Research Article

Competition for Aphid Prey between Different Lady Beetle Species in a Laboratory Arena

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Direct competition for aphid prey (Hemiptera: Aphididae) was evaluated between and among several lady beetle species (Coleoptera: Coccinellidae). The behavior of three native (*Coccinella trifasciata*, *Coleomegilla maculata*, and *Hippodamia convergens*) and four nonnative (*Coccinella septempunctata*, *Harmonia axyridis*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata*) lady beetles was observed in laboratory arenas. The beetles were kept alone, paired with conspecifics or paired with heterospecifics, and presented with potato aphids (*Macrosiphum euphorbiae*). *Harmonia axyridis* was the most successful aphid predator in our study, being able to find aphids more quickly and consume more of them compared to most other lady beetle species. It was also by far the most aggressive of the tested species. *Coccinella septempunctata*, *C. trifasciata*, and *C. maculata* generally followed *H. axyridis* in aphid consumption. Prey discovery, consumption, and aggressive behaviors were dependent on which species were present in the arena. Except for the generally superior *H. axyridis*, there was no obvious dominance hierarchy among the other tested species and no dichotomy between the native and non-native species. Asymmetric interactions between lady beetle species may affect their abilities to coexist in the same habitat.

1. Introduction

Lady beetles comprise an ecologically and economically important group of insects that are also charismatic and well known to the general public [1, 2]. Understanding intraguild interactions among lady beetle species is important both for their conservation and for their maximum utilization as biological control agents. For example, the establishment of nonnative lady beetle species often coincides with declines in native lady beetle abundances [3–9] and has been implicated in having profound effects on the populations of pestiferous prey [4, 9, 10].

Competition is often assumed when predatory species consuming the same prey species are found in the same area [11]. Persistent species that share prey and an evolutionary history are often considered to have achieved a compromise over time, allowing them to coexist by differentially exploiting the same prey species [12, 13]; for example, by foraging

at different times [14]. When species consuming the same prey are newly brought together, the ability of each to acquire the same necessary resources may allow for their coexistence [15, 16]. Intraguild predation, however, does not mean that a sufficient share goes to each predator [6, 17–19]. Consumption by a more efficient predator may eventually result in the competitive exclusion of the less efficient predator [16, 20].

Most comparative studies of different lady beetle species have either dealt with their relative abundances in the field [3–9, 21] or focused on intraguild predation [3, 6, 7, 17, 22–32]. The recent spread of *Harmonia axyridis* (Pallas) outside of its native range has been the impetus for a number of additional behavioral comparisons [33]. *Harmonia axyridis* has been shown to outcompete other lady beetle species in evaluations of intraguild predation [17, 24, 31], prey utilization [6], pathogen tolerance [34], and in the acquisition of prey tended by aggressive ants [35]. Relatively little research effort has been dedicated to competition for prey items among lady

beetle species. In an extensive field survey, Finlayson et al. [21] documented native and nonnative lady beetle species occurring together in a variety of habitats throughout Maine. A series of experiments [35, 36, and this study] were then conducted to compare behavior between different species. In the present study, we investigated behavior of seven lady beetle species competing for prey in a laboratory arena. We hypothesized that recently introduced species that share habitats with the native species [21], but appear to replace them over time [9], are more aggressive aphid predators.

2. Materials and Methods

2.1. Study Species. Aphidophagous lady beetle species, which were known to be abundant in Maine and were found together in the same habitats [21, 36], were chosen for the present study. Three species are native: the three-banded lady beetle *Coccinella trifasciata perplexa* Mulsant, the twelve-spotted lady beetle *Coleomegilla maculata lengi* Timberlake, and the convergent lady beetle *Hippodamia convergens* Guérin. The native range of *C. trifasciata* is north from New Jersey to Labrador and west to California and Alaska [37]. *Coleomegilla maculata* is native to eastern North America from Georgia to Ontario, and west to Texas and Minnesota [37]. The range of *H. convergens* extends from British Columbia and Ontario to South and Central America and the Antilles [37].

The nonnative lady beetles used in the present study were the seven-spotted lady beetle *Coccinella septempunctata* (L.), the multicolored Asian lady beetle *Harmonia axyridis* (Pallas), the variegated lady beetle *Hippodamia variegata* (Goeze), and the fourteen-spotted lady beetle *Propylea quatuordecimpunctata* (L.). *Harmonia axyridis* is native to Central and Eastern Asia [33, 38]. The other three species are of Palearctic origin [39, 40]. All were inadvertently or intentionally introduced into North America. *Coccinella septempunctata* has been established in the eastern United States since 1979 [41]. *Harmonia axyridis* was first documented as established in North America in 1988 [42, 43] and now occurs throughout much of the continental United States [33]. *Hippodamia variegata* is widespread throughout northeastern North America [44–49]. In Maine, *P. quatuordecimpunctata* was first documented in 1988 in Aroostook, Penobscot, and Kennebec Counties, where it is believed to have expanded its range from populations in Quebec dating to 1968 [50].

The potato aphid, *Macrosiphum euphorbiae* (Thomas), served as the prey. *Macrosiphum euphorbiae* is common in Maine and native throughout North America [51]. It is known to feed on over 200 plant species, including potato, apple, aster, and rose [51] and is a common prey item for many lady beetle species [2, 37, 52].

2.2. Insect Origins and Maintenance. Lady beetles were collected 48–72 hours before the initiation of each trial and were provided with water, but no food, for 48 hours before trials began. Beetles were collected in Orono, Maine (44.8835°N, 68.6721°W) from a variety of habitats: mixed shrub (*Solidago* sp., *Rubus* sp., *Prunus* sp., *Rosa* sp., *Cornus sericea*, and *Alnus*

sp.), apple (*Malus* sp.), grain (*Hordeum* sp. and *Avena* sp.), mixed organic crops (*Solanum lycopersicon*, *Allium* sp., *Brassica* sp., *Pisum* sp., and *Phaseolus* sp.), and field (*Phleum pratense*, *Trifolium* sp., *Cirsium* sp., *Vicia* sp., and *Fragaria* sp.). Potato aphids were obtained from a colony maintained in our laboratory. The colony was originally founded from aphids collected in Presque Isle, Maine (46.6528°N, 68.0109°W) from potato (*Solanum tuberosum*, Family: Solanaceae) fields and then maintained on excised potato foliage in the laboratory. Until they were used in trials, lady beetles and aphid colonies were housed separately in ventilated, 0.95 L ball glass jars (Jarden Home Brands, Inc., Daleville, IN, USA) held within Percival I-33VL Intellus environmental chambers (Percival Scientific, Inc., Perry, IA, USA) at 16 (light):8 (dark) hour photoperiod. The temperature was maintained at $20 \pm 1^\circ\text{C}$ during both the photophase and scotophase. Trials were conducted from May 16 to September 8, 2006.

2.3. Competition Trials with Paired Lady Beetles. Each trial took place in an observation arena under a clear, ventilated plastic container (8.9-cm diameter and 9.5-cm height), which was turned upside down and placed inside the bottom of a Petri dish. For each container, a cut potato leaf was placed in a small plastic vial with water. Using a paintbrush, 4 adult wingless aphids were placed on the upper surface of the leaf. Aphid number was chosen based on a previous study [36] in which lady beetles consumed between 5.33 ± 0.4271 (*P. quatuordecimpunctata*) and 9.17 ± 0.2039 (*H. axyridis*) adult potato aphids in a 24-hour period. Therefore, we believe that four aphids provided an adequate, but not overabundant, food supply. The vial containing the vegetation and aphids was then placed in an upright position inside the observation arena. Adult lady beetles were transferred to a different observation arena by allowing each lady beetle to crawl on to the tip of a paintbrush and then onto the interior of the arena. After a 10-minute period of adjustment, the cover holding the lady beetle(s) was switched with the cover under which the vial holding the leaf and aphids was housed, simultaneously exposing the lady beetle(s) to the aphids. Trials were conducted for 45 minutes. Time to prey discovery (of the first aphid), number of prey consumed by each beetle (documented to 0.25 aphid when the entire aphid was not consumed), and behavior (as a count of aggression delivered and received by each beetle in each trial) were recorded. The following behaviors were considered aggressive: chasing, grasping, biting, climbing upon, and attempting to or successfully stealing prey. Ten trials were conducted in random order, with individuals of each species and with pairs of all combinations of each species, including conspecific pairings.

2.4. Prey Consumption and Discovery Time by Single Lady Beetles. To serve as a comparison with the paired trials described above, aphid consumption and time to prey discovery was also documented in trials with single lady beetles. These trials were conducted following the same protocol as described above, but with one individual introduced in each arena. Ten trials were conducted with each of the seven lady beetle species.

TABLE 1: Mean ($\pm$ SE) aphid consumption (number of aphids), prey discovery time (minutes), and aggression delivered (number of occurrences) by seven lady beetle species during laboratory trials. The data were pooled for all trials conducted with a given species (see text for details). Means in each column followed by the same letter are not significantly different from each other (Tukey's HSD tests, $P < 0.05$). Nonnative species are printed in bold font.

	Aphid consumption			Aggression delivered	Prey discovery time	
	Alone	Same species	Other species	Other species	Same species	Other species
<i>C. trifasciata</i>	1.30 $\pm$ 0.34b	1.55 $\pm$ 0.21ab	1.78 $\pm$ 0.17ab	0.22 $\pm$ 0.05b	15.95 $\pm$ 3.11ab	16.47 $\pm$ 2.02b
<i>C. maculata</i>	1.60 $\pm$ 0.37ab	1.55 $\pm$ 0.20ab	1.42 $\pm$ 0.16bcd	0.23 $\pm$ 0.06b	20.30 $\pm$ 2.75a	17.80 $\pm$ 2.01b
<i>H. convergens</i>	1.20 $\pm$ 0.29b	1.35 $\pm$ 0.20ab	1.30 $\pm$ 0.14bcd	0.20 $\pm$ 0.05b	18.40 $\pm$ 3.07a	19.18 $\pm$ 2.18b
<i>C. septempunctata</i>	1.70 $\pm$ 0.42ab	1.50 $\pm$ 0.28ab	1.48 $\pm$ 0.17abc	0.13 $\pm$ 0.04b	18.70 $\pm$ 3.75a	20.80 $\pm$ 2.33ab
<i>H. axyridis</i>	2.70 $\pm$ 0.30a	1.95 $\pm$ 0.23a	2.10 $\pm$ 0.17a	0.57 $\pm$ 0.06a	6.35 $\pm$ 1.47b	13.23 $\pm$ 1.99b
<i>H. variegata</i>	0.70 $\pm$ 0.26b	0.75 $\pm$ 0.12ab	0.84 $\pm$ 0.12d	0.13 $\pm$ 0.04b	24.90 $\pm$ 3.33a	28.13 $\pm$ 2.13a
<i>P. quatuordecimpunctata</i>	1.10 $\pm$ 0.23b	1.03 $\pm$ 0.13b	0.94 $\pm$ 0.11cd	0.33 $\pm$ 0.06b	17.85 $\pm$ 3.39a	20 $\pm$ 2.18 ab
N	10	20	60	60	20	60
P	0.0146	0.0122	<0.0001	<0.0001	0.0002	<0.0001
F	2.90	2.85	5.99	6.27	4.76	5.56
DF	6, 63	6, 133	6, 413	6, 413	6, 133	4, 413

2.5. Measurements of Lady Beetle Weight and Size. Because differences in predator size have been used in some studies to explain differences in competition [6, 17, 53, 54], the weight and volume of 20 lady beetles of each species were documented. The weight of each beetle was determined to the 0.0001 gram using an electronic Ohaus Adventurer Balance AR2140 (Ohaus Corp., Pine Brook, NJ, USA). Width, length, and height were measured using a ruler mounted in the eyepiece of a Stereoscopic Zoom Microscope SMZ800 (Nikon Instruments Inc., Melville, NY, USA) at 10x magnification. Volume was estimated by multiplying width (across the pronotum, dorsal side), length (from the frons of the head to the end of the elytra, dorsal side), and height (the greatest height below the elytra, laterally).

2.6. Statistical Analyses. The Wilk-Shapiro test (PROC UNIVARIATE; SAS Institute, Inc. 2002) was used to test data normality. Data were transformed using rank transformations [55]. Untransformed data were used to calculate the means and standard errors reported in this paper.

Behavioral data were analyzed using one-way ANOVAs followed by Tukey's HSD tests (PROC GLM, SAS Institute, Inc. 2002). First, we compared the overall differences among the species for beetles that were held alone, paired with conspecifics, and paired with heterospecifics (all species other than the species of interest pooled together). Lady beetle species were used as the main effect (Table 1). Secondly, we tested the effects of the competition context (beetle held alone, paired with conspecifics, or paired individually with each of the heterospecific species) separately for each lady beetle species. Competition contexts were used as the main effect (Tables 2–4). Aphid consumption, prey discovery time, aggression received, and aggression delivered were used as dependent variables in both analyses.

TABLE 2: Number of aphids (mean $\pm$ SE) consumed by *C. trifasciata* and *C. maculata* in different competition contexts (see text for details). Means in each column followed by the same letter are not significantly different from each other (Tukey's HSD tests, $P < 0.05$). Nonnative species are printed in bold font.

Competition context	<i>C. trifasciata</i>	<i>C. maculata</i>
Alone	1.30 $\pm$ 0.34ab	1.60 $\pm$ 0.37ab
<i>C. trifasciata</i>	1.70 $\pm$ 0.34ab	0.40 $\pm$ 0.22b
<i>C. trifasciata</i> *	1.40 $\pm$ 0.27ab	N/A
<i>C. maculata</i>	2.60 $\pm$ 0.37ab	1.60 $\pm$ 0.31ab
<i>C. maculata</i> *	N/A	1.50 $\pm$ 0.27ab
<i>C. septempunctata</i>	1.00 $\pm$ 0.42b	1.80 $\pm$ 0.36a
<i>H. axyridis</i>	1.30 $\pm$ 0.37ab	1.00 $\pm$ 0.27ab
<i>H. convergens</i>	2.60 $\pm$ 0.31a	1.55 $\pm$ 0.26ab
<i>H. variegata</i>	1.20 $\pm$ 0.36ab	1.95 $\pm$ 0.51a
<i>P. quatuordecimpunctata</i>	2.00 $\pm$ 0.39ab	1.80 $\pm$ 0.42ab
P	0.0073	0.0262
F	2.87	2.33
DF	8, 81	8, 81

* When beetles were paired with conspecifics, the data are listed separately for each beetle in the pair.

Correlation analysis (PROC CORR; SAS Institute Inc. 2002) was used to test associations between aphid consumption, prey discovery time, aggression delivered, and aggression received. The analyses were conducted both within each species (e.g., correlation between aphid consumption and prey discovery time for *H. axyridis*), as well as between the two paired species (e.g., correlation between aphid consumption by *H. axyridis* and *C. septempunctata*) or the two

TABLE 3: Number of aggression events (mean $\pm$ SE) delivered by *H. axyridis* and *H. variegata* in different competition contexts (see text for details). Means in each column followed by the same letter are not significantly different from each other (Tukey's HSD tests, $P < 0.05$). Nonnative species are printed in bold font.

Competition context	<i>H. axyridis</i>	<i>H. variegata</i>
<i>H. axyridis</i>	0.10 $\pm$ 0.10b	0.50 $\pm$ 0.17a
<i>H. axyridis</i> *	0.10 $\pm$ 0.10b	N/A
<i>C. maculata</i>	0.60 $\pm$ 0.16ab	0.10 $\pm$ 0.10b
<i>C. septempunctata</i>	0.10 $\pm$ 0.10b	0.00 $\pm$ 0.00b
<i>C. trifasciata</i>	0.80 $\pm$ 0.13a	0.00 $\pm$ 0.00b
<i>H. convergens</i>	0.70 $\pm$ 0.15ab	0.00 $\pm$ 0.00b
<i>H. variegata</i>	0.50 $\pm$ 0.17ab	0.00 $\pm$ 0.00b
<i>H. variegata</i> *	N/A	0.00 $\pm$ 0.00b
<i>P. quatuordecimpunctata</i>	0.70 $\pm$ 0.16ab	0.20 $\pm$ 0.13ab
<i>P</i>	0.0003	<0.0001
<i>F</i>	4.70	4.72
<i>DF</i>	7, 72	7, 72

* When beetles were paired with conspecifics, the data are listed separately for each beetle in the pair.

individuals of the same species in case of conspecific trials. Most of the correlations between aphid consumption and prey discovery time were statistically significant. Therefore, for the ease of interpretation, their results are reported separately (Table 5) from statistically significant comparisons between all other combinations of variables (Table 6).

Weights and volumes of different lady beetle species were compared using one-way ANOVA (PROC GLM, SAS Institute, Inc. 2002). Means were separated by Tukey's HSD tests.

3. Results

Aphid consumption was significantly different among the species whether the beetles were held alone, paired with conspecifics, or paired with heterospecifics (Table 1). *Harmonia axyridis* generally consumed the most aphids, while *P. quatuordecimpunctata* and *H. variegata* consumed the least. Also, *H. axyridis* was the most aggressive species towards other lady beetles when held with heterospecifics (Table 1). No difference in delivered aggression was detected among the species paired with conspecifics (d.f. = 6, 133, $F = 2.07$, $P = 0.1544$). The overall amount of received aggression was similar among the tested species ($P > 0.15$).

Prey discovery time did not differ among species when the beetles were held alone (d.f. = 6, 63, $F = 1.01$, $P = 0.4273$). However, in the presence of conspecifics, *H. axyridis* found aphids quicker compared to the other species (Table 1). In the trials with heterospecifics, *H. variegata* discovered prey slower than all other species except *C. septempunctata* and *P. quatuordecimpunctata* (Table 1).

Competition context affected aphid consumption for two of the tested lady beetle species (Table 2). *Coccinella trifasciata* consumed fewer aphids when paired with *C. septempunctata* than when paired with *H. convergens*, while

C. maculata consumed fewer aphids when paired with *C. trifasciata* than when paired with *C. septempunctata* or *H. variegata*. Prey discovery time did not vary within any of the tested species regardless of the competition context ($P > 0.2$).

Harmonia axyridis exhibited significantly more aggression towards *C. trifasciata* than towards the other lady beetle species (Table 3). Interestingly, *H. variegata*, which was a rather peaceful species in our trials, significantly increased its level of aggression when paired with *H. axyridis* (Table 3). *Coccinella trifasciata*, *H. convergens*, *H. variegata*, and *P. quatuordecimpunctata* received different amounts of aggression from different lady beetle species (Table 4). A statistically significant difference was also detected for *C. maculata*, but the effect was relatively weak, inconsistent, and its biological significance is uncertain (Table 4). Beetles from all five aforementioned species received more aggression from *H. axyridis* compared to at least one other species with which they were paired. *Hippodamia variegata* also received as much aggression from *P. quatuordecimpunctata* as from *H. axyridis* (Table 4).

Not surprisingly, aphid consumption was negatively correlated with prey discovery time (Table 5). In other words, the beetles that found their prey the most quickly consumed the most. The only exceptions were *C. trifasciata* paired with *C. maculata*, *H. convergens* paired with *H. axyridis*, and *H. axyridis* paired with *P. quatuordecimpunctata*. Correlation coefficients were marginally significant for *C. maculata* paired with *H. axyridis*, *H. axyridis* paired with *C. trifasciata*, and *P. quatuordecimpunctata* paired with *C. maculata* (Table 5).

Correlation analyses also revealed a number of strong relationships between other measured parameters (Table 6). In six trials, aphid consumption by one species was negatively correlated with aphid consumption by the other species confined in the same arena. Similarly, there were three cases of negative correlations between prey discovery times by two beetles in a pair. In five comparisons, aphid consumption by one species was positively correlated with prey discovery time by the other species. Aggressive behavior increased aphid consumption for *C. maculata* when paired with *C. trifasciata*, and for *H. convergens* when paired with *H. axyridis*. However, prey discovery time for *C. maculata* increased with increased aggression against *C. septempunctata*. Receiving aggression from *P. quatuordecimpunctata* significantly decreased aphid consumption by *C. septempunctata*. Similarly, prey discovery time for three aphid species increased as they received more aggression from another beetle in the pair (Table 6).

Coccinella septempunctata was the largest of the species tested, closely followed by *H. axyridis* (Table 7). *Hippodamia variegata* was the smallest.

4. Discussion

Results of the present study suggest the existence of asymmetric competitive interactions among the tested lady beetle species. There were significant differences in aphid consumption and prey discovery times among the species, and numerous occasions of aggressive encounters among the beetles confined in the observation arenas. The nature and strength

TABLE 4: Number of aggression events (mean $\pm$ SE) received by *C. trifasciata*, *C. maculata*, *H. convergens*, *H. variegata*, and *P. quatuordecimpunctata* in different competition contexts (see text for details). Means in each column followed by the same letter are not significantly different from each other (Tukey's HSD tests, $P < 0.05$). Nonnative species are printed in bold font.

	<i>C. trifasciata</i>	<i>C. maculata</i>	<i>H. convergens</i>	<i>H. variegata</i>	<i>P. quatuordecimpunctata</i>
<i>C. trifasciata</i>	0.20 $\pm$ 0.13b	0.30 $\pm$ 0.15ab	0.20 $\pm$ 0.13ab	0.10 $\pm$ 0.10b	0.30 $\pm$ 0.15ab
<i>C. trifasciata</i> *	0.30 $\pm$ 0.15ab	N/A	N/A	N/A	N/A
<i>C. maculata</i>	0.20 $\pm$ 0.13b	0.00 $\pm$ 0.00b	0.20 $\pm$ 0.13ab	0.30 $\pm$ 0.15ab	0.10 $\pm$ 0.10b
<i>C. maculata</i> *	N/A	0.10 $\pm$ 0.10ab	N/A	N/A	N/A
<i>C. septempunctata</i>	0.20 $\pm$ 0.13b	0.10 $\pm$ 0.10ab	0.30 $\pm$ 0.15ab	0.00 $\pm$ 0.00b	0.10 $\pm$ 0.10b
<i>H. axyridis</i>	0.80 $\pm$ 0.13a	0.60 $\pm$ 0.16a	0.70 $\pm$ 0.15a	0.50 $\pm$ 0.17a	0.70 $\pm$ 0.15a
<i>H. convergens</i>	0.00 $\pm$ 0.00b	0.30 $\pm$ 0.15ab	0.10 $\pm$ 0.10b	0.20 $\pm$ 0.13ab	0.20 $\pm$ 0.13ab
<i>H. convergens</i> *	N/A	N/A	0.10 $\pm$ 0.10b	N/A	N/A
<i>H. variegata</i>	0.00 $\pm$ 0.00b	0.10 $\pm$ 0.10ab	0.00 $\pm$ 0.00b	0.00 $\pm$ 0.00b	0.20 $\pm$ 0.13ab
<i>H. variegata</i>*	N/A	N/A	N/A	0.00 $\pm$ 0.00b	N/A
<i>P. quatuordecimpunctata</i>	0.40 $\pm$ 0.16ab	0.20 $\pm$ 0.13ab	0.30 $\pm$ 0.15ab	0.50 $\pm$ 0.17a	0.10 $\pm$ 0.10b
<i>P. quatuordecimpunctata</i>*	N/A	N/A	N/A	N/A	0.10 $\pm$ 0.10b
<i>P</i>	0.0012	0.0298	0.0132	0.0028	0.0170
<i>F</i>	3.89	1.79	2.39	3.22	2.88
<i>DF</i>	7, 72	7, 72	7, 72	7, 72	7, 72

* When beetles were paired with conspecifics, the data are listed separately for each beetle in the pair.

TABLE 5: Correlations between aphid consumption and prey discovery time for single and paired lady beetles in trials ($N = 10$). Each row represents the relationship between aphid consumption and prey discovery time for the species in the left column when it was alone or paired with the species in the first row of the table. Ct: *Coccinella trifasciata*, Cm: *Coleomegilla maculata*, Hc: *Hippodamia convergens*, Cs: *Coccinella septempunctata*, Ha: *Harmonia axyridis*, Hv: *Hippodamia variegata*, Pq: *Propylea quatuordecimpunctata*. Nonnative species are printed in bold font.

		Alone	Ct	Cm	Hc	Cs	Ha	Hv	Pq
Ct	<i>r</i>	-0.8698	-0.7745	-0.3644	-0.8675	-0.8541	-0.7642	-0.9107	-0.7571
	<i>P</i>	0.0011	<0.0001	0.3005	0.0011	0.0017	0.0101	0.0002	0.0112
Cm	<i>r</i>	-0.9524	-0.7942	-0.8559	-0.9011	-0.6469	-0.6235	-0.8016	-0.7745
	<i>P</i>	<0.0001	0.0061	<0.0001	0.0004	0.0432	0.0541	0.0053	0.0085
Hc	<i>r</i>	-0.7994	-0.8708	-0.8199	-0.9091	-0.9039	-0.5518	-0.9431	-0.9184
	<i>P</i>	0.0055	0.0010	0.0037	<0.0001	0.0003	0.0982	<0.0001	0.0002
Cs	<i>r</i>	-0.8420	-0.8009	-0.8193	-0.8701	-0.8735	-0.9240	-0.9066	-0.8609
	<i>P</i>	0.0022	0.0054	0.0037	0.0011	<0.0001	0.0001	0.0003	0.0014
Ha	<i>r</i>	-0.9389	-0.6010	-0.7980	-0.8140	-0.6836	-0.7743	-0.9708	-0.2439
	<i>P</i>	<0.0001	0.0661	0.0057	0.0042	0.0293	<0.0001	<0.0001	0.4970
Hv	<i>r</i>	-0.9447	-0.7891	-0.8894	-0.9322	-0.7487	-0.8316	-0.8647	-0.8033
	<i>P</i>	<0.0001	0.0067	0.0006	<0.0001	0.0127	0.0029	<0.0001	0.0051
Pq	<i>r</i>	-0.8818	-0.8734	-0.6182	-0.7900	-0.8852	-0.6361	-0.8284	-0.7502
	<i>P</i>	0.0011	0.0010	0.0568	0.0065	0.0007	0.0480	0.0031	0.0001

of the observed interactions varied depending on the species involved.

Harmonia axyridis was the most successful aphid predator in our study, being able to find aphids quicker and consume more of them compared to most other lady beetle species. Furthermore, *H. axyridis* was by far the most aggressive of the tested species. These observations are consistent with a number of studies that have documented the superior competitive abilities of *H. axyridis* among lady beetle species [6, 17, 24, 26, 28, 31, 56, 57]. A superior competitive ability

of invasive species to utilize resources over native species has been also documented in numerous other systems [58–61].

Interestingly, it took about twice as long for *H. axyridis* to find aphids when paired with heterospecifics than when paired with conspecifics (Table 1). It is possible that attacking heterospecifics distracted them from searching for aphids. Indeed, *H. axyridis* attacked heterospecifics 5–8 times more often than conspecifics (Table 3) although the differences were not always statistically significant. The aphid consumption data suggest that such a strategy paid off. Similarly,

TABLE 6: Additional significant correlations between aphid consumption, prey discovery time, aggression delivered, and aggression received by lady beetles in trials ($N = 10$). Nonnative species are printed in bold font.

Correlation between:	And:	r	P
Aphid consumption	Aphid consumption	r	P
<i>C. septempunctata</i>	<i>C. trifasciata</i>	−0.9049	0.0002
<i>C. trifasciata</i>	<i>H. convergens</i>	−0.7356	0.0127
<i>C. maculata</i>	<i>H. axyridis</i>	−0.7098	0.0112
<i>C. septempunctata</i>	<i>H. convergens</i>	−0.8195	0.0053
<i>H. axyridis</i>	<i>H. convergens</i>	−0.9133	0.0003
<i>H. axyridis</i>	<i>P. quatuordecimpunctata</i>	−0.8497	0.0020
Prey discovery time	Prey discovery time	r	P
<i>C. septempunctata</i>	<i>C. trifasciata</i>	−0.7653	0.0085
<i>C. septempunctata</i>	<i>H. convergens</i>	−0.8138	0.0030
<i>H. convergens</i>	<i>P. quatuordecimpunctata</i>	−0.7001	0.0143
Aphid consumption	Prey discovery time	r	P
<i>C. trifasciata</i>	<i>C. septempunctata</i>	0.8350	0.0017
<i>C. septempunctata</i>	<i>H. convergens</i>	0.7069	0.0002
<i>C. septempunctata</i>	<i>C. trifasciata</i>	0.7665	0.0112
<i>H. convergens</i>	<i>C. septempunctata</i>	0.8344	0.0022
<i>P. quatuordecimpunctata</i>	<i>H. variegata</i>	0.7107	0.0088
Aphid consumption	Aggression delivered towards	r	P
<i>C. maculata</i>	<i>C. trifasciata</i>	0.7994	0.0063
<i>H. convergens</i>	<i>H. axyridis</i>	0.7327	0.0029
Aphid consumption	Aggression received from	r	P
<i>C. septempunctata</i>	<i>P. quatuordecimpunctata</i>	−0.7812	0.0080
Prey discovery time	Aggression delivered towards	r	P
<i>C. maculata</i>	<i>C. septempunctata</i>	0.9225	<0.0001
Prey discovery time	Aggression received from	r	P
<i>C. maculata</i>	<i>C. septempunctata</i>	0.8511	0.0017
<i>H. convergens</i>	<i>C. maculata</i>	0.8370	0.0002
<i>C. septempunctata</i>	<i>P. quatuordecimpunctata</i>	0.8392	0.0028
Aggression delivered by	or Aggression received by	r	P
<i>C. trifasciata</i>	<i>C. trifasciata</i>	0.7003	0.0004

Michaud [6] found *H. axyridis* to be a highly evolved inter-specific competitor in the Florida citrus ecosystem.

Harmonia axyridis data generally agree with our hypothesis that recently introduced lady beetle species that replace native species over time are more aggressive aphid predators. However, we did not observe the same situation for the other three nonnative species. There was no distinct dichotomy between supposedly more aggressive nonnative species and supposedly more docile native species. Also, except for the generally superior *H. axyridis*, there was no obvious dominance hierarchy among the other tested species.

The native lady beetle species used in the current study, *C. maculata*, *C. trifasciata*, and *H. convergens* are currently numerous in Maine [21]. Native species, *Coccinella transversoguttata* (Brown) and *Hippodamia tredecimpunctata tibialis* (Say), that have experienced declines in abundance since nonnative lady beetle introductions [9] were excluded be-

cause they were not easily found in numbers sufficient for testing [21]. It would be interesting and valuable to pair native species once numerous in Maine with both the now common nonnative species and the native species that still persist.

Among the species tested, *C. septempunctata*, *C. trifasciata* and *C. maculata* generally followed *H. axyridis* in aphid consumption. *Coccinella septempunctata* and *H. axyridis* were also the heaviest and largest species among the seven species tested (Table 7). Despite *C. septempunctata*'s large size and being among the species consuming the most aphids, *C. septempunctata* generally did not deliver or receive more aggression than other species. Larger lady beetle species have been shown to be competitively favored over smaller ones [6, 17, 53, 54], possibly because they are able to consume more due to their larger size, or perhaps because their size is advantageous in direct fighting. *Coccinella septempunctata* has also been documented to deter aggression by ants

TABLE 7: Mean ($\pm$ SE) weight (mg) and volume (mm^3) of lady beetle species ($N = 20$) used in laboratory trials. Means in each column with the same letter are not significantly different (Tukey's HSD tests, $P < 0.05$). Nonnative species are printed in bold font.

	Weight	Volume
<i>C. trifasciata</i>	$1.04 \pm 0.0007c$	$20.41 \pm 1.2005d$
<i>C. maculata</i>	$0.91 \pm 0.0008c$	$15.10 \pm 0.8356de$
<i>H. convergens</i>	$0.87 \pm 0.0009c$	$32.43 \pm 1.8409c$
<i>C. septempunctata</i>	$2.25 \pm 0.0017a$	$78.87 \pm 2.6835a$
<i>H. axyridis</i>	$1.68 \pm 0.0015b$	$66.30 \pm 2.4081b$
<i>H. variegata</i>	$0.40 \pm 0.0004d$	$8.64 \pm 0.5435e$
<i>P. quatuordecimpunctata</i>	$0.63 \pm 0.0005dc$	$12.87 \pm 0.8090e$
<i>P</i>	<0.0001	<0.0001
<i>F</i>	38.63	280.85
<i>DF</i>	6, 133	6, 133

chemically by producing a defensive alkaloid and bleeding reflectively [62, 63]. It is possible that chemical defense is also used by *C. septempunctata* to prevent aggression from other coccinellids.

It is worth noting that *H. axyridis*, *C. septempunctata*, *H. convergens*, *H. variegata*, and *P. quatuordecimpunctata* showed no difference in aphid consumption and prey discovery time whether they were kept alone or paired with any other species tested in the study, including conspecifics (data not shown). Perhaps if a given species is an efficient predator that can find and consume aphids quickly, its ability to acquire prey may not be significantly hindered by the presence of other lady beetles. Prey consumption by *C. trifasciata* and *C. maculata*, on the other hand, differed depending on which species they were paired with.

Significant negative correlations between the numbers of aphids consumed and prey discovery times in paired trials (Table 6) confirm the existence of competitive interactions. Furthermore, we detected a number of significant positive correlations between the number of aphids consumed by one beetle in a pair and prey discovery time by the other beetle in the pair. In other words, the longer it took a beetle to discover the prey, the more aphids its competitor could consume.

Increased aggression delivered by *C. maculata* and *H. convergens* (Table 6) was correlated with increased aphid consumption by those species in trials with *C. trifasciata* and *H. axyridis*, respectively. In those cases, aggression may have helped deter other species from consuming prey. On the contrary, increased aggression by *C. maculata* was correlated with its own increased prey discovery time, suggesting that it was distracted from foraging.

Receiving aggression from *P. quatuordecimpunctata* increased prey discovery time and decreased aphid consumption for *C. septempunctata* (Table 6). Similarly, prey discovery time increased for *H. convergens* with the increase in aggression it received from *C. maculata*, and for *C. septempunctata* with the increased aggression it received from *P. quatuordecimpunctata*. In a conspecific pairing of *C. trifasciata*, aggression received by one conspecific was

correlated with the aggression it delivered, meaning that aggressive interactions were not one sided, but equally met by the other conspecific.

Overall, our results confirm that behavioral interactions between different lady beetle species affect their ability to secure prey items, with *H. axyridis* generally having a competitive advantage over the other species. Our study was conducted in a relatively simple setting of a laboratory arena with a limited number of aphids. Furthermore, prey choice was limited to a single aphid species. Increased environmental complexity, including variations in prey species and their abundances (including relative abundances of winged and wingless morphs), may modify competitive abilities of and interactions between certain species. Nevertheless, our findings support the idea that behavioral differences in prey discovery, consumption, and intraguild aggressiveness may, in part, lead to reductions in native lady beetle species following the establishment of *H. axyridis*.

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