Larval Responses of Aphidophagous Lady Beetles (Coleoptera: Coccinellidae) to Weevil Larvae Versus Aphids as Prey

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ABSTRACT Adult and larval aphidophagous lady beetles (Coleoptera: Coccinellidae) feed on alfalfa weevil larvae, *Hypera postica* (Gyllenhal), and aphids in alfalfa fields. We studied the development of first and fourth instars of two lady beetle species (*Coccinella septempunctata* L. and *Harmonia axyridis* Pallas) when provided live or dead weevil larvae versus pea aphids, *Acyrthosiphon pisum* (Harris). No individuals of either species survived to the second stadium on a diet of weevils (dead or alive), whereas almost 100% of first instars of both species did so on a diet of aphids. Nearly all individuals of *H. axyridis* that were provided weevils (dead or alive) during the fourth stadium survived and subsequently completed pupation. However, these individuals weighed significantly less as newly molted adults than did conspecifics that had fed on aphids as fourth instars. Only 5% of fourth-instar *C. septempunctata* survived to adulthood when provided live weevils (versus 100% provided aphids), but 70% did so when provided dead weevils. Both first and fourth instars of both species attacked both dead and live weevil larvae much less readily than aphids, and were often deterred from persisting in the attack by the defensive wriggling of live weevil larvae (in contrast to their persistence and success in attacking aphids). Nevertheless, even first instars of the predators succeeded in some instances in overcoming weevil larvae, and proceeded to feed upon the prey for up to the maximum of 10 min of observation. Our results suggest that although weevil larvae are not very suitable as substitute prey for aphids for the larvae of *C. septempunctata* and *H. axyridis,* consumption of weevil larvae especially by older larvae of the predators (particularly *H. axyridis)* may enable them to complete development in alfalfa fields even when aphid populations fall to low levels.

KEY WORDS *Coccinella septempunctata, Harmonia axyridis, Hypera postica,* biological control, foraging behavior, predation

LADY BEETLES (COLEOPTERA: Coccinellidae) return in large numbers each spring to alfalfa fields throughout North America to feed, mate, and reproduce (e.g., Neuenschwander et al. 1975, Frazer and Gill 1976, Wheeler 1977, Elliott and Kieckhefer 1990, Giles et al. 1994). These predators are described as aphidophagous in that they attack aphids in particular (Gordon 1985, Hodek and Honěk 1996) and respond to spatial variation in aphid density (e.g., Evans and Youssef 1992, Ives et al. 1993 and references therein). Although they primarily consume aphids, such as the pea aphid, *Acyrthosiphon pisum* (Harris), that occur in alfalfa fields (e.g., Davis et al. 1976), aphidophagous lady beetles consume a variety of other prey as well (Hagen 1987, Hodek and Honěk 1996). In alfalfa fields, in particular, both adults and larvae also feed on the abundant larvae of the alfalfa weevil, *Hypera postica* (Gyllenhal) (e.g., Webster 1912, Essig and Michelbacher 1933, Barney and Armbrust 1981, Evans and England 1996).

Recent studies of the lady beetles' use of weevil larvae as prey in Utah alfalfa fields have examined the reproductive response of adult lady beetles to diets that include alfalfa weevil larvae (Richards and Evans 1998, Evans et al. 1999). Here, we report the results of laboratory experiments in which we investigated the behavioral and developmental responses of immature lady beetles to weevil larvae. Our objectives were to quantify the relative suitability of weevil larvae versus pea aphids as prey for larval growth and development and to determine the likelihoods of attack and capture when the predator encountered the two prey species.

We studied two lady beetle species that have recently invaded North America and are now found in alfalfa fields throughout the continent. The more abundant of the two in alfalfa is *Coccinella septempunctata* L., which became established in northern Utah in the early 1990s (Evans 1991). Adults of *C. septempunctata* reproduce in alfalfa fields in the spring (E.W.E., unpublished data). These predators readily attack alfalfa weevil larvae as well as aphids but fail to reproduce when maintained on a diet composed solely of the larvae (Richards and Evans 1998, Evans et al. 1999). The apparent necessity of aphids in the diet to stimulate high levels of egg production in this and related species (Hagen 1987, Hodek and Honěk 1988; see also Honěk 1978, 1980) is noteworthy given that offspring appear poorly adapted to survive and develop when aphids are not present in high numbers (e.g., see Dixon 1959). Thus, we hypothesized that larvae of *C. septempunctata* would be relatively unsuccessful in preying upon weevil larvae versus aphids.

Our second study species was *Harmonia axyridis* Pallas, a native of eastern Asia, which was introduced to North America in the late 1970s (Tedders and Schaefer 1994) but did not occur in sizable numbers in northern Utah until the late 1990s (E.W.E., unpublished data). This species primarily occurs on trees and shrubs but to a lesser degree also frequents herbaceous plants including alfalfa (LaMana and Miller 1996, Colunga-Garcia and Gage 1998, E.W.E., unpublished data). The predator primarily attacks aphids but attacks other insect taxa as well (e.g., see host list in Tedders and Schaefer 1994). Larvae in natural populations of this and related species frequently attack beetle larvae (including other coccinellids) (Elliott and de Little 1980, Whitehead and Duffield 1982, Yasuda and Shinya 1997, Ohgushi and Sawada 1998, Yamaga and Ohgushi 1999, Yasuda and Ohnuma 1999). Thus, we hypothesized that larvae of *H. axyridis* would be relatively more successful than those of *C. septempunctata* in preying upon alfalfa weevil larvae.

Materials and Methods

First- and fourth-instar *C. septempunctata* and *H. axyridis* were evaluated for their ability to survive on a diet of aphids versus weevil larvae and their tendency to attack each prey type. Dead rather than live weevils were provided to some lady beetle larvae to determine whether the predators would consume weevils and develop successfully on a weevil diet even if they were unable to capture and kill live weevils. Lady beetle larvae were obtained from eggs laid by females collected from the field in northern Utah during May–June 1999. First instars were not exposed to prey before their use in the experiments. Fourth instars were reared by providing them excess numbers of both aphids and third and early fourth instars of the alfalfa weevil. Before experiments, lady beetle larvae were reared at 20–24°C on a laboratory bench exposed to windows (and natural daylength).

Twenty larvae each of *C. septempunctata* and *H. axyridis* were used both in the study of survivorship and in the study of predator behavior upon encounter with prey. Offspring from five females of each species were used in both studies (four larvae per female per treatment). In the survivorship study, first and fourth instars were reared individually in glass vials held horizontally (1-dram vials for first instars: 14 by 45 mm; and 2-dram vials for fourth instars: 16 by 55 mm). Vials were stoppered with cotton moistened with water. Individuals were randomly assigned to receive one of three prey types: (1) pea aphids, (2) live weevil larvae, or (3) dead weevil larvae (killed by freezing on the day they were provided to the predators). Prey were provided in excess each day such that unconsumed food was still present in the rearing vial on the following day when new prey were added. Both dead and live prey from the previous day (but not frass) were removed before new prey were added. First instars were given either aphids as first and second instars or weevil larvae (live or dead) as second instars and similarly sized early third instars. Fourth instars were given either aphids as third and fourth instars or weevil larvae (live or dead) as third and fourth instars (after the first few days, all weevil larvae provided were fourth instars).

First instars were reared on the experimental diets at 20–24°C on a laboratory bench exposed to natural daylight. Fourth instars were reared at 22°C and a photoperiod of 14:10 (L:D) h in an incubator (previously unavailable when first instars were reared). The number of days spent in the first or fourth stadium was recorded as was the percentage of individuals that survived to the second stadium (first instars) or to the pupal and adult stage (fourth instars). Wet weights were recorded for adults emerging from pupae.

In the study of predatory behavior, larval lady beetles were used 24–48 h after they had molted (by this time, they were actively foraging for prey). Both first and fourth instars of *C. septempunctata* and *H. axyridis* were placed individually with prey in 1-dram vials held horizontally. Predators were randomly assigned to be exposed to five prey individuals of either aphids, or live or dead weevils placed in the vial immediately before the predator was introduced (prey stages studied were the same as those used for predators of corresponding age in the survivorship study).

Behavioral interactions between predator and prey were observed using a dissecting microscope under ambient laboratory conditions. Each predator was observed for up to 10 instances in which there was physical contact with prey. Such instances are referred to hereafter as "encounters," which were considered to end when the predator moved away from the prey after initial physical contact (if the predator physically contacted a prey that it had previously contacted and moved away from, this was scored as a second encounter). Many encounters were brief (i.e., the predator failed to respond to initial physical contact by remaining with the prey and attacking it for at least 2 s). In those instances in which an attack was initiated, its duration (including the time during which the predator fed after subduing the prey) was measured up to a maximum of 10 min (this arbitrary limit was placed on observation time devoted to individual predators to ensure that sufficient numbers of larvae were observed for each predator-prey combination).

Statistical Analyses. Results were analyzed using SAS (SAS Institute 1998). Analyses of variance (ANOVA, with linear contrasts to compare diets of aphids versus weevils and of live versus dead weevils) were used to analyze the number of days spent in the fourth stadium, the live weights of individuals upon reaching adulthood, and the number of encounters with prey before the predator attacked. The number of days spent in the relatively brief first instar was analyzed using the nonparametric Mann–Whitney *U* test to compare individuals consuming aphids versus dead weevils. Because only a single individual of *C. septempunctata* survived to adulthood on a diet of live weevils, the weight of this individual was compared

Table 1. Number of first- and fourth-instar *C. septempunctata* and *H. axyridis* that survived to the second instar (n_2) and pupal and adult stages (n_p and n_a), and the mean number of days (± 1 SE) spent in the first or fourth stadium by individuals that completed the stadium (n = number of individuals at the outset)

Diet	Predator	First instars			Fourth Instars			
		n	n_2	Days (± [SE])	n	n_p	n_a	Days (± [SE])
Aphids	*C. septempunctata*	20	20	2.4 (0.1)	20	20	20	4.8 (0.1)
	H. axyridis	20	19	2.1 (0.1)	20	20	20	5.1 (0.2)
Dead weevils	*C. septempunctata*	19	4	4.0 (−)	20	17	14	6.6 (0.3)
	H. axyridis	20	3	4.0 (1.0)	20	20	20	6.0 (0.1)
Live weevils	*C. septempunctata*	20	0	−	19	13	1	7.2 (0.4)
	H. axyridis	20	0	−	20	20	19	7.3 (0.2)

with weights of conspecifics that had fed on dead weevils using a t-test comparison of a single observation with the mean of a sample (Sokal and Rohlf 1981). The numbers of predators that fed versus did not feed on aphids, live weevils or dead weevils for the full ten minutes of observation (or until the prey was consumed fully) were compared using χ^2 tests.

Results

Survival and Growth on Aphid Versus Weevil Diets. First instars of both *H. axyridis* and *C. septempunctata* attacked and killed second– early third instar weevil larvae (at most, one or two per day), but neither predator survived to the second instar on a diet of live weevils (Table 1). In contrast, all but one *H. axyridis* and all 20 *C. septempunctata* survived on a diet of aphids. A low percentage of individuals (≈20%) survived to the second instar when dead weevil larvae were provided as prey. Rates of development were similar for the two species of predators; individuals of both species required a little over 2 d to mature to the second instar on a diet of aphids versus 4 d on diet of dead weevils (Table 1; Mann–Whitney $U = 256$, $n_1 = 40$, $n_2 = 7$, $P < 0.001$, for number of days on the two diets [both predator species combined]).

Both species of predators survived better as fourth than as first instars on a diet of weevils; individual predators attacked and killed weevil larvae in large numbers (as many as 15–20 per day, although many of these were not fully consumed by the predator). All but one larva of *H. axyridis* pupated and molted into an adult when maintained on diets of either live or dead weevils (Table 1). Individuals of *C. septempunctata* were less successful in completing development on weevil diets. Although 13 of 19 individuals completed the fourth stadium and pupated when fed live weevils, only one of these individuals successfully molted into an adult. Individuals survived better when provided dead weevils during the fourth instar, but still only 70% succeeded in molting into adults (Table 1).

Rates of development were similar for fourth-instar *H. axyridis* and *C. septempunctata* that survived to pupate (Table 1). Overall, both species combined developed faster on a diet of aphids versus weevils and on a diet of dead versus live weevils (linear contrasts in ANOVA for number of days spent in the fourth stadium [ln-transformed]: aphids versus weevils, $F = 138.7$; df = 1, 107; $P < 0.0001$; live versus dead weevils, $F = 18.7$; df = 1, 107; $P < 0.0001$).

Individuals of both *H. axyridis* and *C. septempunctata* differed substantially in weight upon reaching adulthood when they had fed as fourth instars on weevil larvae versus aphids (Fig. 1). Adults of *H. axyridis* that had fed as fourth instars on aphids were significantly heavier than adults that had fed on weevils (linear contrast in one-way ANOVA: $F = 115.35$; df = 1, 55; $P < 0.0001$). Adults of *H. axyridis* were also heavier on average when they had fed as fourth instars on dead versus live weevils, but the difference was not significant (linear contrast in one-way ANOVA: $F = 2.14$; df = 1, 55; $P = 0.15$). Adults of *C. septempunctata* that had fed as fourth instars on aphids were significantly heavier than adults that had fed on dead weevils (one-way ANOVA: $F = 23.69$; df = 1, 32; $P < 0.0001$). The lone individual of *C. septempunctata* that survived to adulthood on a diet of live weevils weighed less than the mean weight of individuals that had fed on dead weevils but the difference was not significant (t-test comparison of a single observation with the mean of a sample: $t_s = 0.51$, df = 13, $P > 0.50$).

Observations of Foraging Behavior. As first instars, both *C. septempunctata* and *H. axyridis* readily attacked aphids but not weevil larvae once they en-

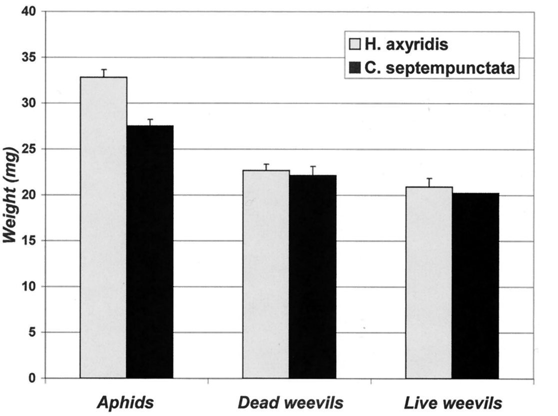

Fig. 1. Mean wet weight (±1 SE) of *H. axyridis* and *C. septempunctata* as newly molted adults, following consumption as fourth instars of pea aphids, or live or dead alfalfa weevil larvae.

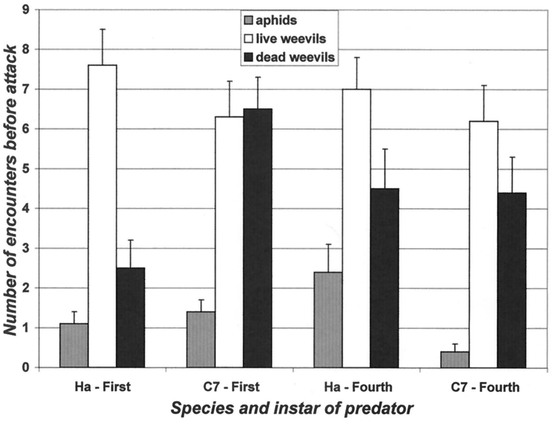

Fig. 2. The mean (±1 SE) number of encounters with prey (i.e., instances of physical contact with pea aphids, or live or dead alfalfa weevil larvae) occurring before a first or fourth instar of *H. axyridis* or *C. septempunctata* remained with the prey and attacked it for at least 2 s. Predators were observed for up to a maximum of 10 encounters without attack.

countered (i.e., physically contacted) them. Thus, the mean number of encounters before the predator remained with the prey and attacked it for at least 2 s differed significantly among prey types (two-way ANOVA of number of encounters [transformed as $\ln(x + 1)$]: effect of prey, $F = 31.87$; df = 2, 114; $P < 0.0001$). Both species of predators attacked aphids after fewest encounters (Fig. 2; linear contrast for predators of both species attacking aphids versus weevils [both live and dead]: $F = 53.91$; df = 1, 144; $P < 0.0001$). A significant interaction occurred in the effects of predator and prey ($F = 6.32$; df = 2, 114; $P = 0.0025$), reflecting that the two predator species contrasted in their response to live versus dead weevils (*H. axyridis* but not *C. septempunctata* attacked dead weevils more readily than live weevils; Fig. 2).

As fourth instars, both species of predator again differed significantly in their likelihood of attacking different prey (Fig. 1; two-way ANOVA of number of encounters [transformed as $\ln(x + 1)$]: effect of prey, $F = 22.65$; df = 2, 114; $P < 0.0001$; effect of predator, $F = 3.06$; df = 1, 114; $P = 0.08$; interaction of prey with predator, $F = 2.15$; df = 2, 114; $P = 0.12$). Both species of predators attacked aphids much more readily than weevils, and dead weevils more readily than live weevils (linear contrasts for predators of both species: aphids versus weevils [both live and dead]: $F_{1,114} = 37.86$; $P < 0.0001$; live versus dead weevils: $F = 37.86$; $P < 0.008$).

As first instars, both species of predators were almost always successful in capturing aphids when they attacked, and all individuals succeeded eventually even in those few instances when initial attacks were unsuccessful. Furthermore, all individuals proceeded to consume the aphid for the maximum observation period of 10 min. In contrast, predators that attacked live weevils often abandoned the attack quickly in response to defensive wriggling by the prey. Only two *C. septempunctata* first instars (10% of individuals observed) and no *H. axyridis* first instars succeeded in subduing a live weevil in the course of 10 encounters. Both successful predators thereupon fed on the weevils for the full 10 min of subsequent observation. First-instar predators provided dead weevils typically either failed to attack the prey or (in a few instances) fed for only 1 min or less or fed on the prey for the full 10 min of observation. Overall, 35% of *C. septempunctata* and 45% of *H. axyridis* individuals fed on a dead weevil for the full 10 min ($\chi^2 = 73.44$, df = 2, $P < 0.01$, for number of predators for both species combined [out of 40] that fed for the full 10 min on an aphid, live weevil, or dead weevil).

Similar results were obtained for fourth instars. Both species of predators always succeeded in capturing aphids upon attack and fed on them until they were fully consumed (in most instances, this took less than 10 min). Both species had difficulty overcoming struggling weevil larvae, but when successful, they typically consumed the prey for the full 10 min of observation. Overall, 50% (*H. axyridis*) and 30% (*C. septempunctata*) of the predators fed on a weevil for the full ten minutes when live prey were provided, and 55% (*H. axyridis*) and 70% (*C. septempunctata*) did so when dead weevils were provided ($\chi^2 = 27.19$, df = 2, $P < 0.01$, for number of predators for both species combined [out of 40] that fed for the full 10 min [or until the prey was fully consumed] on an aphid, live weevil, or dead weevil).

Discussion

Larvae of both *C. septempunctata* and *H. axyridis* were less successful in developing when offered alfalfa weevil larvae rather than pea aphids as prey. First instars did succeed in killing and consuming small weevil larvae (second and early-third instars) but did not survive to the second instar when these prey were the only food available. Fourth instars of *H. axyridis* (but only a single such individual of *C. septempunctata*) were successful in maturing, pupating, and subsequently emerging as adults on a diet of larger live weevil larvae (late-third and fourth instars) but gained significantly less weight than did fourth instars that fed on aphids. Behavioral observations suggest that the unsuitability of the weevil diet arises largely from the reluctance of the predators to attack weevils after contacting them, and from the ability of weevils to defend themselves against attack. Thus, *C. septempunctata* fourth instars, in particular, were much more successful in completing development to adulthood when presented dead rather than live weevils. Our results are consistent with previous laboratory observations (Yadava and Shaw 1968, Ouayogode and Davis 1981) that lady beetle larvae and adults generally consume aphids in greater numbers than alfalfa weevil larvae (but see Hussain 1975).

The ability of larvae of aphidophagous lady beetles to complete development on a diet of active stages of nonaphid prey has not been well documented. Most previous studies on the suitability of nonaphid prey for larvae of aphidophagous lady beetles have used eggs as substitute prey. Various species of lady beetles have been reared successfully on diets of beetle eggs (including those of conspecifics) (e.g., Elliott and de Little 1980, Hazzard and Ferro 1991, Agarwala and Dixon 1992, Munyaneza and Obrycki 1997, Cottrell and Yeargan 1998) and lepidopteran eggs (Schanderl et al. 1988, Phoofolo and Obrycki 1997). Yasuda and Ohnuma (1999) examined the ability of fourth-instar *C. septempunctata* and *H. axyridis* to complete development by feeding on conspecific larvae or on each other (note, however, that legs were removed from prey before the prey were offered to predators). Larvae of *H. axyridis*, in particular, developed equally well on diets of either conspecific or heterospecific larvae or cotton aphids, *Aphis gossypii* Glover. In contrast, larvae of *C. septempunctata* consumed other larvae less readily and were less successful in gaining weight and completing development on a diet of lady beetle larvae (especially heterospecifics) versus aphids. The greater ability of *H. axyridis* versus *C. septempunctata* larvae to subsist and develop on a diet of beetle larvae as shown here and by Yasuda and Ohnuma (1999) is consistent with reports of associations of larvae of *H. axyridis* and close relatives with beetle larvae as prey in natural settings (Elliott and de Little 1980, Whitehead and Duffield 1982, Yasuda and Shinya 1997, Ohgushi and Sawada 1998, Yamaga and Ohgushi 1999).

Our finding that first instars of the two lady beetle species are unable to survive on a diet of young weevil larvae alone is especially interesting when viewed from the perspective of lady beetle reproductive habits. Adult females of both predator species survive well and maintain body weight but fail to produce eggs when provided only alfalfa weevil larvae as prey (Richards and Evans 1998, Evans et al. 1999, and unpublished data). Our results support the hypothesis that the lady beetles' failure to produce eggs is an adaptive response to unsuitable prey availability for larval development (see also Evans and Dixon 1986). In alfalfa fields, it appears that consumption of weevil larvae may be particularly valuable to lady beetles in enabling older instars to complete development, especially in those instances in which pea aphid populations are declining (e.g., Evans and England 1996; see also Yasuda and Shinya 1997 and Schellhorn and Andow 1999 for discussion of the similar importance of cannibalism and intraguild predation under such circumstances). The ability of *H. axyridis*, in particular, to complete the fourth stadium and pupal stage on a diet of weevil larvae alone may enable this polyphagous predator to survive even when aphid populations collapse entirely.

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