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The role of vision and color in the close proximity foraging behavior of four coccinellid species

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Abstract The role of vision and color in close-proximity foraging behavior was investigated for four species of lady beetles: *Coccinella septempunctata*, *Hippodamia convergens*, *Harmonia axyridis*, and *Coleomegilla maculata*. The effect of light level and color cues on consumption rates varied among the four predator species. The consumption rates of these predators on the pea aphid *Acyrtosiphon pisum* (Harris) was measured under light and dark conditions. *C. septempunctata*, *H. convergens*, and *Ha. axyridis* consumed significantly more aphids in the light than in the dark, while the consumption rate of *Col. maculata* was not affected by light level. Foraging ability was also measured on red and green color morphs of the pea aphid on red, green, and white backgrounds. *C. septempunctata* consumed significantly more of the aphid morph that contrasted with the background color, and showed no difference between morphs on the white background. *H. axyridis* consumed significantly more red morph aphids regardless of background. The remaining two species showed no difference in consumption rates on the two color morphs. The variation in the use of visual cues demonstrates how different species of predators can exhibit different foraging behaviors when searching for the same prey.

Key words Coccinellidae · Foraging behavior · Vision

Introduction

The chemical and biological cues used by insect predators are important to understanding the predators' effectiveness as biological control agents. Many major

insect predators use visual cues to find prey, including some carabids (Wheater 1989), Heteroptera (Ambrose et al. 1991; Awan et al. 1989), and mantids (Bowdish and Bultman 1993). There was a long-held view that coccinellids could not detect prey until contact and therefore that vision is not an important factor in close-proximity foraging (Fleschner 1950; Robinson 1952; Banks 1954, 1957; Putnam 1955; Dixon 1959; Kaddou 1960; Kehat 1968; Hodek 1973; Storch 1976). Many of these conclusions were drawn from broad-based foraging behavior studies which had included many factors besides vision, and results were often generalized across multiple species and life-stages.

More recent studies have been specifically performed to investigate the possibility of visual cues in coccinellid foraging. While studies involving larvae have found no evidence for the use of vision (Fleschner 1950; Banks 1954; Storch 1976; Stubbs 1980; Hattingh and Samways 1995), experiments involving adults have shown the use of visual cues in the foraging behavior of several species. Stubbs (1980) found that *Coccinella septempunctata* L. discovered immobile aphid and dummy prey significantly faster than would be expected by random movement within experimental arenas. Nakamuta (1984) found that *C. septempunctata* foraging in the dark did not attempt to capture an immobilized aphid prey until direct contact with it, while in the light, it would orient towards the prey from 7 mm away. In other experiments, *Harmonia axyridis* (Pallas) and *Chilocorus nigritus* (Fabricius) were found to use both olfactory and visual cues in detecting individual prey from a short, but undetermined distance (Obata 1986; Hattingh and Samways 1995).

While these experiments suggest the use of visual cues in the foraging of some species of coccinellids, there has been no comparative study of the use of visual cues among several species. We experimentally examined the effects of light and color on the foraging efficiency of four coccinellid species, *Coccinella septempunctata* L., *Hippodamia convergens* Guerin, *Harmonia axyridis*, and *Coleomegilla maculata* DeGeer (Coleoptera: Coccinell-

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idae). These species are commonly found in agricultural fields of southern Wisconsin during most of the summer. All four are generalist predators that have the potential to influence populations of the pea aphid, *Acyrtosiphon pisum* (Harris), a common pest of some agricultural crops (Clausen 1978). The pea aphid occurs as a red and a green color morph which are both regularly found in the field (Losey et al. 1997). The two aphid color morphs provide the opportunity to examine whether coccinellids use color cues in foraging.

Our specific objectives were (1) to determine the importance of visual cues for detecting aphid prey by comparing ladybird foraging in light and dark conditions, (2) to investigate the role of color cues by allowing the coccinellids to choose between red morph and green morph pea aphids in arenas with a cryptic or neutral colored background, and (3) to ascertain if these visual and color cues are used differently among the species.

Materials and methods

Natural history

C. septempunctata and *Ha. axyridis* are Palearctic species that were introduced into the United States to control several economically important aphid species in different agroecosystems (Hodek 1973; Honek 1985; Dreistadt et al. 1995). From 1974 to 1989, *C. septempunctata* was released through a USDA redistribution program in several midwestern states including Wisconsin (Angalet et al. 1979). *C. septempunctata* is now one of the most common coccinellid species east of the Rocky Mountains (Gordon and Vandenberg 1991). *Ha. axyridis* had been introduced in various North American locations since 1916; however, no recoveries were reported before a major release in the orchards of Georgia as part of a biological control program for pecan aphids (*Monellia caryella* and *Monelliopsis pecanis*) during the late 1970s and early 1980s (Teddors and Schaefer 1994). Since then, large populations of *Ha. axyridis* have been found in the southeastern United States (Chapin and Brou 1991), and its range has spread to Canada (Coderre 1995) and the Pacific Northwest (Dreistadt et al. 1995).

Col. maculata and *H. convergens* are native to North America. *H. convergens* is an aphidophagous species commonly used by organic farmers to augment coccinellid populations (Yebsen 1976). Certain populations are known to migrate, notably those from California which overwinter in the Sierra Nevada Mountains where they are collected for distribution (Hagen and Sluss 1966). *Col. maculata* is also widely distributed east of the Rocky Mountains (Gordon 1985). It is an omnivorous species (Hodek 1973) that feeds on prey such as aphids, as well as pollen from a variety of different plant species (Maredia 1992; Putnam 1964).

A. pisum is an Old World aphid species that was first introduced in the mid-19th century (Clausen 1978). It feeds on alfalfa, peas, and other agricultural crops, in some areas reaching levels great enough to cause significant economic damage (Clausen 1978). Like other aphids, including the English grain aphid (Araya et al. 1996), the pea aphid has more than one color morph (Müller 1983). This experiment used a red morph and a green morph of the pea aphid. The two morphs have been found to be very similar in terms of growth rates, host specificity, and defensive behaviors, and both color morphs are common in agricultural fields of southern Wisconsin (Losey et al. 1997).

Experimental animals

Coccinellids were collected as adults or as pupae from agricultural fields at the Arlington Agricultural Research Station in south-

central Wisconsin, from late June to late August in 1996 and 1997. In the laboratory pupae were allowed to emerge, and adults were maintained on pea aphids and sugar water until the experiment. Most coccinellids were in the laboratory less than 1 week before experiments, and no coccinellid was in the laboratory for over 1 month. Pea aphids used for feeding and in the experiment were from a large laboratory colony. The aphids were reared on fava beans and were no more than 4 months removed from field stock.

Light/dark experiment

To determine if the presence or absence of visual cues had any effect on the foraging efficiency of coccinellids, individual adult *C. septempunctata*, *H. convergens*, *Ha. axyridis*, or *Col. maculata* were placed in a cage with ten green morph aphids and allowed to forage for 30 min in either absolute darkness or under fluorescent light. Prior to each experiment, the coccinellids were satiated and then starved for 18–24 h to maximize searching activity (Frazer and Gilbert 1976). Twenty-four adults of each species were used in both the light and the dark, with different individuals used in the light/dark conditions. After 30 min of foraging, coccinellids were removed and the number of aphids partially or completely eaten were counted.

Since these experiments were focusing only on the close proximity use of visual cues, the experiments were carried out in small circular arenas 20 cm in diameter and 10 cm high. The cages were constructed of clear mylar sides and white construction paper bottoms (Canson brand 66% rag-acid-free paper white #335). The bottom and mylar sides were connected with clear silicone. To ensure that the aphids would always be accessible and viewed against the same background, a 5 cm strip of white construction paper was attached around the bottom, outside of the mylar, and the bottom 5 cm of the inside was coated with Fluon (a slippery substance) to keep aphids from climbing on the sides. A nylon mesh screen was fitted at the top of the cage with a removable plastic rim. The experiment was conducted in a plant growth chamber at a constant temperature of 25°C under florescent lighting or in total darkness. Data were analyzed as a factorial analysis of variance with two levels of light (light, dark) and four levels of species.

Color experiment

To determine whether the coccinellids use color as a foraging cue, choice tests were performed in which coccinellids were allowed to forage for red and green color morphs of the pea aphids in arenas. The arena was the same as used in the light/dark experiment except that the background color was varied. The cages each had either a red, green, or white background, (Canson brand 66% rag-acid-free paper green #475, amber #504) to provide either a cryptic or neutral background. To the human eye, a red aphid on the red background was cryptic, the green morph was cryptic on the green background, and on the white background neither form was cryptic. Five red aphids and five green aphids were placed in each cage and allowed to disperse. Aphids used were older than first instar, and the age structure of the two color morphs was equal. Coccinellid adults that had been satiated and then starved for 18–24 h were placed inside each cage and allowed to forage for 30 min. Twenty individual coccinellids from each species were allowed to forage on the red background, another twenty individuals foraged on the green background, and an additional group of twenty were used on the white background. After 30 min of foraging, the coccinellid was removed, and the number of aphids eaten was counted. The experiment took place under constant fluorescent lighting at room temperature (20–22°C). Data from each species of coccinellid were analyzed as a separate split-plot analysis of variance with background as the whole plot and aphid color morph as the split plots.

Non-visual cues experiment

To determine if any of the species could detect relevant non-visual differences between the red and green aphid morphs, an additional set of preference tests was performed on a white background in absolute darkness. With the exception of the lighting, the procedure was the same as the color experiment test; 20 coccinellids of each species were placed in white background cages with five aphids of each color morph. The coccinellids were satiated and starved before the experiment, and each coccinellid was allowed to forage for 30 min and the number of aphids consumed were counted. The experiment took place in a completely dark growth chamber at 25°C. Data were analyzed as a factorial analysis of variance with two levels of light (light, dark) and four levels of species.

Results

The effect of light level on aphid consumption varied significantly across the four coccinellid species (Table 1). *C. septempunctata* consumed significantly more aphids in the light (4.29 ± 0.40) than in the dark (2.36 ± 0.27) ($P = 0.0003$, Fig. 1) as did *H. convergens* (4.13 ± 0.41 in light vs. 2.25 ± 0.33 in dark; $P = 0.0004$; Fig. 1). *Ha. axyridis* also consumed more aphids in the light, but

the results were not significant (2.67 ± 0.44 in light vs. 1.63 ± 0.49 in dark; $P = 0.064$; Fig. 1). *Col. maculata* showed no significant difference in the number of aphids eaten in the presence versus the absence of light ($P > 0.1$; Fig. 1).

The relative consumption rates on green and red morph aphids by *C. septempunctata* was significantly affected by background color (Table 2). *C. septempunctata* consumed significantly more red aphids than green aphids on the green background (2.10 ± 0.182 vs. 1.45 ± 0.182 ; $P = 0.0144$), significantly more green aphids than red aphids on the red background (1.45 ± 0.182 vs. 0.80 ± 0.182 ; $P = 0.0144$) and exhibited no difference in the consumption of the two morphs on the white background ($P = 0.5627$; Fig. 2).

Table 1 Analysis of variance results for the effects of light level (light, dark), coccinellid species (*Coccinella septempunctata*, *Coleomegilla maculata*, *Harmonia axyridis*, and *Hippodamia convergens*), and their interaction on the number of aphids (*Acyrtosiphon pisum*) consumed

Source of Variation	df	MSE	F	P
Species	3	14.58	4.47	0.005
Light level	1	68.42	20.97	<0.001
Species × light level	3	9.89	3.03	0.031
Error	180	3.26		

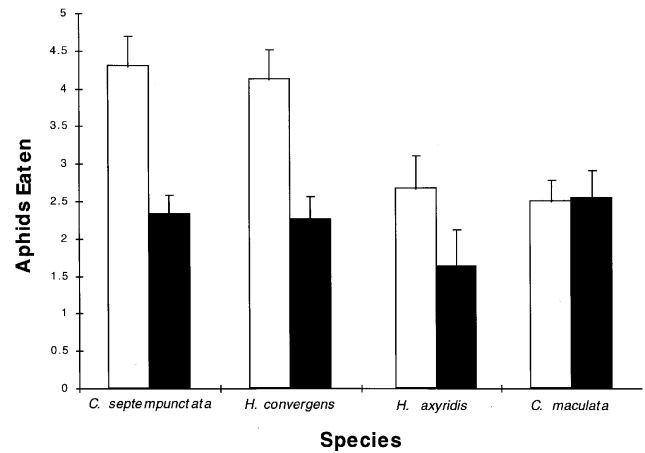
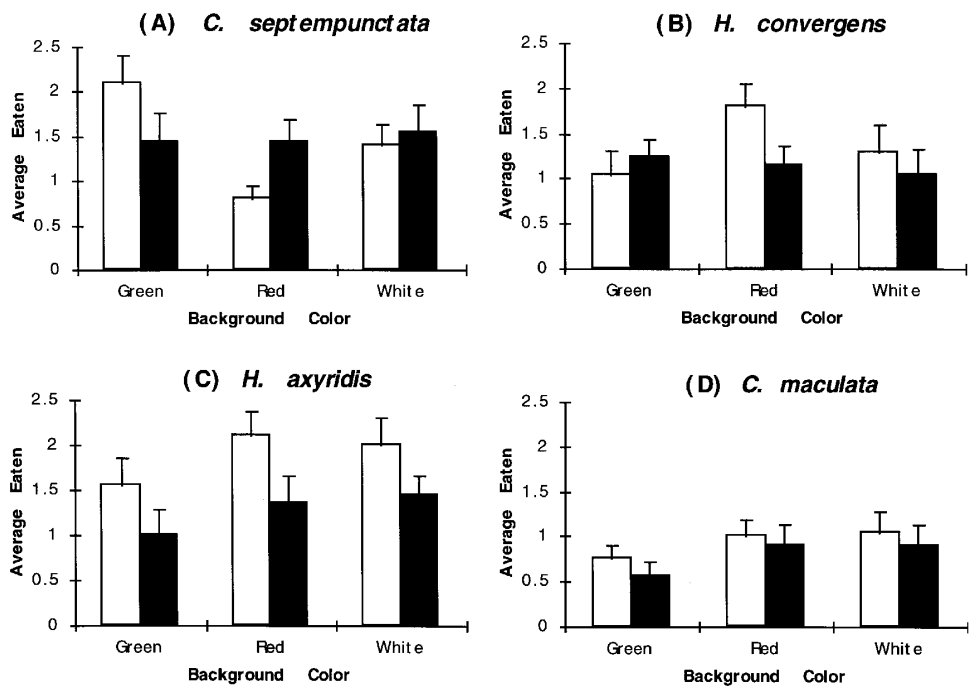


Fig. 1 Mean (+SEM) aphid consumption by four species of coccinellids in light (open bars) and dark (filled bars) conditions

Fig. 2A–D Mean (+SEM) consumption of red (open bars) and green (filled bars) morph aphids on green, red, and white backgrounds: **A** *Coccinella septempunctata*, **B** *Hippodamia convergens*, **C** *Harmonia axyridis*, **D** *Coleomagilla maculata*



The effect of aphid color morph on consumption by *Ha. axyridis* did not vary significantly across the color backgrounds (Table 2). *Ha. axyridis* consumed significantly more red morph than green morph aphids (1.88 ± 0.128 vs. 1.27 ± 0.128 ; $P = 0.0012$; Fig. 2) regardless of background color. The aphid consumption rates of *Col. maculata* and *H. convergens* were not significantly effected by differences in background color or differences in morph color ($P > 0.1$; Table 2; Fig. 2).

In the dark, *Col. maculata* consumed significantly more green morphs than red morphs (0.65 ± 0.116 vs. 0.33 ± 0.083 ; $P = 0.029$; Table 3). *C. septempunctata*, *H. convergens*, and *Ha. axyridis* showed no significant difference in the consumption rates of red and green aphids in the dark ($P > 0.1$; Table 3).

Discussion

The most striking aspect of our results is the variation in foraging cues used by these coccinellid species that all feed on a common prey species in the same habitat. The four species we examined exhibited wide variation in

Table 2 Significance values (P) for the effects of background (red, green, and white), and aphid morph (red and green) and their interaction on the number of aphids consumed by four species of coccinellids

	Background	Aphid morph	Background × morph
<i>C. septempunctata</i>	0.1585	0.7380	0.0029
<i>H. convergens</i>	0.4714	0.1680	0.1248
<i>Ha. axyridis</i>	0.2980	0.0012	0.8730
<i>Col. maculata</i>	0.2872	0.2973	0.9599

Table 3 Mean number (\pm SEM) of green and red aphids consumed in total darkness by four species of coccinellids and the significance values (P) of the differences

	Green morph	Red morph	P
<i>C. septempunctata</i>	1.850 ± 1.182	1.450 ± 1.468	0.349
<i>H. convergens</i>	0.750 ± 0.716	0.800 ± 0.696	0.824
<i>Ha. axyridis</i>	0.950 ± 0.999	1.000 ± 0.973	0.873
<i>Col. maculata</i>	0.650 ± 0.736	0.325 ± 0.526	0.026

Table 4 Summary of the difference in consumption rates by the four coccinellid species in the three experiments with P values listed in parantheses

	Light/dark	Color	Non-visual cues
<i>C. septempunctata</i>	Light > Dark* (0.0003)	Contrasting > Cryptic** (0.0144 green background) (0.0144 red background)	ns (0.349)
<i>H. convergens</i>	Light > Dark* (0.0004)	ns (0.1248)	ns (0.824)
<i>Ha. axyridis</i>	Light > Dark (0.064)	Red > Green* (0.0012)	ns (0.873)
<i>Col. maculata</i>	ns (0.935)	ns (0.9599)	Green > Red (0.029)

* Indicates significance after Bonferroni for multiple comparison correction; 12 corrections, adjusted P value = 0.004 (Neter et al. 1989)

** Combined P value is < 0.004 ($\chi^2_{4} = 16.96$; Sokal and Rohlf 1981)

their use of light, color, and non-visual cues in their close-proximity foraging behavior (Table 4). *C. septempunctata*, which is known to be an important aphid predator, was affected dramatically by both color and light. Conversely, *Col. maculata*, a known pollenivore, appears not to make use of color or any other visual cue. *H. convergens* and *Ha. axyridis* had varying responses to light and color.

Three of the four species showed decreased foraging efficiency in dark versus light conditions. One explanation for this is that ladybird foraging efficiency is reduced because the ladybirds cannot see the aphids. An alternative explanation is that ladybird activity is reduced in dark conditions. Nakamuta (1987) found that most of *C. septempunctata*'s locomotor activity occurred during photophase and that they consumed significantly fewer aphids in the dark period of a day than they consumed in the light period. However, Nakamuta (1987) also showed that *C. septempunctata* exhibits a dominant circadian rhythm in its activity behavior with a distinct active phase from 0900 to 1600 hours, during which all of our experiments were conducted. Hence, although we cannot distinguish between these two explanations of reduced foraging efficiency in the dark, it is likely that the inability to see aphids is important.

The color experiment results show that *C. septempunctata* consumes different numbers of the two color morphs depending on the color of the background, but it consumes the same amount of both morphs in the dark. These results imply that *C. septempunctata* uses color contrast to increase its foraging efficiency. *C. septempunctata* has photoreceptors in the UV, blue, and green, suggesting that this coccinellid is sensitive to green stimuli and that it has the ability to distinguish between red and green colors (Agee et al. 1990; Lin and Wu 1992; Lin 1993). A consequence of these color cues is that the green morphs of the pea aphids could have a distinct advantage over the red morphs since the primary background, the host plant, of the pea aphids is green. High *C. septempunctata* densities in the field relative to the density of the parasitoid *Aphidius ervi* (Harris) are associated with a decrease in the fraction of red morph relative to green morph aphids (Losey et al. 1997). Thus, as one of the most effective predators of aphids in agricultural settings, *C. septempunctata* predation could be

an important factor in the relative abundance of red and green color morphs in the field.

H. convergens probably use visual cues, as implied by their decrease in foraging efficiency in the dark. However, no significant difference was found between its foraging efficiencies for either color morph in the dark or in the light on any of the three backgrounds. These results imply that although they use general visual cues, color cues do not play a significant role in this species' foraging for pea aphids.

Ha. axyridis consumed significantly more aphids in the light than in the dark, more red aphids than green aphids regardless of background color in the light, and exhibited no preference for either color in the dark. The preference for one morph regardless of background suggests the use of non-visual possibly olfactory cues. However, this conclusion is not supported by the lack of preference for either aphid in the dark. What relationship there may be between visual and olfactory cues (Obata 1986) or other sensory cues is unclear. Further tests designed to investigate specific non-visual cues may resolve this question.

Col. maculata did not have a higher predation rate in light compared to the dark, suggesting that visual cues are not a primary component of this species' foraging behavior. Furthermore, the results of the color experiment suggest that color cues are either unused or unimportant in its prey foraging efficiency. *C. maculata* was the only species to consume more of one morph than the other in the dark. However, when corrected for multiple comparisons, the results are not statistically significant. The diet of this species is significantly different from the other species in that pollen constitutes the principal component of its diet (Putnam 1964), and visual cues in close proximity foraging behavior may not be as important as other senses.

Visual cues have a significant role in the foraging behaviors of *C. septempunctata*, *Ha. axyridis*, and *H. convergens*, and color cues play a part in the foraging of *C. septempunctata* and possibly *Ha. axyridis*. The use of visual and color cues are not the only factors that have been shown to have different effects on different coccinellid species foraging in similar habitats. Plant architecture has been found to influence coccinellid behavior differently among species (Kareiva and Sahakian 1990; Frazer and McGregor 1994). In larvae, the role of light has been found to differ among species and by stage of development (Ng 1986). All of these differences can have a significant impact on predator and prey population dynamics and may influence community composition. Native coccinellid species have been decreasing in at least one location since *C. septempunctata* has been introduced (Elliott et al. 1996), one possible reason for this could be the differences in visual cues among members of the coccinellid community.

While the historical trend has been to generalize behavioral traits found in one species to all coccinellids, our study demonstrates the wide variation in the use of foraging cues. By finding differences and similarities among species, we may be able to understand better how

multiple species of coccinellids coexist in the same habitat on the same prey, and how we can most effectively employ these predators to control pest populations.

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