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Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve a defensive function?

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Abstract

Laboratory experiments examined interspecific interactions between larvae of three coccinellid species, *Curinus coeruleus* Mulsant (Chilocorinae), *Harmonia axyridis* Pallas and *Olla v-nigrum* (Mulsant) (Coccinellinae), and between these and larvae of the green lacewing, *Chrysoperla rufilabris* (Burmeister). Larvae of *C. coeruleus*, although defended on their dorsal surface with long spines, had the smallest mandibles, were the slowest-moving, and the least successful in interspecific larval combat. The long spines of third instar *C. coeruleus* appeared to reduce their palatability as food to *H. axyridis* and *O. v-nigrum* larvae in choice tests with dead larvae, but were not an effective defence against these species in Petri dish arenas. Larvae of *O. v-nigrum* had a smooth dorsal surface, were intermediate in terms of mandible size, but were the fastest moving, a trait that benefited their survival in intraguild combat. Larvae of *H. axyridis* were intermediate with respect to dorsal spines and speed of movement, but had the largest mandibles. This species was the most effective intraguild combatant among the coccinellids and the only one to successfully compete against *C. rufilabris* larvae of similar age. The speed, manoeuverability and long mandibles of *C. rufilabris* enabled them to impale coccinellid larvae at a relatively safe distance. The spines of *C. coeruleus* larvae impeded laterally oriented attacks by *C. rufilabris*, but did not provide sustained protection from repeated attacks. Success in these interactions appeared largely a function of offensive weaponry (mandible size and morphology) and speed of movement, although the role of dorsal spines as defensive structures was not ruled out. Rates of larval cannibalism were highest for *C. rufilabris* and largely mirrored the level of aggression observed in interspecific combat for each species.

Introduction

The defensive behaviours of adult Coccinellidae such as thanatosis (death feigning) and 'reflex bleeding' have received considerable research attention (Hodek & Honek, 1996). The potential defences of predacious coccinellid larvae have received far less research attention, although these possess a variety of distinctive morphological features specific to various subfamilies and tribes. Whereas the larvae of the subfamily Coccinellinae are typically spineless and naked (with a few exceptions), those of the subfamily Chilocorinae are usually covered with long, branched spines that grow in length with each successive larval moult until later instars take on almost a 'pin-cushion' appearance (J.P. Michaud, personal observation). On the other hand, the larvae of most species of Scymninae produce filamentous waxy secretions that can cover their dorsal surface

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completely (Pope, 1979). Both waxy secretions and dorsal spines cannot be produced without some physiological cost, a cost that is likely offset by some adaptive function. The most apparent function for such dorsal structures is defensive.

The waxy secretions of the Scymninae have been theorized to serve either as camouflage, or as a deterrent to predation. For example, the larvae of *Cryptolaemus montrouzieri* Mulsant bear a striking resemblance to many of their mealybug prey. The sugar cane woolly aphid, *Ceratovacuna lanigera* Zehntner (Hemiptera: Aphididae), has a soldier caste that vigorously defends the colony against attacks by predators, but the larvae of *Pseudoscymnus kurohime* (Miyatake) secrete a waxy covering very similar to that of the aphids themselves and are not attacked by soldier aphids (Arakaki, 1992). Samways (1983) referred to the waxy larvae of *Scymnus* spp. as 'ant-tolerant', although it is likely that it is the ants that actually tolerate *Scymnus* larvae, rather than vice versa. Kaneko (2002) observed that wax-covered larvae of *Scymnus posticalis* Sicard foraging in colonies of *Aphis gossypii* Glover were ignored by *Lasius niger* Linnaeus (Hymenoptera: Formicidae) workers that attacked all other aphid predators. Völkl & Vohland (1996) demonstrated that the larval wax covers of *Scymnus niginus* Kugelann and *Scymnus interruptus* (Goeze) protected them from intraguild predation by larger coccinellids and a carabid beetle, as well as from attacks by workers of *L. niger* and *Formica polyctena* Förster (Hymenoptera: Formicidae). While the adaptive advantages of wax secretions have thus been demonstrated in a number of Scymninae, there have no efforts to date to demonstrate a similar defensive function for the dorsal spines carried by larvae of the Chilocorinae.

There are no published reports of chilocorine larvae foraging effectively within colonies of ant-tended Homoptera as there are for the Scymninae, so their spines may not function in defence against ants. It seems more likely that the spines could serve to deter attacks from other predators, such as larvae of their own or other coccinellid species. A series of laboratory experiments was designed to test for potential defensive functions of these spines in a chilocorine species, *Curinus coeruleus* Mulsant. Two coccinelline species were employed in experiments for sake of comparison, and to serve as potential intraguild predators, *Harmonia axyridis* Pallas and *Olla v-nigrum* Mulsant. These three species are all sympatric with *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae) on citrus trees in east-coast Florida where they share a range of similar prey (Michaud, 2002a). *Curinus coeruleus* is primarily a scale feeder, while the other species are all primarily aphid predators. The dorsal surface of *O. v-nigrum* larvae is entirely smooth, while that of *H. axyridis* has several rows of short, barbed spines. However, other behavioural and morphological differences among these species such as mandible size and speed of movement are factors that could also influence the outcome of competitive larval interactions. A high activity level could either increase the frequency of aggressive encounters with competitors in an experimental arena, or increase escape frequency in response to attacks. Mandible size can be considered a measure of the weaponry available to a larva in combat encounters. Larvae of *C. rufilabris* were included in some experimental combinations as it is known to be effective as an intraguild predator of coccinellids (Phoofolo & Obrycki, 1998). Four hypotheses were tested:

1. Larvae of *C. coeruleus* are less susceptible to intraguild predation by larvae of other coccinellids than are larvae of coccinelline species that lack dorsal spines.
2. Larvae of *C. coeruleus* are less susceptible to attacks by *C. rufilabris* larvae than are coccinelline larvae that lack spines.
3. The spines of *C. coeruleus* larvae render them less palatable as intraguild prey independent of defensive functions.
4. Rates of larval cannibalism among the three coccinellid species will reflect their level of aggression in interspecific interactions.

Materials and methods

Beetle colonies were established using between 20 and 40 adults of each species collected from the following localities on the following dates: *H. axyridis*, Polk County, October, 2000; *O. v-nigrum*, St Lucie County, March, 2001; *C. coeruleus*, St Lucie County, August, 2001. Voucher specimens of all species were deposited in the insect collection at the Florida Department of Agriculture and Consumer Affairs, Division of Plant Industry, Gainesville, Florida, 32608, USA. Pairs of adult beetles of each species were placed into plastic Petri dishes (5.5 cm × 1.0 cm) and provided daily with frozen eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), bee pollen, and water encapsulated in polymer beads (Entomos, Gainesville, Florida, USA). Once oviposition began, males were removed so that females could continue to oviposit in isolation. Voucher specimens of all species were deposited at the Florida State Arthropod collection at the Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville.

Eggs of *H. axyridis* and *O. v-nigrum* were usually laid directly on the surface of the plastic Petri dishes, and sometimes directly on the polymer water beads. Females of *C. coeruleus* were provided with small fragments of black carpet fibre as this species prefers to secrete its eggs in concealed locations. Eggs of all species were held in a plexiglass terrarium at 24 ± 1°C, 60 ± 10% rh under fluorescent lights set to a daylength of 16:8 (L:D) until hatching. Larvae for stock colonies were reared in groups of five to six in plastic Petri dishes (as above) provisioned with *Ephestia* eggs daily, and fresh water beads every three days. Larvae pupated in the dishes and emerging adults of each species were placed in 1-litre wide-mouth, glass Mason jars covered with muslin cloth. The jars had water provided on a cotton wick, and were provisioned daily with *Ephestia* eggs and bee pollen. Mating occurred under these conditions, but for reproduction, females were removed after one or more weeks in the jars and isolated in Petri dishes for oviposition (as above).

Eggs of *C. rufilabris* were obtained by mail order from Beneficial Insectary (Redding, California, USA) and held in an incubator at 24 ± 1°C, 60 ± 10% rh until hatching. Larvae used in experiments were either transferred to the experimental arenas immediately following hatching (first instars) or were isolated in individual Petri dishes (2.5 cm × 1.0 cm) and raised to the third instar on a diet of *Ephestia* eggs.

All experiments were performed on a laboratory bench under fluorescent light at an ambient temperature of 24 ± 1°C. Larval combat experiments were conducted with different combinations of larvae of various ages in plastic Petri dishes (5.5 cm × 1.0 cm). The spines of *C. coeruleus* larvae are quite short in the first instar but become increasingly longer with each successive instar, so it was deemed necessary to test different ages of larvae. Similarly, larvae of *C. rufilabris* and the various coccinellid species do not all develop at the same rate, nor are they the same size at a given age, so various intraguild predations trials were conducted with different aged larvae to generate combinations of similar or disparate sizes. Trials were also conducted with and without food. Intraguild predation events in trials with continuous food availability presumably reflect aggressive attacks toward competitors, rather than attacks driven by hunger. In contrast, trials without food may reflect hunger-driven attacks, but there is no larval growth during the experiment and therefore no change in relative size prior to intraguild predation events. Trials with food present were run until all surviving larvae pupated; trials without food were run until only one larva remained alive in each replicate. Intraguild predation events were recorded twice daily for each experiment, once in the morning and again in the late afternoon, and direct observations of combat interactions were also made at these times. Replicates in which a larva died from causes other than predation were excluded from analysis. Data from the larval contests were analysed using a Chi-square, goodness of fit test with expected values derived from the assumption that all species should win an equal share of contests if no competitive assymetries existed.

Measurements of mandible gape and motility

Larvae of each species were reared to the third instar and then measured for mandible width and speed of movement. Larvae were first starved for 6–8 h by confining them individually in plastic Petri dishes with access only to water. One by one, larvae of each species (n = 17–20) were transferred to a circle (1.0 cm diameter) drawn in the centre of a white filter paper disc (9.5 cm diameter) and placed on the surface of a black laboratory bench under fluorescent light. The white surface provided a high-contrast background that was expected to stimulate rapid movement of larvae off the filter paper circle. Speed of movement was measured with a stop watch as the time from release of the larva in the circle until it exited the filter paper disc completely onto the surface of the laboratory bench. Larvae were killed by quick freezing, relaxed in 70% ethanol solution, and then measured for mandible width under a binocular dissecting microscope with a graduated ocular lens. Mandible width was measured as the distance between the outer edges of the mandibles at their tips when spread to maximum gape. Data for mandible width and speed of movement were compared among species using a one-way ANOVA followed by an LSD test for separation of means ($\alpha = 0.05$).

Experiment 1 – contests among coccinellid species with food

Four combinations of coccinellid larvae were reared together from the first instar with continuous access to food and water beads that were both refreshed every second day. Larvae of *H. axyridis* or *O. v-nigrum* were introduced into experimental arenas at < 24 h old, whereas larvae of *C. coeruleus* were 48 ± 6 h, since the larval developmental time of this species averages about a week longer than that of the others at 24°C. The four series (n = 40 replicates in each) comprised all three pairwise combinations of species, plus a series with all three species confined together. The experiment was continued until all insects either pupated successfully, or were victims of intraguild predation.

Experiment 2 – contests among coccinellid species without food

The same experimental design was employed as in experiment 1 except that larvae were combined when they were in the third instar (*H. axyridis* and *O. v-nigrum* 120 ± 12 h old, *C. coeruleus* 240 ± 12 h old) and only water was provided. Between 60 and 100 replicates were performed for each combination of larvae.

Experiment 3 – contests between C. rufilabris *and same-aged coccinellid larvae with food*

Newly hatched larvae of *C. rufilabris* (< 24 h old) were combined pairwise with first instars of each of the three coccinellid species (*H. axyridis* and *O. v-nigrum* < 24 h old, *C. coeruleus* 48 ± 6 h old) in plastic Petri dishes (as above) with continuous access to food and water beads, both refreshed every second day. In a fourth series, larvae of all four species were reared in each dish. Fifty replicates were performed for each treatment. The experiment was continued until all insects either pupated successfully, or were victims of intraguild predation.

Experiment 4 – contests between C. rufilabris and same-sized coccinellid larvae without food

The same experimental design was followed as in experiment 3 except that second instar coccinellid larvae were paired with third instar *C. rufilabris* larvae and only water was provided. Larvae in each replicate were selected to be approximately the same size (*H. axyridis* and *O. v-nigrum* 48 ± 6 h, *C. coeruleus* 96 ± 6 h, *C. rufilabris* 120 ± 12 h old). Fifty replicates were performed for each treatment and the experiment was continued until only one insect remained in each dish.

Experiment 5 – contests between C. rufilabris *and larger coccinellid larvae with food*

The same experimental design was followed as in experiment 3 except that second instar coccinellid larvae were combined with first instar *C. rufilabris* larvae. Larvae of *C. rufilabris* were < 24 h old, whereas larvae of *H. axyridis* and *O. v-nigrum* were 48 ± 6 h old and those of *C. coeruleus*, 120 ± 12 h old. Fifty replicates were performed for each treatment.

Experiment 6 – contests between C. rufilabris *and larger coccinellid larvae without food*

The same experimental design was followed as in experiment 4 except that all insects were combined in the third instar (*H. axyridis* and *O. v-nigrum* 120 ± 12 h old, *C. coeruleus* 240 ± 12 h old, and *C. rufilabris* 192 ± 12 h old,) with coccinellid larvae averaging two to three times the size of the *C. rufilabris* larvae. Fifty replicates were performed for each treatment.

Experiment 7 – choice tests with larval corpses

In order to test the third hypothesis, a series of choice tests were performed with dead larvae to evaluate their acceptability as food to larvae of their own and other species in the absence of defensive behaviour. Third instar larvae (n = 25) of each coccinellid species were transferred to individual plastic Petri dishes (as above) and presented with a choice of three dead third instar larvae (killed by rapid freezing), one of each species. Each dead larva was carefully orientated in the dish to ensure that the dorsal surface was upright. Each replicate was examined 24 h later and the number of larvae consumed was tallied. Data were analysed using a χ^2 goodness of fit test with expected values derived from the assumption that corpses of each species would be consumed in equal numbers in the absence of any preference.

Experiment 8 – comparative larval cannibalism

Six newly hatched larvae of each species, each obtained from the egg cluster of a different female in the case of coccinellids, were transferred to each of 40 Petri dishes (as above) and provisioned with excess *Ephestia* eggs and water beads. A surplus of food was provided fresh every second day and water beads were replaced as required. Cannibalism events were recorded daily until all surviving larvae pupated. Data were compared among species using a one-way ANOVA followed by an LSD test ($\alpha = 0.05$) to resolve differences between means. The experiment was continued until all surviving insects pupated.

Results

Measurements of mandible gape and speed of movement

The mean period required for dispersal of larvae off the filter paper discs differed among species ($F = 71.90$; 2,54 df; $P < 0.001$). Larvae of *O. v-nigrum* were significantly faster moving than larvae of *H. axyridis*, that were in turn faster than larvae of *C. coeruleus* (fig. 1). There were also significant differences among the three species in the mandible gape width of third instar larvae ($F = 166.69$; 2,51 df; $P < 0.001$). The mandibles of *H. axyridis* had a significantly larger gape than those of *O. v-nigrum*, that in turn had larger gape than those of *C. coeruleus* (fig. 2).

Experiment 1 – contests among coccinellid species with food

The results of the first experiment are depicted graphically in fig. 3. In the three-way trial, *H. axyridis* was the sole survivor in 15 of 40 replicates, *O. v-nigrum* in 24, *C. coeruleus* in none, and *O. v-nigrum* and *H. axyridis* pupated together in one replicate. Thus *C. coeruleus* won fewer than expected contests ($\chi^2 = 13.3$, $P < 0.001$), *O. v-nigrum* won more than expected ($\chi^2 = 8.54$, $P < 0.01$) and *H. axyridis* won an expected number ($\chi^2 = 0.05$, ns). The mean time to a predation event (± SEM) was 3.7 ± 0.21 days and there was no difference among species in the order of attack. In pairwise contests, *H. axyridis* won 17 of 39 with *O. v-nigrum* ($\chi^2 = 0.32$, ns) with both larvae pupating in one replicate, *H. axyridis* won 39 of 40 contests with *C. coeruleus* ($\chi^2 = 18.1$, $P < 0.001$), and *O. v-nigrum* won 36 of 40 contests with *C. coeruleus* ($\chi^2 = 12.80$, $P < 0.001$).

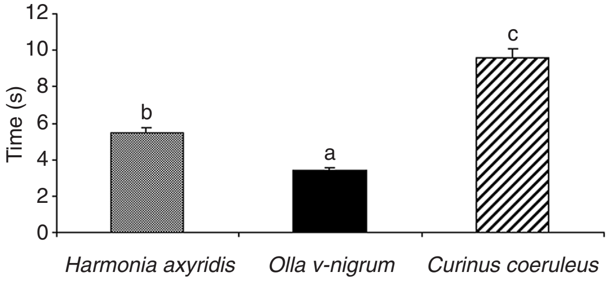

Fig. 1. Mean time in seconds (+ SEM) required for third instar larvae (n = 20) of each of three coccinellid species to completely exit a filter paper circle of radius 4.25 cm. All means were significantly different in a one-way ANOVA followed by LSD ($\alpha < 0.001$).

Experiment 2 – contests among coccinellid species without food

In the three-way trial, an *H. axyridis* larva was the sole survivor in 42 of 75 replicates, *O. v-nigrum* in 24, and *C. coeruleus* in nine. Thus *C. coeruleus* won fewer than expected contests ($\chi^2 = 10.2$, $P < 0.001$), *H. axyridis* won more contests than expected ($\chi^2 = 11.6$, $P < 0.001$), and *O. v-nigrum* won an expected number ($\chi^2 = 0.04$, ns). The mean time (± SEM) to a

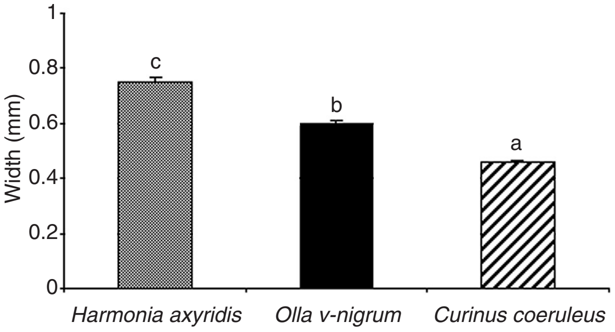

Fig. 2. Mean width of mandible gape in mm (+ SEM) for third instar larvae (n = 20) of each of three coccinellid species. All means were significantly different in a one-way ANOVA followed by LSD (P < 0.001).

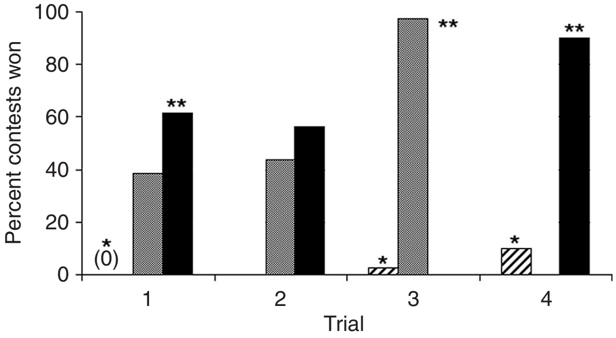

Fig. 3. Percent of contests won by (▨, *Curinus coeruleus*; ░, *Harmonia axyridis*; ■, *Olla v-nigrun*) larvae of three different coccinellid species reared together from the first instar in groups of three (trial 1) or in species pairs (trials 2–4). Data were analysed by a χ^2 goodness of fit test ($P < 0.05$). * indicates fewer than expected contests won within a trial, ** indicates more than expected contests won within a trial.

predation event was 1.4 ± 0.07 days and there was no difference among species in the order of attack. In pairwise contests, *H. axyridis* won 62 of 88 with *O. v-nigrum* ($\chi^2 = 7.36$, $P < 0.01$), and 49 of 58 with *C. coeruleus* ($\chi^2 = 13.8$, $P < 0.001$), whereas *O. v-nigrum* won 48 of 61 with *C. coeruleus* ($\chi^2 = 10.0$, $P < 0.001$).

Experiment 3 – contests between C. rufilabris *and same-aged coccinellid larvae with food*

When first instar *C. rufilabris* larvae were paired with first instar coccinellid larvae, *C. rufilabris* won 17 of 30 contests with *H. axyridis* ($\chi^2 = 0.27$, ns) and both larvae pupated in 20 of 50 replicates. Larvae of *C. rufilabris* won 38 of 42 contests with *O. v-nigrum* ($\chi^2 = 13.7$, $P < 0.001$), with both larvae pupating in six replicates, and all 50 contests with *C. coeruleus* ($\chi^2 = 25.0$, $P < 0.001$).

Experiment 4 – contests between C. rufilabris *and same-sized coccinellid larvae without food*

When third instar *C. rufilabris* larvae were paired with second instar coccinellid larvae that were approximately the same size, *C. rufilabris* won 42 of 50 contests with *H. axyridis* ($\chi^2 = 11.5$, $P < 0.001$), 46 of 49 contests with *O. v-nigrum* ($\chi^2 = 18.8$, $P < 0.001$), and all 50 contests with *C. coeruleus* ($\chi^2 = 25.0$, $P < 0.001$).

Experiment 5 – contests between C. rufilabris *and larger coccinellid larvae with food*

When first instar *C. rufilabris* larvae were paired with second instar coccinellid larvae that were approximately two to three times larger, *H. axyridis* won all 36 contests with *C. rufilabris* ($\chi^2 = 18.0$, $P < 0.001$), both larvae pupating in the other eight replicates. Larvae of *C. rufilabris* won 28 of 37 contests with *O. v-nigrum* ($\chi^2 = 4.88$, $P < 0.05$) and in no case did both larvae pupate. Larvae of *C. rufilabris* won 42 of 44 contests with *C. coeruleus* ($\chi^2 = 18.2$, $P < 0.001$), both larvae pupating in four replicates.

Experiment 6 – contests between C. rufilabris *and larger coccinellid larvae without food*

When third instar *C. rufilabris* larvae were paired with third instar coccinellid larvae that were two to three times as large, *H. axyridis* won 46 of 47 contests ($\chi^2 = 21.5$, $P < 0.001$), *O. v-nigrum* won 30 of 50 ($\chi^2 = 1.00$, ns), and *C. coeruleus* won 11 of 45 ($\chi^2 = 5.88$, $P < 0.05$).

Experiment 7 – choice tests with larval corpses

There were significant differences in the total number of larval corpses consumed by the three species when third instar larvae were presented with a three-way choice between larval corpses of their own and other species ($F = 24.2$; 2,72 df; $P < 0.001$; fig. 4), *H. axyridis* consuming significantly more corpses than either *O. v-nigrum* or *C. coeruleus* (LSD, $P < 0.001$). However, *H. axyridis* larvae consumed *C. coeruleus* corpses at a significantly lower than expected frequency ($\chi^2 = 9.28$, $P < 0.01$) whereas *O. v-nigrum* larvae consumed corpses of their own species with significantly higher than expected frequency ($\chi^2 = 5.11$, $P < 0.05$). Larvae of *C. coeruleus* were the only species to consume *C. coeruleus* corpses at the same rate as corpses of other species.

Experiment 8 – comparative larval cannibalism

There were highly significant differences among species in rates of larval cannibalism when larvae were reared six per dish ($F = 222.4$; 3156 df; $P < 0.001$; fig. 5). *Chrysoperla rufilabris* was significantly more cannibalistic than any of the coccinellid species, and *H. axyridis* was more cannibalistic than either *O. v-nigrum* or *C. coeruleus* (LSD, $P < 0.01$ in both cases).

Discussion

Overall, aggressive behaviour and size of weaponry appeared to be the important determinants of victory in these intraguild combat experiments and the dorsal spines of *C. coeruleus* appeared to have minor value as defensive structures. Among the coccinellids, *H. axyridis* and *O. v-nigrum* appeared to be closely matched competitors. Although *O. v-nigrum* was most often the lone survivor in the three-way contest in experiment 1, *H. axyridis* had an advantage over *O. v-nigrum* in experiment 2 when third

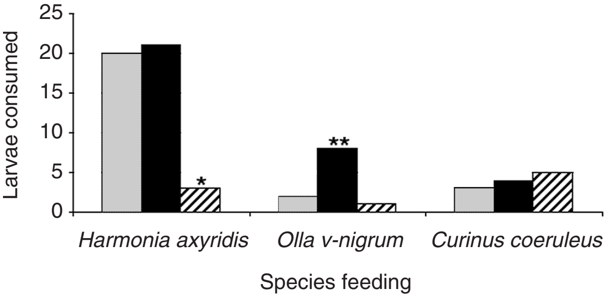

Fig. 4. Total numbers of third instar larval corpses consumed by third instar larvae of three coccinellid species (▨, *Curinus coeruleus*; □, *Harmonia axyridis*; ■, *Olla v-nigrun*) in choice trials. Each larvae was presented with a choice of three larval corpses, one of each species, for a period of 24 h. * indicates fewer than expected consumed, ** indicates more than expected consumed, based on a χ2 goodness of fit test ($P < 0.05$).

Table 1. Summary of results for experiments pitting larvae of *Chrysoperla rufilabris* against larvae of three coccinellid species in pair-wise contests. The species with a significant combat advantage (χ^2, $P \leq 0.05$) is indicated for each contest.

Insect combinations	Food	*Harmonia axyridis*	*Olla v-nigrum*	*Curinus coeruleus*
All 1st instars, *C. rufilabris* smaller	Yes	No advantage	*C. rufilabris*	*C. rufilabris*
C. rufilabris 3rd instar, coccinellids 2nd instar, same size	No	*C. rufilabris*	*C. rufilabris*	*C. rufilabris*
C. rufilabris 1st instar, coccinellids 2nd instar, 2–3 times larger	Yes	*H. axyridis*	*C. rufilabris*	*C. rufilabris*
All 3rd instars, coccinellids 2–3 times larger	No	*H. axyridis*	*O. v-nigrum*	*C. rufilabris*

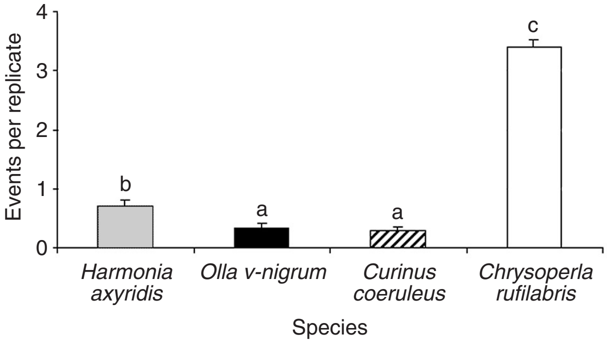

Fig. 5. Mean number of cannibalism events per replicate for larvae of four predatory species confined together in groups of six from eclosion in plastic Petri dishes and provided with excess food, refreshed every second day. Columns bearing the same letter were not significantly different in a one-way ANOVA followed by LSD ($\alpha = 0.05$).

instars were confined together without food. Events occurred much faster in the second experiment and food deprivation appeared to have unequal impact on the two species; it either stimulated aggressive behaviour disproportionately in *H. axyridis*, or negatively impacted the ability of *O. v-nigrum* to either mount attacks or use its superior speed to escape. It was evident from the direct observations that the initiator of an attack often experienced a significant advantage. An intended victim, depending on how it was gripped, was often physically unable to reach the attacker with its mandibles, despite visibly contorting its body in attempts to do so. Direct observations also suggested that the rapid movement and quick response time of *O. v-nigrum* larvae often facilitated their escape following contact with a would-be attacker, although this could not be quantified. However, once larvae engaged in combat, the large mandibles of *H. axyridis* appeared to be especially effective for maintaining a grip on a potential victim and immobilizing it rapidly. By contrast, *C. coeruleus* larvae had the slowest rate of movement and the smallest mandibles, and won the fewest contests in all experiments. Therefore, the hypothesis that larval spines would protect *C. coeruleus* larvae against attack by larvae of other coccinellid species was not supported, at least under the conditions of these experiments.

The results of experiments 3–6 that pitted *C. rufilabris* larvae against the various coccinellids are summarized in table 1. Larvae of *C. rufilabris* appeared to be more formidable intraguild predators than any of the coccinellid species, a finding in agreement with the results of Phoofolo & Obrycki (1998). Larvae of *C. rufilabris* are fast-moving (not quantified) but more importantly, the morphology of their long, sickle-shaped mandibles enabled them to impale their victims while remaining beyond the reach of their (coccinellid) opponent's mouthparts, regardless of the angle of attack. Thus offensive weaponry again emerged as a trait of overarching importance in intraguild combat. Among the coccinellids, relative success against *C. rufilabris* followed the order of mandible size, rather than speed of movement or the presence of defensive spines. *Harmonia axyridis* was better able to defend itself against *C. rufilabris* than the other coccinellid species; *C. rufilabris* did not win in combat against *H. axyridis* unless it was older and at least the same size. *Olla v-nigrum* only vanquished *C. rufilabris* when third instars were matched and *O. v-nigrum* was substantially larger. Dixon (2000) stated that '…the spiny covering and large mandibles would appear to protect the larvae of *H. axyridis* against intraguild predators'. In the light of our results, it is tempting to conclude that mandible size is the trait of key importance in interspecific larval combat. These trials also revealed that relative body size is a factor influencing the outcome of intraguild interactions among predatory larvae, although traits such as level of aggression (propensity to attack) and mandible morphology probably account for species-specific differences when size is similar.

Larvae of *C. coeruleus* did not win against *C. rufilabris* in any experimental configuration, even when they were two to three times the size of the lacewing larva. Although larval spines did not enhance survival as hypothesized, there was some indication that the spines made *C. coeruleus* a difficult prey item to handle, especially in later instars when the spines reached considerable length. Direct observations indicated that broadside attacks by *C. rufilabris* were rarely successful on third instar *C. coeruleus* because the spines on the medial abdominal segments were longer than the length of *C. rufilabris* mandibles. Repeated attacks were eventually successful when *C. rufilabris* impaled *C. coeruleus* either in the neighbourhood of the head capsule, which is spineless, or directly in the terminal abdominal segment, where spines are shortest. Therefore, our results do not rule out a defensive function of larval spines in combination with evasive behaviour, since the insects in these experiments had no possibility of escape as they would in nature.

Results of the choice tests with larval corpses revealed that *H. axyridis* larvae were less likely to feed on *C. coeruleus* corpses than on conspecific corpses or those of *O. v-nigrum* (fig. 4). Similarly, larvae of *O. v-nigrum* consumed the naked larvae of its own species in preference to either the short-spined larvae of *H. axyridis* or the long-spined larvae of *C. coeruleus*. Only larvae of *C. coeruleus* consumed corpses of that species at the same frequency as those of the other species. The results for *O. v-nigrum* are consistent with the nutritional suitability of conspecific larvae being generally greater than that of other species. If spines generally reduce the palatability of larvae, this could explain why no preference for conspecific larvae was evident in either *H. axyridis* or *C. coeruleus* when spineless *O. v-nigrum* larvae were available. These results collectively lend support to the third hypothesis, that the spines of *C. coeruleus* larvae would reduce their palatability as intraguild prey independent of defensive behaviour.

The results of the cannibalism trials revealed that a species' cannibalism rate largely reflected its level of aggression in interspecific combat situations, supporting the fourth hypothesis and suggesting that common factors may influence behavioural responses to both conspecific and heterospecific competitors. *Chrysoperla rufilabris* was the most aggressive intraguild predator and also had the highest intrinsic propensity for larval cannibalism under these laboratory conditions (fig. 5). Larval cannibalism is a common behaviour among the Chrysopidae (Duelli, 1981; Michaud, 2001) and is a major pitfall to mass-rearing these insects for biological control applications. Similarly, *H. axyridis* had the highest rate of larval cannibalism among the coccinellids and was the most effective intraguild predator. It is also a highly adapted larval cannibal, capable of successful development on an exclusive diet of conspecific larval corpses (Michaud, 2002b). The higher cannibalism rate of *H. axyridis* relative to *O. v-nigrum* confirms previous results for these two species (Michaud, 2003). *Curinus coeruleus* tied with *O. v-nigrum* for the lowest rate of cannibalism. Since these two species are the most disparate with respect to larval morphology (long spines versus no spines), an important role for larval spines in deterring attacks by conspecifics does not seem indicated. However, cannibalism rates might also reflect some effects of diet if the acceptability of *Ephestia* eggs varied among species.

Aggression toward heterospecific larvae must scale with offensive capabilities for it to constitute adaptive behaviour. Species that are successful in intraguild combat tend to display high levels of aggression toward competitors, levels that can only evolve in concert with behavioral and morphological traits that improve offensive, rather than defensive, capability in aggressive interactions. Consequently, size of weaponry and speed of movement both tend to be correlated with success in intraguild combat. Less aggressive species that lack such offensive capabilities might evolve foraging behaviours that reduce their risk of exposure to intraguild predation, or defensive structures and behaviours that improve their chances of escape, rather than victory, in intraguild combat situations.

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