in each treatment. The level of significance for all statistical tests was $P = 0.05$; treatment means were compared by using the Bonferroni method (Milliken and Johnson 1984). An analysis of variance (ANOVA) (PROC GLM, SAS Institute 1985) was used to compare the effects of the single species and 2 species treatments on developmental time from 1st instar to adult and the adult weight for each coccinellid species in each year. Separate comparisons were made for the adult weights of females and males. Cages were used as replicates in the analyses. However, because of the low survival of coccinellids in some cages ($n = 2$ adults), an ANOVA using cages as replicates could not be conducted for certain measurements. Thus, for analysis of developmental time and adult weight, we tested for cage effects, and then analyzed the data using individual values.

Survival data were arcsine transformed (square root of the proportion that survived) before a repeated measures ANOVA was performed and the treatments were compared (Steel and Torrie 1980). The transformed proportion survival was compared between the single species treatment and the 2 species treatment for each species in each year.

The density of *M. persicae* was compared among the 4 treatments for each year. An ANOVA (PROC GLM, SAS Institute 1985) was performed on the estimated *M. persicae* density per cage on the last day coccinellid larvae were observed each year.

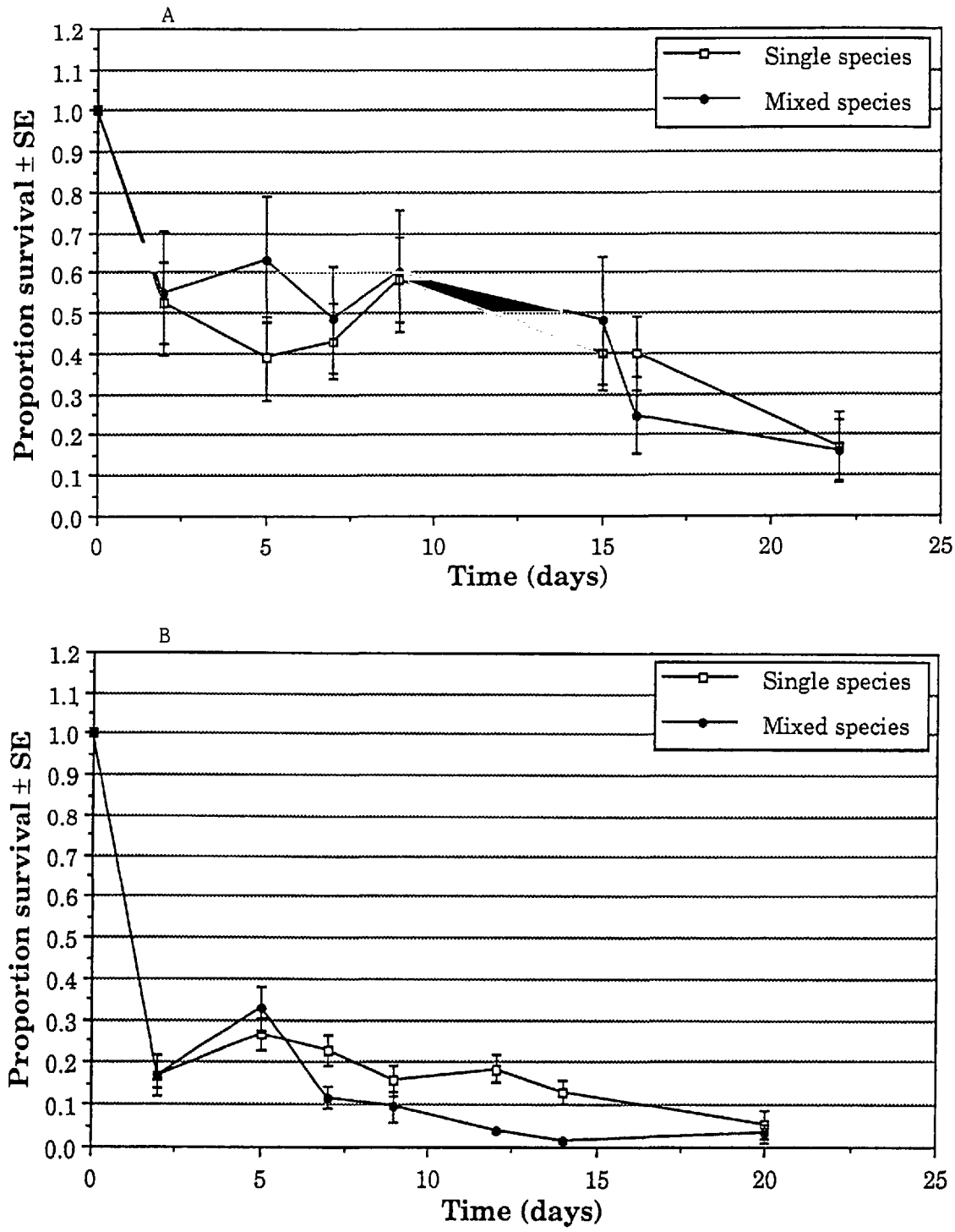

Fig. 1. Estimated proportion survival of *Coleomegilla maculata* reared with other *Coleomegilla maculata* larvae only (Single species) and when reared with *Coccinella septempunctata* (Mixed species); (A) 1992; (B) 1993.

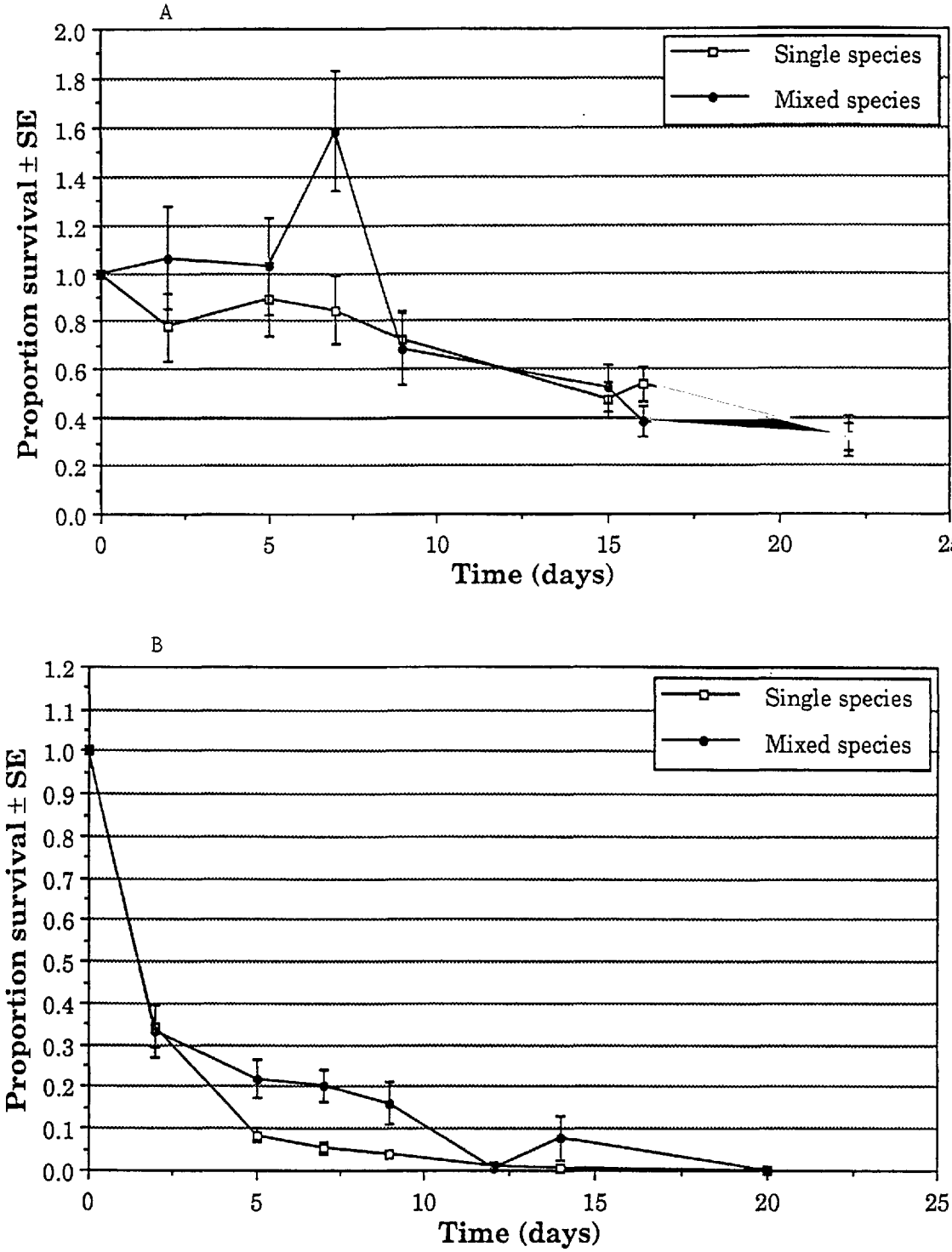

Fig. 2. Estimated proportion survival of *Coccinella septempunctata* reared with other *Coccinella septempunctata* larvae only (Single species) and when reared with *Coleomegilla maculata* (Mixed species); (A) 1992; (B) 1993.

Results

Larval Survival. The repeated measures ANOVA of the arcsine (square root) transformed survival from 1st instar to adult showed no significant treatment effect for *C. maculata* in 1992 ($P = 0.8520$) or 1993 ($P = 0.0762$) (Table 1). Survival of *C. maculata* in 1992 from 1st instar to adult in the single species treatment was 19.6 and 18.3% in the 2 species treatment (Table 2). In 1993, survival from 1st instar to adult was 5.7% in the single species treatment and 3.3% in the 2 species treatment (Table 2).

The repeated measures ANOVA of the arcsine transformed survival from 1st instar to adult showed no significant treatment effect for *C. septempunctata* in 1992 ($P = 0.5833$) or 1993 ($P = 0.1626$) (Table 1). In 1992, survival from 1st instar to adult for *C. septempunctata* was 38.3% in the single species treatment and 39.2% in the 2 species treatment (Table 2). In 1993, no *C. septempunctata* survived to the adult stage (Table 2).

Five days after release in 1992, the number of *C. maculata* larvae decreased to between 25 and 60% of those released (Fig. 1 a and b). Five days after release in 1992, the estimated number of *C. septempunctata* was 80% of the number released, which then gradually declined over the experimental period (Fig. 2 a and b). By contrast, in 1993, the number of *C. septempunctata* larvae decreased within 5 d to between 10 and 20% of the number released. The variation in the estimated proportion surviving from days 2 to 7 was caused by the difficulty in sampling early coccinellid instars. For example, on day 7 in 1992, the estimated proportion of *C. septempunctata* was greater than on day 1 (Fig. 2a). This was caused by an overestimation of the number of small larvae in the cage as a result of sampling variation in the number of young larvae observed; it was not because of the movement of *C. septempunctata* larvae into the cage.

Developmental Time. In 1992, *C. maculata* average developmental time (24.5 d) from 1st instar to adult in the single species treatment was similar to the 25.4 d observed in the 2 species treatment (Table 2). In 1993, the average developmental time of *C. maculata* from 1st instar to adult was 20.4 d in the single species treatment and 20.6 d in the 2 species treatment (Table 2). In 1992, developmental time from 1st instar to adult of *C. septempunctata* was 20.5 d in the single species cages and 20.0 d in the mixed species cages (Table 2).

Adult Weight and Sex Ratio. The ANOVA of adult weight of male and female *C. maculata* showed a significant treatment effect in 1992 ($P = 0.0421$) and 1993 ($P = 0.0492$) (Table 1). In 1992, weight of *C. maculata* males in the single species cages (11.73 mg) was significantly greater than that from the 2 species cages (10.28 mg) ($P < 0.05$) (Table 2). In 1993, weight of *C. maculata* males in the single species cages (9.99 mg) was similar to that from the 2 species cages (7.51 mg) (Table 2). In 1992, *C. maculata* females were not significantly different in the single species treatment (13.85 mg) than in the mixed species treatment (13.58 mg) (Table 2). No *C. maculata* females survived in the interspecific cages in 1993.

Table 3. ANOVA table for *M. persicae* population per cage in 1992 and 1993

Year	Source	df	MS	Pr>F
1992	Treatment	3	4.0370	0.0080
	Error	12	0.6360	
1993	Treatment	3	89.8388	0.0001
	Error	16	6.4541	

Treatments are control (no coccinellid larvae), *C. septempunctata* larvae only, *C. maculata* larvae only, and both *C. septempunctata* and *C. maculata* larvae.

In 1992, *C. septempunctata* males from the single and 2 species cages weighed between 27 and 28 mg (Table 2). *C. septempunctata* females from the single species cages weighed 33.2 versus 34.5 mg in the 2 species cages (Table 2) An analysis could not be performed on adult weight of *C. septempunctata* in 1993 because no individuals survived to the adult stage.

In 1992, the single species treatment of *C. maculata* had a high percentage of females—71%, compared with 36% females in the 2 species treatment. In 1993, the single species treatment was 65% female, whereas no females survived in the 2 species cages. In 1992, *C. septempunctata* was 45% female in the single species cages compared with 49% female in the 2 species cages.

***Myzus persicae* Densities.** The ANOVA of *M. persicae* density per cage for the last day when coccinellid larvae were observed showed significant treatment effects in 1992 ($P = 0.0080$) and 1993 ($P = 0.0001$) (Table 3). In 1992 the control treatment (41,933 aphids per cage) had significantly ($P < 0.05$) higher *M. persicae* densities than any of the treatments with coccinellid larvae (Fig. 3a). A similar result was observed in 1993; the highest density of aphids was observed in the control cages (8,138 aphids per cage; $P < 0.05$) (Fig. 3b). Temperatures during the field study were higher in 1993 (25 ± 1.1°C) than in 1992 (22 ± 0.9°C), but the potatoes grew less vigorously in 1993 compared with 1992. These 2 factors may have affected the growth of the *M. persicae* populations.

Aphid densities in the 2 species treatments were between these 2 single species treatments, but were not significantly different from either ($P > 0.05$) (Fig. 3a). In 1993, no significant differences in *M. persicae* densities were observed among the coccinellid larval treatments ($P > 0.05$) (Fig. 3b).

Discussion

Competitive interactions between species are based on a resource being in limited supply (Keddy 1989, Connell 1983, Schoener 1983). Competition between 2 species may result in a measurable reduction in the survival, growth, or fecundity of both species involved. In this field cage study, food (i.e., *M. persicae*) was the basis for competition between *C. maculata* and *C. septempunctata* larvae.

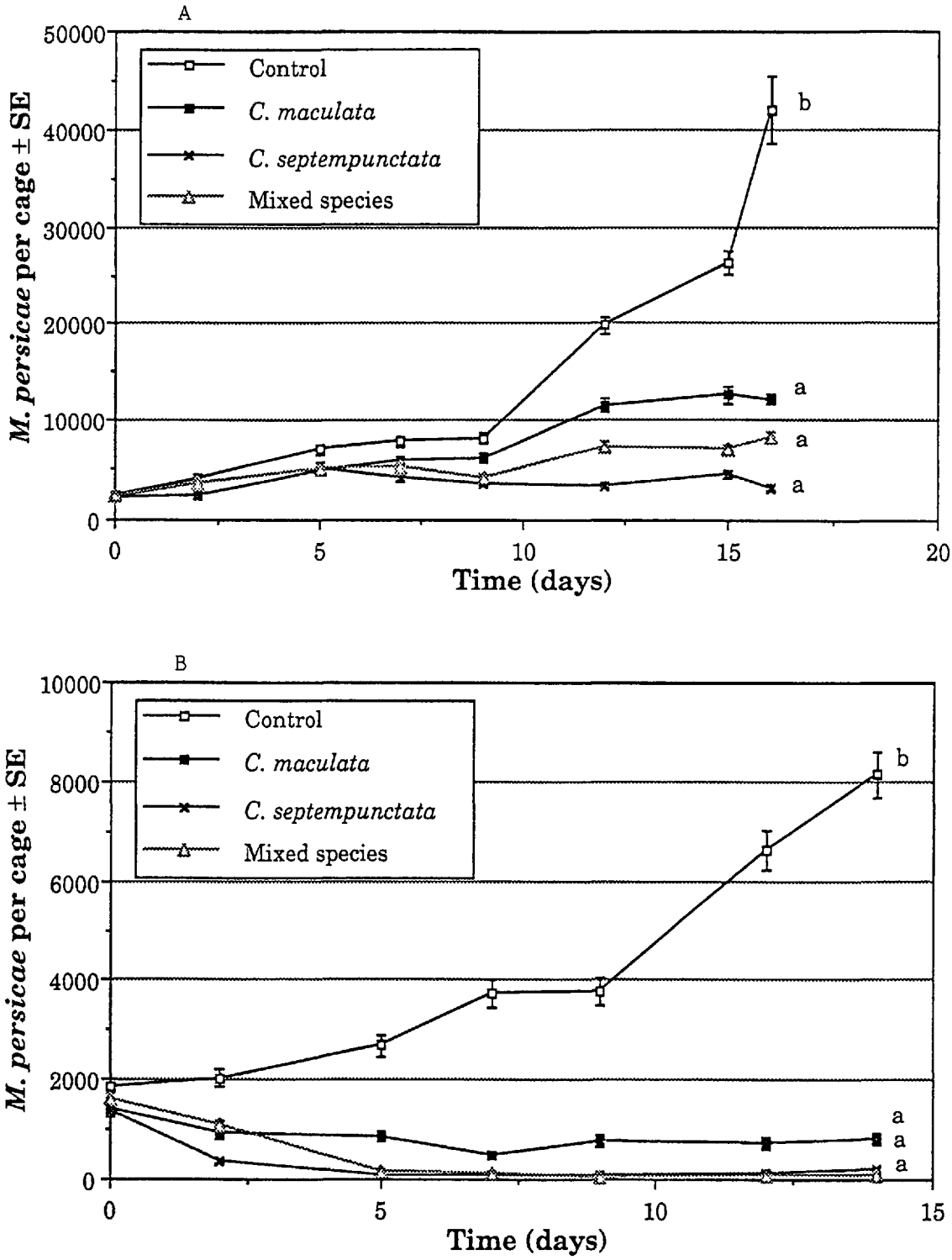

Fig. 3. Estimated number of *Myzus persicae* ± SE per cage on each sampling day in each treatment; letters indicate significant differences on the last sampling day ($P < 0.05$); (A) 1992; (B) 1993.

Reduced prey availability results in decreased survival of *C. septempunctata* larvae, increased larval developmental time, and decreased adult weight and fecundity (Sundby 1968, Hodek and Honek 1996). Reduced aphid prey levels [*A. pisum* or *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphididae)] decreased larval survival of *C. maculata* and reduced adult weight (Smith 1965). In a previous laboratory study, limited aphid prey (*A. pisum*) increased larval developmental time and reduced larval survival and adult weight of both *C. maculata* and *C. septempunctata* (Ormord 1994). Competition or intraguild predation between *C. maculata* and *C. septempunctata* larvae at a low prey density is asymmetric, favoring survival of *C. septempunctata* over *C. maculata* (Obrycki et al. 1998).

Using larval survival and adult weight as measures of competition in this field cage study, no significant differences for *C. septempunctata* were observed between the intra- and interspecific treatments. No differences were observed between the effects of the intra- and interspecific treatments on larval survival or preimaginal developmental time of *C. maculata*. In 1992, weight of *C. maculata* males was significantly reduced in the interspecific cages compared with the intraspecific cages. This may indicate that less food was consumed by *C. maculata* larvae when *C. septempunctata* larvae were present, because restricted prey consumption results in smaller adults (Ormord 1994). Additionally, *C. maculata* adults were generally smaller in 1993 when aphids were less abundant in all treatments (Table 2).

In a laboratory study, adult *C. maculata* were smallest at the lowest prey density of 1 *A. pisum* per day (average weight of 10.78 mg for females and 8.90 mg for males) and largest at the highest prey density of >20 *A. pisum* per day (average weight of 13.93 mg for females and 10.96 mg for males) (Ormord 1994). In the field cages, weights ranged from 11.63 to 13.85 mg for females and 7.51 to 11.73 mg for males of *C. maculata*. This indicates that diets were probably not optimal in the field cages for *C. maculata*.

Similarly, adult *C. septempunctata* in the laboratory study were smallest at 1 *A. pisum* per day (average weight of 14.63 mg for females and 14.22 mg for males) and largest at >20 *A. pisum* per day (average weight of 40.0 mg for females and 32.6 mg for males) (Ormord 1994). In the field cages, adult weights of *C. septempunctata* ranged from 33.2 to 34.5 mg for females and 27.2 to 27.8 mg for males. Aphid densities in the field cages were limiting for *C. septempunctata* as well.

In 1993, when prey was less abundant, no *C. septempunctata* survived to the adult stage in the intra- or interspecific treatments. However, although survival of *C. maculata* was reduced in 1993 compared with 1992, some *C. maculata* survived (3.3%) to the adult stage, even in the interspecific treatment where *C. septempunctata* was present.

In a laboratory study at a low prey density *C. septempunctata* preyed on or outcompeted *C. maculata* more often than *C. maculata* did on *C. septempunctata*, and survival of *C. septempunctata* was greater than that of *C. maculata* when together at low prey densities (Ormord 1994). In contrast, in this field cage study in 1993, *C. maculata* survived even although *C. septempunctata* was present. This observation may be explained based on Huffaker's (1958) work in which prey and predators did not coexist for extended periods in a simple laboratory environment, but persisted for extended periods when complexity was added to an artificial environment. *M. persicae* persisted to the end of the experiment in all treatments, even though *C. septempunctata* larvae were evidently starving because they were not finding prey. In the more complex environment of the field cages, compared with a simple laboratory cage arena (Ormord 1994), both *C. maculata* and *M. persicae* escaped predation by *C. septempunctata*.

In addition to environmental complexity, the lower food requirements of *C. maculata* may have facilitated its survival. Larger species (e.g., *C. septempunctata*) have a competitive advantage in interference competition, including intraguild predation, in which they physically interfere with their competitors or prey upon them. But, smaller species have a competitive advantage in exploitative competition during periods of low food availability because they require less food to develop (Lawton and Hassell 1981, Persson 1985).

This study suggests that under field conditions, even when *C. maculata* and *C. septempunctata* feed on the same aphid species in the same crop, they may coexist because aphid densities typically fluctuate within and between years. We predict that in years or locations of low aphid densities, *C. maculata* would have a competitive advantage because of its smaller size and lower food requirements. But when higher aphid densities occur, *C. septempunctata* would have a competitive advantage because of its larger size, which would favor it in interference competition and intraguild predation (Spiller 1986, Wissinger and McGrady 1993).

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