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# The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids

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**Abstract.** By manipulating plant variety and predator species, we investigated the interactions of plant and predator traits in determining predation effectiveness. The predators were all coccinellid adults (*Hippodamia convergens, Hippodamia variegata, Coccinella apunctata,* and *Coccinella septempunctata*) and the prey were cabbage aphids *(Brevicoryne brassicae)*. Foraging behavior of the four predators was observed on four crucifers that differed widely in their structures and surface textures (*Brassica oleracea caulorapa, Brassica campestris, Brassica juncea crispifolia,* and *Hirschfeldia incana*). Predation rates were significantly influenced by plant variety, a result we attribute to direct effects of plant morphology on predator mobility, falling frequency, and prey accessibility. Predation rates did not vary significantly among the ladybirds, although the four species did exhibit distinct foraging strategies as measured by time spent actively foraging, the rate of encountering aphids, and the fraction of aphids encountered that were consumed. The coccinellids also differed in their propensity for flying away from the plant, and in the frequency with which they fell from the plant. We did not detect any significant interaction effects between plant and predator species, suggesting that the main effects of plant and predator species may overwhelm their interactions in this kind of system. Our results suggest that the level of predation upon herbivorous insects may depend more upon plant architecture than on the particular species of natural enemies present.

**Key words:** *Coccinellidae* – Crucifers – Foraging behavior – Plant architecture – Predation efficiency

The efficiency with which predatory insects pursue prey can be affected by the texture and structure of the surfaces that they search. Morphological features of plants such as dense trichomes (Belcher and Thurston 1982; Kauffman and Kennedy 1989), slippery leaves (Way and Murdie 1965; Carter et al. 1984; Kareiva and Sahakian 1990), and complex surfaces (Andow and Prokrym 1990) have all been shown to reduce the effectiveness of predators or parasites. However, these studies typically have focused on one predator or parasite species at a time, while manipulating one aspect of plant architecture. Yet even closely related predators may have unique strategies for locating and consuming prey and we need to know how a plant's structure affects all predators that may forage on the plant if we are to predict the consequences of plant architecture for the intensity of herbivory. We quantified the effects of plant architecture on a suite of predatory coccinellid beetles (*Hippodamia convergens, Hippodamia variegata, Coccinella apunctata* and *Coccinella septempunctata*) foraging for aphids on four morphologically diverse, but closely related crucifers (*Brassica oleracea caulorapa, Brassica campestris, Brassica juncea crispifolia,* and *Hirschfeldia incana*).

Our research had three objectives: 1) to compare the foraging behavior of the four ladybirds (i.e. time budgets, rates of falling and flying from the plant, and predation rates) to assess their effectiveness as predators and to look for differences between non-native coccinellids introduced into the U.S. as biocontrol agents and native coccinellids that are their close relatives; 2) to examine the effects of plant architecture on the foraging behavior of these predators, looking for plant features that have either sweeping effects on all species, or different effects on different species; and 3) to investigate the level of behavior at which the plant architecture interacts with the ladybird foraging (i.e. the causes for discrepancies in feeding efficiency).

## Methods

We selected ladybird species that would allow us to make several interesting a priori comparisons. Our sample included two native species, *H. convergens* and *C. apunctata* (HC and CA), which we collected from natural populations at the Mount St. Helens Nation-

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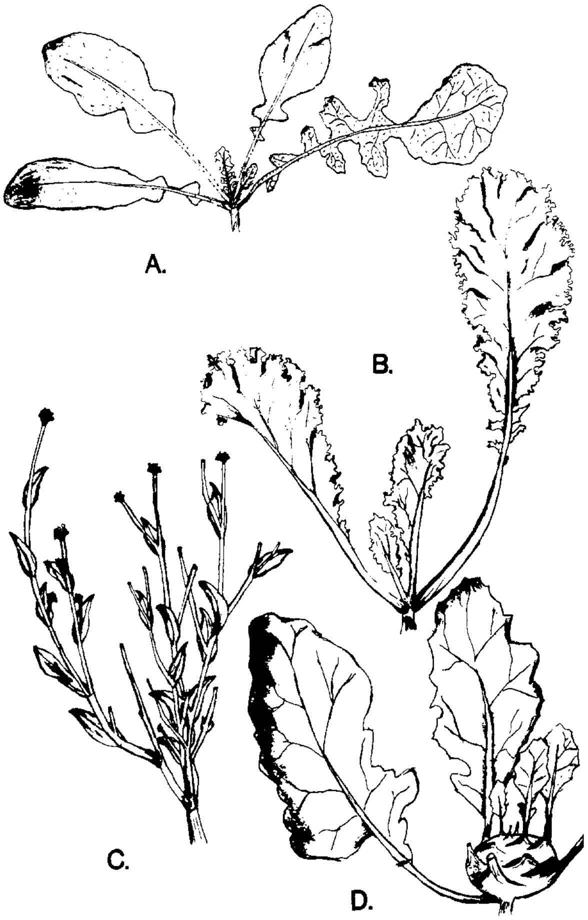

**Fig, 1A–D.** Plant species used in experiments, showing diverse morphology. **A** *Hirshfeldia incana;* **B** *Brassica juncea crispifolia;* **C** *Brassica campestris;* **D** *Brassica caulorapa*

al Volcanic Monument, Washington State, and at the Western Washington Agricultural Experimental Station in Mt. Vernon, and two non-native species, *H. Variegata* and *C. Septempunctata* (HV and C7), which we obtained from U.S. Department of Agriculture stock. This selection allowed us to compare foraging behavior among species, between genera, and between natives and non-natives. In addition, the species represented a wide range of body sizes. HC is 8 mm in length, HV 5 mm, C7 9 mm, and CA 6–7 mm. Their weights are HC 17.2 mg (Elliot pers. comm.), HV 7.8 mg, C7 35.3 mg (Kauffman pers. comm.), and CA approximately 20 mg. Ladybird collections took place between August 30 and September 8, 1990 and we maintained the beetles in cardboard cannisters and fed them aphids and sugar water. We used both male and female adult ladybirds in all experiments. Beetles were starved for 24 h prior to using them in the experiments.

We chose plants to represent particular morphological contrasts (Fig. 1A–D). Kohlrabi *(B.o.c.)* is characterized by its smooth, waxy leaf and stem surfaces and a globose stem on which the petioles converge at the base of the plant (Fig. 1D). *Brassica campestris (B.c.)* has small smooth leaves, branching stems, and at the time of the experiment, both seed pods and flower buds (Fig. 1C). Mustard greens *(B.j.c.)* have large textured leaves with densely ruffled edges (Fig. 1B). Hirschfeldia *(H.i.)* has leaves similar in structure to *B.o.c.,* but the surfaces are covered with 1–2 mm hairs (Fig. 1A).

Seeds of *B.o.c.* and *B.j.c.* were planted abundantly in 17 cm round pots on July 30, 1990, and seedlings were later thinned to one per pot. *B.c.* and *H.i.* were transfered to the pots as seedlings, one plant per pot. Three plants of each species were selected that we felt were morphologically typical. All plants were of comparable overall size at the time of the experiments, though their surface areas varied (Table 1).

**Table 1.** Architectural characteristics and total surface areas of experimental plants. Surface area values represent averages across the 3 plants of each species used in the experiments

| | Stem shape | Leaves | | Surface area ($cm^2$) |
|---|---|---|---|---|
| | | Edges | Surface | |
| B.O.C. | Globose | Smooth | Waxy | 534 |
| B.C. | Linear, branching | Smooth | Waxy | 203 |
| B.J.C. | Linear, short | Ruffled | Wrinkled | 260 |
| H.I. | Linear | Smooth | Hairy | 472 |

Our experiment represented a two-way factorial design, with plant species and ladybird species as main factors. Each of the resulting sixteen ladybird-plant combinations were replicated 11 to 13 times. Although we measured several different variables while conducting our experiment, the protocol itself was quite simple.

Two days before the start of the experiments, we initiated colonies of cabbage aphids *(Brevicoryne brassicae),* which are crucifer specialists, on the plants. Prior to running the experiments, we adjusted the number to between 50 and 100 aphids per plant and added aphids during the course of the day, if needed, to replace individuals consumed by ladybirds.

For each replicate, we randomly selected one of the three plants of the appropriate variety and placed a single beetle on it. We then watched the beetle for ten minutes or until it flew away. Using portable computers, we recorded the amount of time spent foraging and the location of foraging; and occurrences of falling from the plant, flying away, contacts with aphids, and consumption of aphids. The location of search was recorded as leaf, stem, or ground. We included all structures for which foraging movement is one dimensional, such as petioles and seedpods, in the category of "stem". Foraging on the pot was grouped with "ground". If a ladybird fell outside of the pot it was placed on the ground inside of the pot so that it had a chance to find the plant again. Observations were done in sets of four using a single plant for sequential observations of the four coccinellid species, thus insuring that the four ladybird species were equally represented on all individual plants. Individual ladybirds were randomly chosen from a pool of approximately 50 beetles and were not used more that once in a day. The pools were restocked periodically due to the loss of ladybirds that flew away. At the end of a day's observations, all ladybirds were fed and then starved for twenty-four hours prior to using them again. This insured that all experimental beetles were at similar hunger levels.

All experiments took place out of doors on the University of Washington campus between September 6 and September 12, 1990.

## *Data analysis*

Two-way analysis of variance was used to test all components of behavior except the frequency of observations that were terminated by flight from the plant, for which a loglinear test was used. All occurrence data other than flight (number of falls, contacts, and consumptions per unit time) were square root transformed prior to statistical analysis. An arcsine square root transformation was used for all time budget data. In addition to comparing foraging activities across all ladybird species, we examined two pairwise comparisons: 1) We compared the natives to non-natives within each genus (HC vs. HV and CA vs. C7); and 2) We lumped congeneric species to compare Hippodamia with Coccinella. Our analysis of predation rates included a comparison of the overall rates at which aphids were consumed as well as examinations of several refined measures of foraging behavior that give information about the particular components of foraging that are affected by plant architecture. Specifically, we dissected the overall rate of prey consumption into four components: 1) The amount of time spent actively searching, 2) the location of searching, 3) the rate at which prey are contacted, and 4) the proportion of contacted prey that are actually eaten. The two additional behaviors that we analyzed, falling and flying, come into play in determining predation rates primarily by changing the location of foraging from the plant to the ground or from one plant to another.

## Results

Because of the multifactorial design of our experiment and the large number of variables that we measured, and because of the many possible ways of breaking up the data, we simplify matters by first presenting one large analysis of variance summary table that reports whether or not results were significant (Table 2). The degrees of freedom were the same for all entries within each grouping and are listed in the table. In all cases we tested for interaction effects.

From Table 2 it is apparent that all foraging behaviors that we measured varied significantly either among species of ladybird or among plants. However, for none of the seven response variables we examined did we find a significant interaction between ladybird species and plant architecture. We therefore focus on the main effects of ladybird and plant species by presenting ladybird effects averaged across the four plant species and plant effects averaged across the four ladybird species.

### *Overall predation rates*

The most direct measure of foraging effectiveness is the rate at which a predator consumes prey. We found that the number of aphids killed per unit time was influenced more by the plant factor than by the ladybird factor. Feeding rates were 78% higher on *B.c.* than they were on *B.o.c.* (Fig. 2A) but differences in overall kill rate between the four ladybirds were not significant (Fig. 3A, Table 2).

**Table 2.** Effects of ladybird species, plant species, and interactions of the two on six components of ladybird foraging behavior. All behaviors were analyzed by two-way analysis of variance, except flight which was analyzed with loglinear modeling (df = 3 for main effects, 9 for interactions)

Behavior

| | Kills /min | Contacts /min | Kills /cont | Forage /total | Falls /min | Flights /obs. |
|---|---|---|---|---|---|---|
| Ladybird | NS | NS | * | *** | * | *** |
| Plant | * | * | * | * | *** | NS |
| Ladybird × plant | NS | NS | NS | NS | NS | NS |

* $p< =0.05$; ** $p< =0.01$; *** $p< =0.001$; NS: $p>0.05$

### *Refined measures of foraging efficiency*

The rate at which a predator encounters prey is a measure of how effective its searching strategy and its pattern of movement are for locating prey on a given plant surface. As with overall predation rate, we found that contact rates were significantly affected by plant species but not by ladybird species. Approximately 1.5 more aphids were encountered per minute on *H.i.* than on the other three plants (Fig. 2B). Ladybirds consume only some of the aphids they contact, however, and the ratio of aphids killed to aphids contacted did vary significantly for both plants and ladybirds (Fig. 2–3C). By this measurement C7 had the highest efficiency, consuming 54% of the aphids it encountered, and HC had the lowest, 28%.

The amount of time the ladybirds spent actively searching for prey, and the fraction of that time spent on the ground, also depended on both ladybird and plant species (Figs. 2–3D). C7 spent much less time foraging than the others. HC spent a large percentage of its total foraging time on the ground. Time spent on the ground does not contribute to finding aphids since these aphids are almost never found off of the plant.

In light of these refined measures of foraging behavior, it is clear that the comparable overall feeding rates that we measured for the four ladybirds are not the result of similar foraging strategies. Instead, the combinations of very different foraging behaviors at the refined levels resulted in similar feeding rates for the four species.

### *Falling*

The time that ladybirds spend on the ground is largely a result of falling off the plant. The frequency with which ladybirds fell from a plant varied significantly among the different ladybirds, and for different plants on which they foraged. In particular, C7, the most agile species, was 19 times less likely to fall than its congener CA, which fell the most (Fig. 3E). All ladybirds fell nearly four times as often on *B.o.c.* as on the other plants (Fig. 2E); we attribute this to the slippery surface of *B.o.c.*

### *Flight*

The propensity to fly away from a plant was highly variable among ladybird species but apparently independent of plant species (Fig. 2–3F). Interestingly, flight activity among the four ladybirds showed a similar pattern to falling frequency (compare Figs. 3E and F). CA flew the most (62% of observations), C7 the least (10%), and HV and HC were intermediate in their propensity for flight.

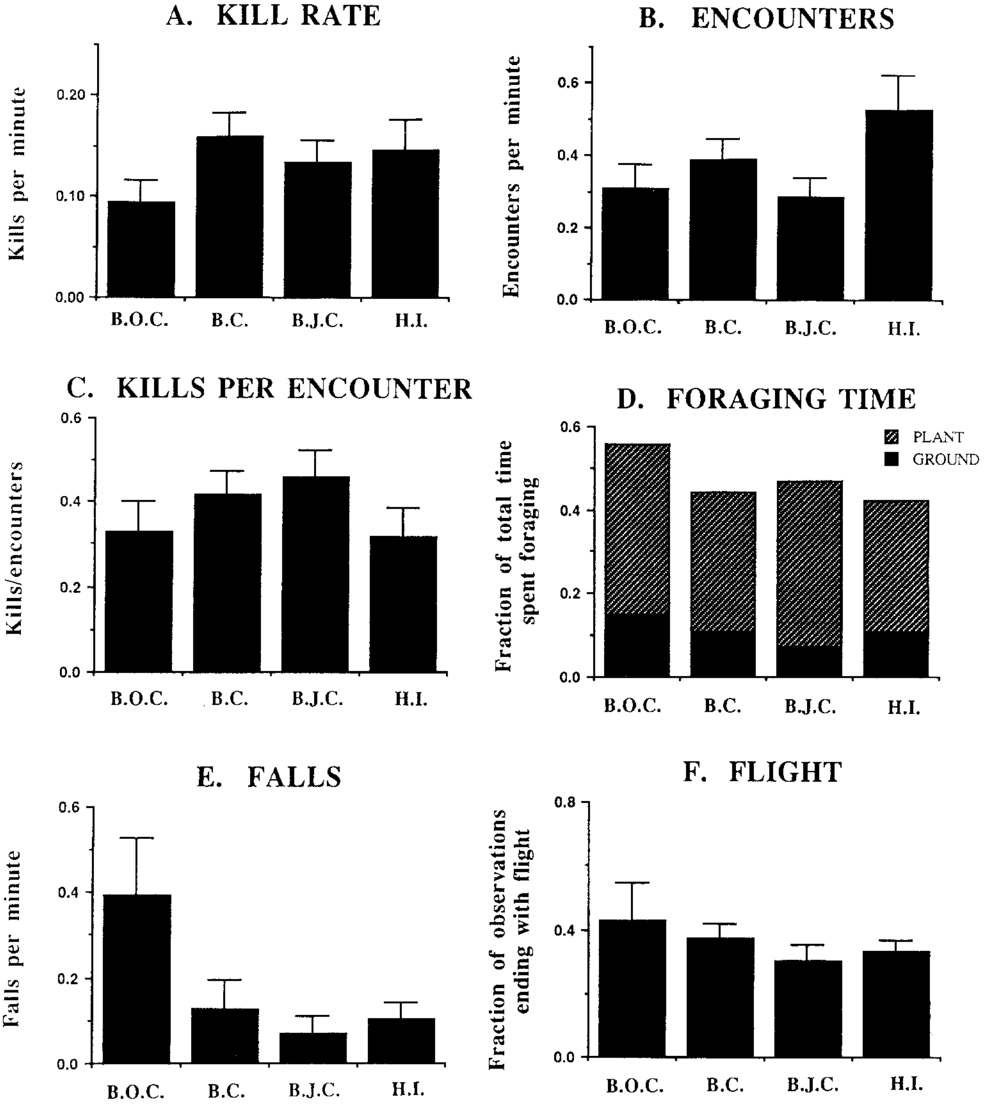

**Fig. 2A–F.** Effects of plant species on foraging behavior of ladybirds. Columns represent the mean and one standard error for all four ladybird species. **A** Rate at which aphids are consumed; **B** rate at which aphids are contacted; **C** fraction of aphids encountered that are actually consumed; **D** fraction of time spent foraging; **E** frequency of falls from the plant; **F** fraction of observations in which the ladybird flew away

### *Pairwise comparisons*

In a priori comparisons among ladybirds, the two genera differed from one another both in the ratio of kills per contact and in the amount that they fell from the plants (Table 3). In addition, the two Hippodamia congeners proved to be very similar in their foraging strategies whereas the two coccinella species were very different. For all measurements except kills/min., C7 proved to be less active and more efficient.

## Discussion

Our study shows that plant morphology can substantially alter the foraging success of predators that search for prey on the plant surface. We found that the rates of prey consumption by ladybirds varied among crucifers of diverse architectures and that these discrepancies in feeding rates could be further explained by the differences in the amount of time spent foraging, the location of foraging, the rate of contacting aphids, and the ratio of aphids killed to aphids contacted. Plants acted directly on the predator by impeding or facilitating movement, causing the predator to fall, or otherwise making prey difficult to reach. The most striking effect of plant architecture was on the frequency with which the ladybirds fell. In particular the slippery surface of *B.o.c* made the plant difficult for ladybirds to traverse. In order to move more efficiently, all ladybird species tended to follow the leaf edges and stems rather than the flat leaf surfaces on this plant. Interestingly, we observed slipping on *B.c.*, which also has smooth leaves, but the complex structure of this plant (more edges and fewer flat surfaces), apparently made it more maneuverable; consequently, ladybirds did not fall as often. Thus the detrimental effects of surface texture on the ability of predators to maneuver on a plant can be ameliorated to some extent by plant morphology.

The impeded movement of ladybirds and other predators on certain plant surfaces may provide refuges for the prey. On *B.o.c.*, for example, many of the aphids were located on the middle of the undersides of leaves, an area impossible for the ladybirds to get to because they could not grip the under surface. Indentations in the ruffled

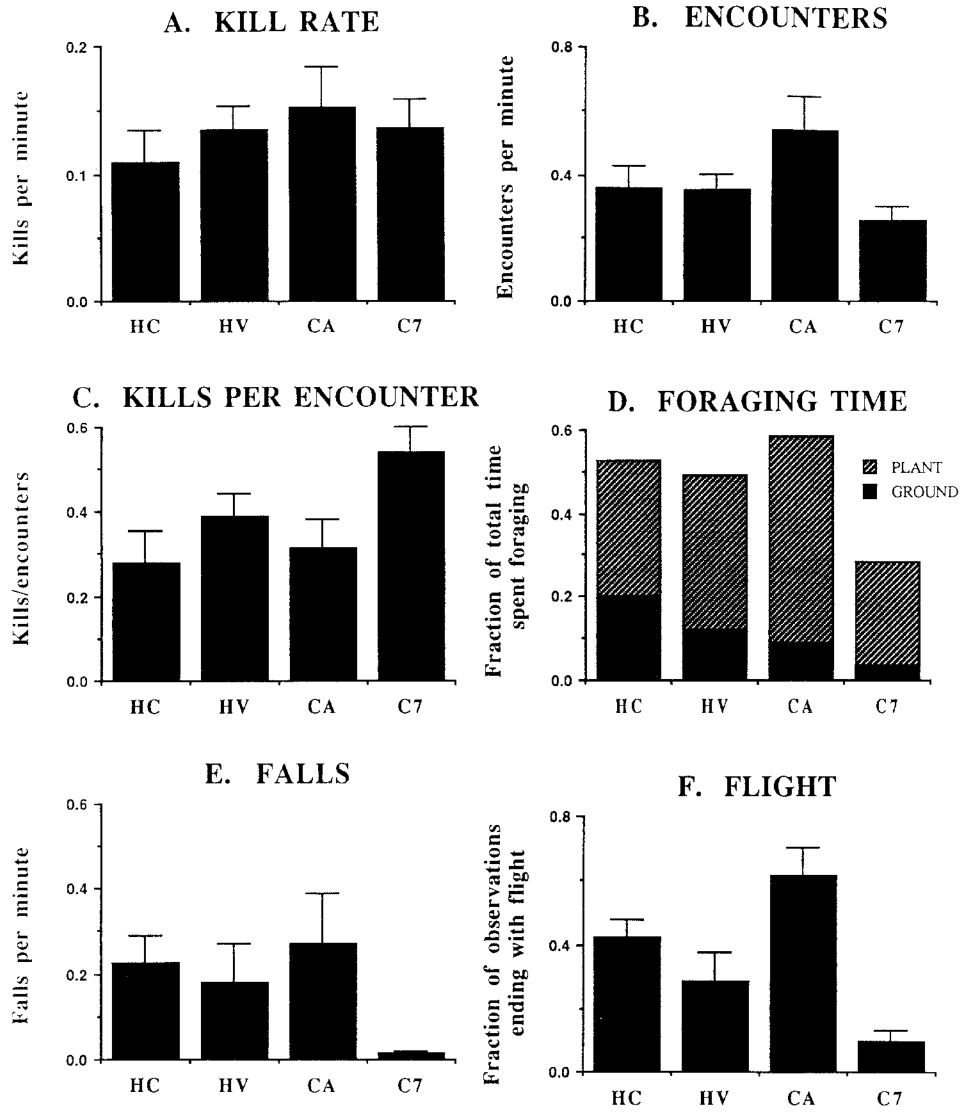

**Fig. 3A–F.** Differences in foraging behaviors of the four species of ladybirds. Columns represent the mean values across all plants and one standard error. **A** Rate at which aphids are consumed; **B** rate at which aphids are contacted; **C** fraction of aphids encountered that are actually consumed; **D** fraction of time spent foraging; **E** frequency of falls from the plant; **F** fraction of observations in which the ladybird flew away

**Table 3.** Effects of ladybird species, or genus, on six components of ladybird foraging behavior with ladybirds grouped by genus. All behaviors were analyzed with analysis of variance, except flight for which a *G* test was used (df = 1 for all entries)

| | Behavior | | | | | |
|---|---|---|---|---|---|---|
| | Kills /min | Contacts /min | Kills /cont | Forage /total | Falls /min | Flights /obs. |
| Coccinella vs. hippodamia | NS | NS | * | NS | *** | NS |
| CA vs. C7 | NS | * | * | *** | * | *** |
| HC vs. HV | NS | NS | NS | NS | NS | NS |

* $p<=0.05$; ** $p<=0.01$; *** $p<=0.001$; NS: $p>0.05$

leaves of *B.j.c.* sometimes provided refugia where aphids were apparently safe from the larger bodied predators. From an evolutionary standpoint, plants are faced with the sometimes contradictory process of adapting their architecture and surface qualities not only as protection from direct environmental pressures and herbivory, but also as a venue accessible to the natural enemies of the plant's pests.

Surprisingly, the overall predation rates of the four ladybird species did not differ significantly. However, significant differences in other aspects of behavior suggest that their search strategies were actually quite different even though the outcome (kill rate) was similar. For example C7 had a high ratio of kills to contacts but low contacts per minute and spent the least amount of time foraging. In contrast, CA spent the most time foraging, and had a high rate of contacts per minute, but killed few of the aphids that it contacted. Thus the level of behavior at which the plant architecture interacts with the ladybird's foraging is not the same for all four ladybird species.

Among the four species of ladybirds we observed, the non-native C7 was distinctive in its foraging strategy – falling, flying, encountering aphids, and actively searching less than the other three species, yet consuming a comparable number of aphids. Interestingly, this species has been successfully introduced into the U.S. for biological control of aphids. Its successful establishment may perhaps be due to the efficiency with which it forages. Longer term studies at the population level would clarify the importance of overall feeding rate vs. feeding efficiency and would also reveal how short term behavioral studies, such as this one, relate to long term effects.

The other distinctive difference in species behavior was CA's propensity for flying. It is not clear whether this activity helps or hinders its foraging efficiency in the long run. While flying away from a plant with aphids may seem like it would reduce effectiveness, high flight activity may insure that the beetle will find isolated colonies and not waste time in areas uninfested with aphids.

The effects of plant morphology on predator efficiency have important implications for biological control of plant pests. For successful biocontrol programs, in addition to assessing predator effectiveness in controlling aphids, we need to assess "plant effectiveness" in allowing predators to gain access to the prey. Programs to breed pest resistant plants may benefit by investigating the effects that particular plant phenotypes have on the pests natural enemies as well as on the pest itself. Thus our results argue that trials for pest resistance should be conducted not only in the presence of pest species, but in the presence of the pests' natural enemies as well (see also e.g. Starks et al. 1972).

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