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Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids

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Summary. The nature and relative strengths of intra versus interspecific interactions among foraging ladybeetle larvae were studied experimentally by measuring short-term growth rates of predators and reductions in population sizes of prey in laboratory microcosms. In these microcosms, ladybeetle larvae foraged singly or as conspecific or heterospecific pairs, for pea aphids on bean plants over a two-day period. Similarly sized third instar larvae of *Hippodamia convergens* and *H. tredecimpunctata, H. convergens* and *H. sinuata*, and *H. convergens* and *Coccinella septempunctata*, were tested in experiments designed to ensure that paired larvae experienced moderate competition. Interspecific competition in these experiments did not differ significantly from intraspecific competition, in that an individual's weight gain did not depend on whether its competitor was heterospecific or conspecific. Furthermore, aphid populations were reduced equally by heterospecific and conspecific pairs. These results suggest that there is little or no difference between intra and interspecific interactions among larvae of these ladybeetles when two similarly sized individuals co-occur on a host plant. Thus, the species diversity *per se* of assemblages of ladybeetle larvae may have little influence over the short term on the reduction of aphid populations by ladybeetle predation.

Key words: Aphid – Biological control – Coccinellidae – Competition – Predation

High prey populations of insects generally attract large numbers of predators representing numerous species (e.g., Kirkland 1898; Morris 1972; Huffaker et al. 1976; Carter et al. 1980). In sharing a local prey population, individual predators may affect each other's foraging success (e.g., Wise 1975; Evans 1976; Hassell 1978; Evans 1983; Spiller 1984a, b). For these mixed species assemblages of predators, it is therefore of great interest to consider whether interactions among different species of predators affect their joint capacity to control numbers of their prey. Of particular concern are the intensity and nature of inter versus intraspecific interactions among the predators. How is the foraging success of individual predators, for example, affected by the activities of heterospecific versus conspecific individuals also attacking the prey? For a given number or biomass of predators, how is the prey population affected when subjected to varying diversities of predators? Do equal numbers of two predator species, for example, depress a prey population more or less than twice as many predators of either species alone?

These questions are important in assessing the significance of predator diversity in both natural and agroecosystems. They are also important in designing biological control programs, where researchers may have the option of manipulating the diversity of natural enemies attacking a target pest species, e.g., by introducing one or more natural enemies (Turnbull and Chant 1961; Ehler and Hall 1982; Ehler 1990). A new predator, for example, may simply join existing predators without affecting their impact on the prey, or the new predator may interfere with or even enhance the ability of already existing predators to control numbers of their prey.

I have explored these issues by examining inter versus intraspecific interactions of ladybeetle larvae (Coleoptera: Coccinellidae) attacking aphids (Homoptera: Aphididae). Ladybeetles are one of a number of major groups of aphidophagous arthropods, and multispecific associations of ladybeetles at local aphid outbreaks are common throughout the world (e.g., Hodek 1970; Neuenschwander et al. 1975; Obrycki and Tauber 1985; Elliot and Kieckhefer 1990). In Utah alfalfa fields, for example, as many as a dozen species of ladybeetles may co-occur in exploiting dense populations of the pea aphid, *Acyrthosiphon pisum* (Harris) (E.W. Evans, personal observations). Experimental evidence indicates that ladybeetles and other aphidophagous arthropods often keep natural populations of aphids at low densities (e.g., Way and Banks 1969; Frazer et al. 1981b; Kring

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et al. 1985; Rice and Wilde 1988), and it is therefore likely that ladybeetles commonly compete at least consumptively (sensu Schoener 1983) in nature (e.g., Frazer et al. 1981a). The basic foraging behaviors of ladybeetle larvae appear similar among species (e.g., see Banks 1957; Dixon 1959, 1970; Wratten 1973, 1976; Carter and Dixon 1984; Hajek and Dahlsten 1987), but subtle differences in the searching patterns, capture efficiencies, and/or tendencies to disturb the prey may exist among co-occurring species. Such differences may lead to a variety of outcomes in inter versus intraspecific interactions.

To examine the nature and relative strengths of intra versus interspecific interactions among foraging ladybeetle larvae, I measured short-term growth rates of individual predators and reductions in population sizes of prey in laboratory microcosms in which one or two ladybeetle larvae of one or two species foraged for pea aphids on bean plants. I used three ladybeetle species of the genus *Hippodamia* (*H. convergens* Guerin, *H. sinuata crotchi* Casey, and *H. tredecimpunctata tibialis* (Say); Gordon 1985), that are common and widespread throughout much of North America. They are among the most abundant ladybeetle species in alfalfa fields in Utah, and larvae of the three species are found frequently in proximity to each other (E.W. Evans, personal observations). I also used larvae of *Coccinella septempunctata* (L.). This Old World species is rapidly spreading across North America, aided in large part by a major USDA program to establish it and other introduced species as part of the North American fauna of ladybeetles attacking aphids (Angalet et al. 1979; Schaefer et al. 1987). At present, it occurs only in very small numbers in Utah alfalfa fields (E.W. Evans, personal observations), but as observed elsewhere in North America, its numbers will likely increase with time. The impact on native ladybeetles of interactions with this introduced predator is at present a matter of considerable concern (e.g., Obrycki et al. 1987; Schaefer et al. 1987; Elliot and Kieckhefer 1990; Kieckhefer and Elliot 1990); for example, *C. septempunctata* possibly has already competitively displaced the native *C. novemnotata* Herbst in Maryland nurseries (Staines et al. 1990).

Methods

Laboratory methods

Aphids and adult ladybeetles of the three *Hippodamia* species were collected from alfalfa fields in Cache County, Utah, while adults of *Coccinella septempunctata* were obtained from the USDA Beneficial Insects Laboratory in Niles, Michigan. The aphid colony was reared on broadbean (*Vicia faba* L., Windsor variety) at ambient temperature in the laboratory (20–29° C) and 15L:9D photoperiod. Ladybeetles were maintained as pairs in 9 cm diameter petri dishes and held in an incubator at 23° C and 15L:9D photoperiod. Larvae produced primarily by these adults and secondarily by the first generation of adults reared in the laboratory were used in foraging experiments (until used in experiments, these larvae were also reared in the incubator). Both adult and larval ladybeetles were maintained in the laboratory on a diet of frozen aphids collected in the field from alfalfa, supplemented by live aphids from the lab colony. In each of three experiments, the performances of individuals of two species of predators were compared when these individuals foraged alongside a conspecific or heterospecific individual (the first experiment also included treatments with individuals foraging singly).

In the first experiment, *Hippodamia convergens* and *H. tredecimpunctata* larvae were used. Broadbean plants were grown in square pots (13.5 cm on a side) in the lab, and used in the experiment approximately two weeks after germination, when they were 12–25 cm high with 6–8 fully expanded leaves. A clear plastic cylinder (28 cm high, and 9 cm in diameter) was placed over each plant. Plants then received 16 aphids (late instar nymphs and young adults), and one of six predator treatments: (a) no ladybeetle larvae, (b) one or (c) two larvae of *H. convergens*, (d) one or (e) two larvae of *H. tredecimpunctata*, or (f) one larva of *H. convergens* and one larva of *H. tredecimpunctata* (ladybeetles in the third of four larval instars were used in all treatments). The experimental densities of predators and prey fall well within the range of densities found in nature (e.g., Banks 1955; Wratten 1973; Mills 1982), including those in Utah alfalfa fields (E.W. Evans, personal observations).

The experiment was completed in blocks by using groups of six, similarly sized plants, and randomly assigning one plant to each predator treatment (i.e., one replicate per treatment per block). The aphids were allowed to settle on the plants for several hours (3–7) before ladybeetle larvae were added (settling times varied among but not within blocks). Ladybeetles were weighed (to the nearest 0.01 mg) immediately prior to being placed on plants (larvae were assigned randomly to plants). The larvae were allowed to forage on the plants for 40–48 (generally 44–45) hours, thus permitting them to consume a number of aphids without exhausting entirely the prey supply before the experiment was terminated. They were then removed and reweighed (wet weight), and the aphids remaining on the plants (including nymphs produced but not consumed during the experiment) were counted. The plants were placed under artificial lighting (15L:9D) on a lab bench during the experiments.

In the second and third experiments, the same protocols were followed except that I employed only the three treatments in which two ladybeetle larvae were added to a plant. I compared *H. convergens* and *H. sinuata* in the second experiment, and *H. convergens* and *C. septempunctata* in the third experiment. Seven (1.1%) of the 634 ladybeetle larvae tested died or disappeared during experiments: one of 81 *H. sinuata* larvae disappeared in the second experiment; one of 168 *H. convergens* died and another disappeared in the the third experiment (both were from conspecific pairs); and four of 168 *C. septempunctata* died in the third experiment (two each from conspecific and heterospecific pairs). Results from all treatments in blocks where larvae died were eliminated from analysis. The total numbers of replicates for each treatment remaining for analysis were 17, 26, and 50 for the first, second, and third experiment, respectively.

Statistical analyses

The growth performance of ladybeetle larvae in the experiments was measured as the percentage gain in weight (final minus initial weight, divided by initial weight). Because it was not possible to distinguish individuals in replicates where two conspecific larvae were placed together, a mean percentage gain in weight was computed for these individuals from their combined initial and final weights. In the first experiment, a two-way analysis of variance (ANOVA) was performed to compare the percentage gain in weight when one vs two individuals of either *H. convergens* or *H. tredecimpunctata* were added to plants bearing aphids. One-way ANOVA with a completely randomized block design was performed in each experiment to compare the percentage gain in weight of individuals when they were paired with conspecific versus heterospecific larvae. Because the performances of the two species were not independent in replicates where heterospecific larvae were paired, separate ANOVAs were performed for each species in each experiment.

Variances in percentage gain in weight were not significantly different among treatments within experiments (F_{max} test, Sokal and Rohlf 1981), legitimizing use of ANOVA. I also compared variances in final weight between treatments in each experiment, however, as a further test of whether larvae associated with different treatments were equally variable in their growth. To test whether one larva tended to prosper while the second suffered when conspecifics were paired, for example, I used an F test to compare the variation associated with final weight for this treatment with the variation observed when larvae foraged singly. I estimated the variation for individuals foraging in conspecific pairs by randomly selecting one of the two final weights recorded for each replicate. To compare variation between treatments independently of the magnitude of treatment means, I transformed final weights by taking their natural logarithms; I then performed F tests on the variances associated with the natural logarithms of final weights (Sokal and Rolhf 1981).

I used one-way ANOVA with linear contrasts (planned, orthogonal comparisons; Sokal and Rohlf 1981) to compare the number of aphids remaining on plants when trials were terminated in the first experiment. Comparisons included the number of aphids remaining when (1) predators (one or two) were present or absent, (2) one versus two predators were present, (3) one *H. convergens* versus one *H. tredecimpunctata* was present, (4) two *H. convergens* versus two *H. tredecimpunctata* were present, and (5) two conspecific (either *H. convergens* or *H. tredecimpunctata)* larvae versus two heterospecific larvae were present. I then performed one-way ANOVA on the numbers of aphids remaining for only the three treatments in which two ladybeetle larvae were present; I made a posteriori comparisons among these three treatments using the Tukey studentized range test. I also used one-way ANOVA with the Tukey test to compare the numbers of aphids remaining among the three treatments (all with two ladybeetle larvae present) in the second and third experiments.

Results

In all three experiments, the ladybeetles generally molted from the third to the fourth instar during the experiment. When larvae of *H. convergens* and *H. tredecimpunctata* foraged as single individuals on experimental plants, they nearly doubled their (wet) weight over the two-day experimental period (Fig. 1). The percentage gain in weight of larvae was significantly reduced when they foraged as paired conspecifics versus as solitary individuals (Table 1 and Fig. 1). There was no significant difference between species, however, in percentage weight gain at a given predator density, nor was there a significant interaction between predator species and density (Table 1). While paired conspecific individuals gained less weight than

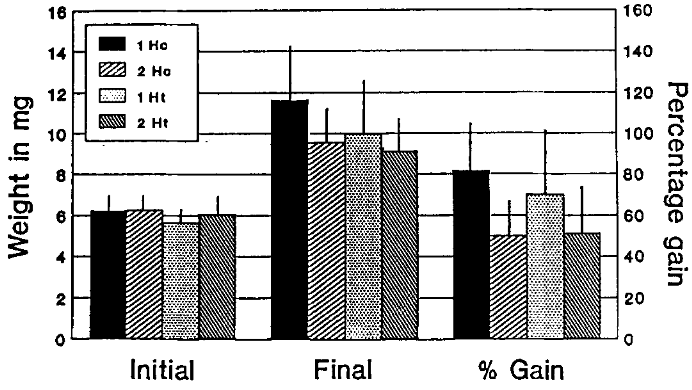

Fig. 1. Initial and final weights (in mg), and percentage gain in weight, of larvae of *H. convergens* (Hc) and *H. tredecimpunctata* (Ht) in the first experiment, when they foraged singly vs in conspecific pairs (vertical bars indicate 2 standard errors)

Table 1. Two-way analysis of variance for the percentage gain in weight of larvae of *H. convergens* and *H. tredecimpunctata* foraging alone or as conspecific pairs (first experiment; $N=68$, or 17 for each of four treatments)

Source of variation	df	MS	*F*	*P*
Species	1	0.0454	0.18	0.67
# Predators	1	1.0907	4.41	0.04
Interaction	1	0.0665	0.27	0.61
Error	64	0.2475		
Total	67			

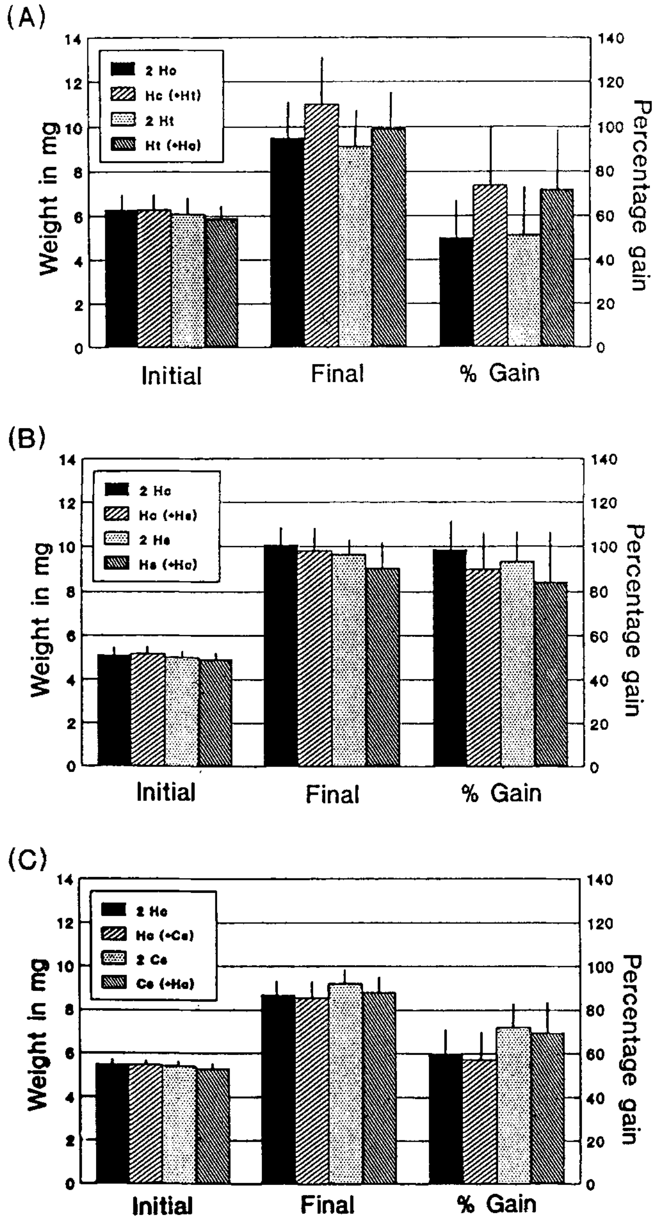

Fig. 2A–C. Initial and final weights (in mg), and percentage gain in weight, of larvae of (a) *H. convergens* (Hc) and *H. tredecimpunctata* (Ht), (b) *H. convergens* (Hc) and *H. sinuata* (Hs), and (c) *H. convergens* (Hc) and *C. septempunctata* (Cs), when they foraged as conspecific vs heterospecific pairs (vertical bars indicate 2 standard errors) solitary individuals, they were not significantly more variable in their final weights (transformed to natural logarithms) than were their solitary counterparts (d.f. = 16,16, F = 1.02 and 1.71, $P > 0.10$ in both instances, for *H. convergens* and *H. tredecimpunctata*, respectively).

The percentage gain in weight was not significantly different for individuals foraging in conspecific versus heterospecific pairs for either species (Fig. 2a; d.f. = 1,16, F = 3.84 and 1.70, $P = 0.068$ and 0.21, for *H. convergens* and *H. tredecimpunctata*, respectively). There was also no significant difference for either species between the variances associated with final weights of individuals when they foraged with conspecifics versus heterospecifics (d.f. = 16,16, F = 1.00 and 1.17, $P > 0.10$ in both instances, for *H. convergens* and *H. tredecimpunctata*, respectively).

In microcosms without ladybeetles, aphids occurred throughout the plant. They often were clustered especially on the undersides of upper leaves. In microcosms with ladybeetles, aphids were relatively rarely found near the tops of plants; instead they tended to be clustered on the stem and leaves near the bottom of the plant. This difference in aphid spatial patterns probably reflects that aphids disturbed by ladybeetles often drop to the ground, later returning to the plant and settling on those plant parts first encountered (i.e., lower leaves and stem). In the absence of ladybeetle larvae, 13.9 ± 1.0 (x ± 2 standard errors) adult and 102.9 ± 21.3 nymphal aphids were counted per replicate at the termination of the first experiment. While ladybeetle larvae significantly depressed aphid population growth, individuals of *H. convergens* and *H. tredecimpunctata* did not differ significantly, either as solitary or as paired conspecific foragers, in their capacities to reduce aphid numbers (Table 2 and Fig. 3). Solitary larvae reduced numbers of aphid nymphs and adults to 40–50% of numbers recorded in the absence of

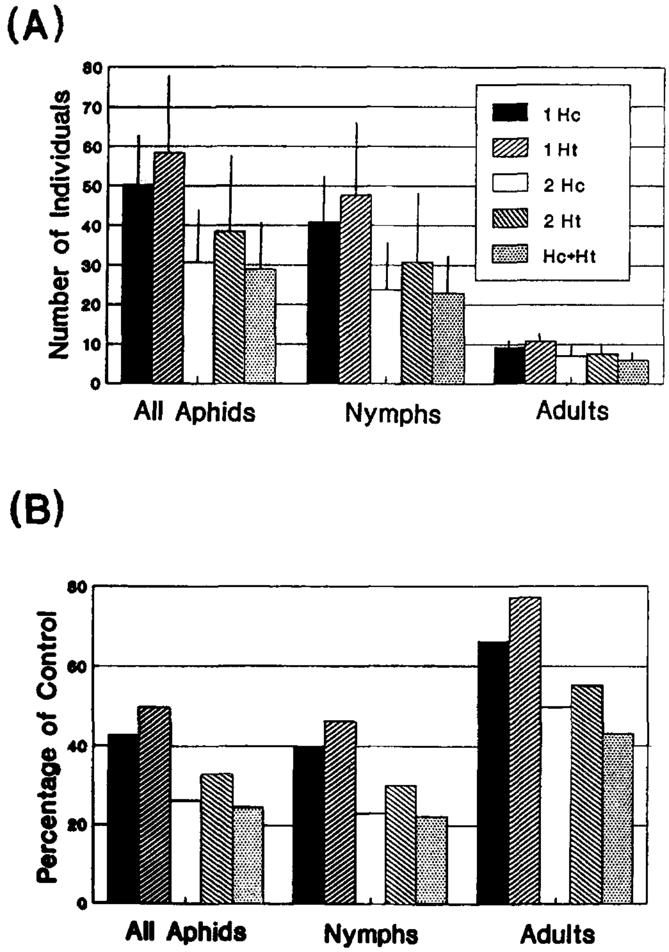

Fig. 3. (A) The number of individuals of aphids remaining when larvae of *H. convergens* (Hc) and *H. tredecimpunctata* (Ht) were removed from bean plants in the first experiment (vertical lines indicate two standard errors), also expressed (B) as the percentage of the number remaining in the control treatment (without ladybeetles)

Table 2. One-way analysis of variance with linear contrasts for the number of aphids remaining when ladybeetle larvae were removed from plants in the first experiment. Linear contrasts include: aphids on plants with no predators vs predators ("no pred vs pred"), with one vs two (conspecific or heterospecific) predators, with one or two predators of *H. convergens* or of *H. tredecimpunctata* ("one pred: Hc vs Ht" and "two pred: Hc vs Ht", respectively), or two conspecific or heterospecific predators ("two preds: consp vs heterosp")

Source of variation	df	All Aphids			Aphid Adults			Aphid Nymphs		
		MS	F	P	MS	F	P	MS	F	P
Block	16	3359.35	4.38	****	45.33	4.43	****	2996.69	4.41	****
Treatment	5	18619.11	24.28	****	144.30	14.11	****	15365.87	22.64	****
No pred vs Pred	1	82029.45	106.95	****	478.50	46.77	****	68788.10	101.33	****
One vs two Pred	1	9585.33	12.50	***	198.29	19.38	***	7011.23	10.33	**
One Pred: Hc vs Ht	1	568.26	0.74	NS	19.88	1.94	NS	375.56	0.55	NS
Two Preds: Hc vs Ht	1	528.12	0.69	NS	4.92	0.48	NS	430.62	0.63	NS
Two Preds: consp vs heterosp	1	384.25	0.50	NS	19.85	1.94	NS	223.54	0.33	NS
Error	80	766.98			10.23			678.84		

P values: **** <0.0001, *** <0.001, ** <0.01, NS>0.10. N = 102, or 17 for each of six treatments

Table 3. One-way analysis of variance for the number of aphids remaining when conspecific and heterospecific pairs of ladybeetle larvae were removed from plants in the first ("Hc and Ht": *H. convergens* and *H. tredecimpunctata*), second ("Hc and Hs": *H. convergens* and *H. sinuata*) and third ("Hc and Cs": *H. convergens* and *C. septempunctata*) experiments

Source of variation	df	All Aphids			Aphid Adults			Aphid Nymphs		
		MS	F	P	MS	F	P	MS	F	P
Hc and Ht										
Block	16	1591.83	2.39	*	46.25	5.31	***	1232.46	2.20	*
Treatment	2	452.37	0.68	NS	12.41	1.43	NS	327.08	0.58	NS
Error	32	665.79			8.70			560.72		
Hc and Hs										
Block	25	585.98	1.55	*	12.67	1.20	NS	456.41	1.57	*
Treatment	2	517.86	1.37	NS	1.65	0.16	NS	540.47	1.86	NS
Error	50	377.99			10.59			290.57		
Hc and Cs										
Block	49	653.09	2.05	**	13.41	0.94	NS	534.81	2.24	***
Treatment	2	155.09	0.49	NS	30.91	2.17	NS	70.65	0.30	NS
Error	98	319.26			14.22			238.97		

P values: *** <0.001, ** <0.01, * <0.10, NS>0.10. $N=51$, 78, and 150 (176, 26, and 50 for each of three treatments), for the first, second, and third experiments, respectively

larvae, and numbers of adults to 66–77%. Pairs of larvae reduced numbers of aphid nymphs and adults to significantly lower levels (Table 2 and Fig. 3). When just the three treatments with pairs of larvae (conspecific and heterospecific) were compared, however, no significant differences occurred in the number of aphids remaining (Table 3 and Fig. 3).

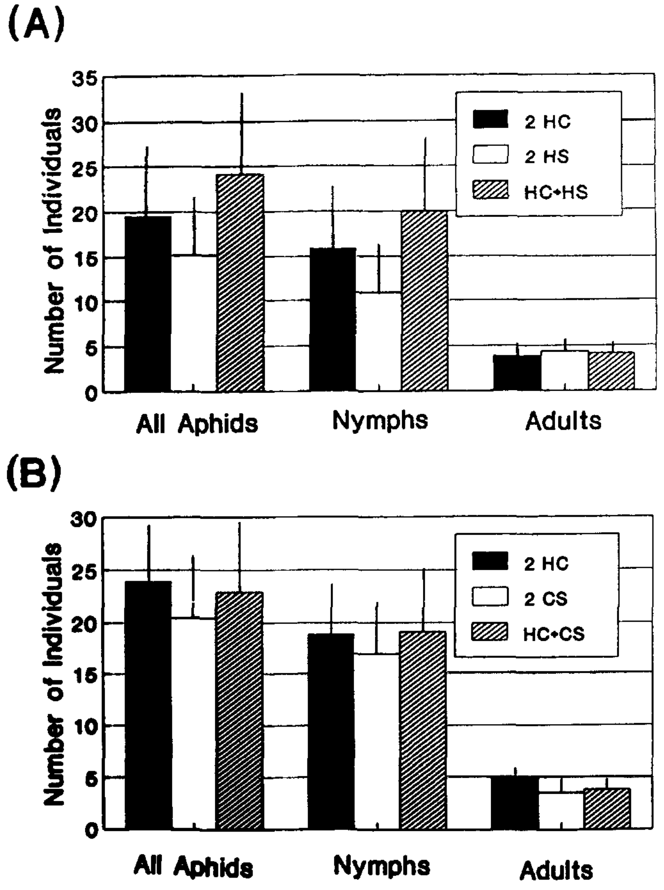

Fig. 4A, B. The number of individuals of aphids remaining when larvae of (**A**) *H. convergens* (Hc) and *H. sinuata* (Hs), and (**B**) *H. convergens* (Hc) and *C. septempuncata* (Cs) were removed from bean plants in the second and third experiments (vertical lines indicate two standard errors)

In the second and third experiments, larvae of *H. convergens* and *H. sinuata* (second experiment) or *C. septempunctata* (third experiment) did not differ significantly from each other in their mean percentage gain in weight when foraging as conspecific pairs (Fig. 2b and c; second experiment: d.f. = 1,25, F = 0.35, $P>0.55$; third experiment: d.f. = 1,49, F = 2.54, $P>0.11$). Individuals of the different species also did not differ significantly in the variance associated with the final weights they achieved when foraging with conspecifics (*H. convergens* vs. *H. sinuata:* d.f. = 25,25, F = 1.17, $P>0.10$; *H. convergens* vs. *C. septempunctata:* d.f. = 49,49, F = 1.03, $P>0.10$).

Within a species, larvae foraging in conspecific versus heterospecific pairs in the second and third experiments did not differ significantly in their mean percentage gain in weight (Fig. 2b and c; second experiment: d.f. = 1,25, F = 0.55 and 0.52, $P>0.44$ and 0.47, for *H convergens* and *H. tredecimpunctata,* respectively; third experiment: d.f. = 1,49, F = 0.11 and $P>0.75$ for both *H. convergens* and *C. septempunctata).* Finally, individuals in heterospecific vs conspecific pairs did not differ significantly in the variance associated with final weight achieved (second experiment: d.f. = 25,25, F = 1.00 and 1.85, $P>0.10$ in both instances, for *H. convergens* and *H. sinuata,* respectively; third experiment: d.f. = 49,49, $F=1.16$ and 1.22, $P>0.10$ in both instances, for *H. convergens* and *C. septempunctata,* respectively). Corresponding to the absence of significant differences in predator growth parameters between treatments in the second and third experiments, no significant differences occurred among treatments in the degree to which pairs of larvae (conspecific and heterospecific) consumed aphids and reduced aphid reproduction (Table 3 and Fig. 4).

Discussion

Ladybeetle larvae generally experience low rates of success in attacking aphids; as much as 50 to 100% of attacks may fail, depending on the ages and species identities of the predator and prey (e.g., Dixon 1959, 1970; Wratten 1973, 1976; Hajek and Dahlsten 1987). Aphids often escape by moving along or dropping from the plant surface as the ladybeetle larva approaches (e.g., Roitberg and Myers 1978, 1979; Clegg and Barlow 1982; Brodsky and Barlow 1986, McConnell and Kring 1990). Aphids that drop from the host plant become unavailable to predators for variable lengths of time. Thus, a ladybeetle larva may reduce the foraging success of another larva both by consuming the prey and by disturbing them. The effects of predator disturbance were evident in the present experiments in the contrasting spatial patterns of aphids on the host plant in the presence and absence of ladybeetle larvae.

If ladybeetle species differ in their foraging habits (e.g., by capturing prey that differ in age or microhabitat), then larvae of different species may interfere less with each other's foraging efforts than larvae of the same species (i.e., interspecific competition may be less intense than intraspecific competition). Consequently, mixed species assemblages of ladybeetle larvae may depress local aphid populations more than single species assemblages containing the same number or biomass of individuals. Alternatively, larvae of different species may overlap extensively in their foraging patterns. These species may interact such that larvae of competitively superior species prosper more in mixed than in single species assemblages, while larvae of competitively inferior species fare less well. Under these circumstances, it is not clear whether the prey population will be most depressed by a more or less diverse predator assemblage (e.g., see Turnbull and Chant 1961; Frazer et al. 1981a; Ehler and Hall 1982, 1984; Keller 1984; Ehler 1985; Spiller 1986). Finally, the foraging habits of closely related ladybeetle species may be so similar that there is little or no difference between intra and interspecific interactions. In such cases, the species diversity of the predator assemblage *per se* may minimally influence the degree to which the prey population is depressed by the predators.

The experiments were intended to test these general hypotheses by ensuring that larvae foraging in pairs experienced moderate competition. Intraspecific competition was clearly evident for both *H. convergens* and *H. tredecimpunctata* in the first experiment, as larvae of each species gained significantly less weight when paired with a conspecific versus when allowed to forage singly. Intraspecific competition, however, did not differ significantly from interspecific competition for either species, in that larvae foraging in pairs gained similar amounts of weight when paired with a heterospecific versus with a conspecific. Furthermore, aphid populations were neither more nor less reduced by heterospecific pairs than by conspecific pairs. These same basic results also emerged in the second and third experiments when *H. convergens* was tested with *H. sinuata* and *C. septempunctata*. In summary, the foraging habits of these ladybeetle larvae appear sufficiently similar such that there is little or no difference between intra and interspecific interactions among these predators when two similarly sized individuals co-occur on a plant.

The results thus suggest that the species diversity *per se* of the ladybeetle assemblage associated with any given local aphid population, e.g., in alfalfa, does not affect substantially how much that aphid population is depressed by the ladybeetles' predatory actions. In particular, there is no evidence from the present study to suggest that a local population of aphids will be controlled more or less effectively by a combination of co-occurring ladybeetle species than one would predict from simple consideration of the impact of these same predator species when they occur singly at equivalent densities.

The relative strengths of intra and interspecific competition have long been of central interest as ecologists have sought to understand the nature of coexistence of similar species (e.g., Lack 1947; MacArthur and Levins 1967; Wise 1981; Creese and Underwood 1982; Schoener 1986). In a review of field experiments, Connell (1983) found that intraspecific competition is generally more intense than interspecific competition. Among very similar species, however, interspecific competition may in some instances be just as intense as intraspecific competition (e.g., Fenchel and Kofoed 1976), as was observed in the experiments reported here.

This study focused on direct effects of ladybeetles on each other and on their aphid prey. Indirect effects of predator-prey interactions, although not studied here, must also be considered in assessing the implications of species diversity in predator assemblages. It is possible, for example, that the degree to which aphids were disturbed and dropped from the host plant differed when the prey were exposed to heterospecific versus conspecific pairs of ladybeetles, with potentially great implications for the spread of plant diseases by aphid vectors (Roitberg and Myers 1979, A. Power, *pers. comm.*). One must also exercise caution in extrapolating short-term laboratory results to the field, where over the long-term, less straightforward interactions among ladybeetles are likely to occur. For example, in nature ladybeetle species may segregate over space and time (e.g., Gagné and Martin 1968; Corderre et al. 1987) such that the species diversity of predators plays a key role in the impact of ladybeetles on aphid populations across heterogeneous landscapes. Ladybeetles are also to some degree cannibalistic, especially on eggs (e.g., Banks 1955; Mills 1982), such that the potential exists for interactions through intraspecific and/or intraguild predation (e.g., Polis 1981; Polis et al. 1989).

Keeping these caveats in mind, the results of the present study are nevertheless of considerable interest in light of potential implications of introducing the Old World ladybeetle, *C. septempunctata*, to North America. This purposeful introduction may have profound impact on the ladybeetle fauna native to North America through complex interactions of Old and New World ladybeetles, e.g. as mediated by differences in life cycle timing and/or habitat and prey preference. If indeed ladybeetle numbers in North America are to some degree limited by the global availability of prey (e.g., see Heathcote 1978), then the successful establishment of *C. septempunctata* in North America may necessarily result in some reduction in population levels of native species. One possibility associated with such reduction is that in coming years, the assemblage of ladybeetles aggregating at a local outbreak of aphids (e.g., in Utah alfalfa) may be more diverse (with the addition of *C. septempunctata)* but relatively little changed in density or biomass compared with present-day ladybeetle assemblages. The experimental results presented here suggest that a simple change in predator species diversity alone, if not accompanied by a change in density and/or biomass of predators, would have minimal influence on the foraging success of individual ladybeetles, and on their combined effects on aphid numbers in local prey populations.

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