PREY SPECIFICITY IN *CHRYSOPA*: AN INTERSPECIFIC COMPARISON OF LARVAL FEEDING AND DEFENSIVE BEHAVIOR

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Abstract. To examine pathways in the evolution of prey specialization in insects, we conducted a comparative experimental analysis of larval behavior in two sympatric predaceous sister-species (*Chrysopa quadripunctata*, a generalist, and *C. slossonae*, a specialist on the woolly alder aphid). Responses of the larvae to food (*Myzus persicae*) and camouflaging material (waxy secretions from woolly alder aphids or exuviae from *M. persicae*) were quantified during four discrete developmental periods. Our analysis revealed species-specific, ontogenetic, and environmentally induced variation in larval defensive and feeding behavior. The pattern of interspecific variation indicates that larval behavior could have subserved two processes in the evolution of prey specialization in the sister-species’ progenitor: establishment on a specific prey and adaptation to the prey. First, the presence of the woolly alder aphid’s secretions results in generalist larvae camouflaging themselves to a degree that rivals that of the specialist. Such phenotypic plasticity could have promoted the progenitor’s initial adoption of the ant-tended woolly alder aphid as prey and its wool as a source of camouflaging material. Second, quantitative differences between the generalist’s and specialist’s behavior indicate that adaptation to the woolly alder aphid did not require the acquisition of novel behavioral traits in the larvae. It involved modifications in the expression of defensive behavior that existed in the generalist ancestor and alterations in the ability to attack and feed on robust prey.

Key words: ants; *Chrysopa*; defensive behavior; feeding behavior; *Insecta*; interspecific variation; phenotypic plasticity; predation; prey specificity.

INTRODUCTION

It is usually assumed that most predacious insects are not specific in their choice of food; yet, in reality many of them have relatively narrow diets (Hagen et al. 1976, Sih 1987b; for other terrestrial arthropods see Stowe 1986, McMurty and Rodriguez 1987, Riechert and Harp 1987). Furthermore, even predators with general feeding habits frequently have complex behavioral mechanisms for finding, choosing, and consuming their prey (e.g., Hagen 1987, Dicke et al. 1989, Pekarsky and Wilcox 1989, Sabelis 1990, Scott and Barlow 1990, Provencher and Riechert 1991). For a variety of reasons, little is known about how these mechanisms vary among closely related species, and consequently both the evolution and the stability of predator–prey associations remain problematic (e.g., Tauber and Tauber 1987, Bristow 1988, Gilbert 1990).

The evolution of a predator’s foraging and feeding behavior may be influenced not only by the characteristics of its prey, but also by encounters with competitors and natural enemies associated with the prey (e.g., Sih 1980, 1987a, b, Feder and Lauder 1986, Strong 1988, Lima and Dill 1990). For example, some ants (and other hymenoptera) protect honeydew-producing homopterans from predators. In turn, some homopterophilic predators have behavioral and other adaptations that allow them to circumvent the prey-tending ants (e.g., Buckley 1987, Pierce 1987, Hölldobler and Wilson 1990, Huxley and Cutler 1991). Thus, an understanding of the evolutionary development of predator–prey associations requires comparative studies of how predators balance the conflicting demands of foraging/feeding vs. defence.

To be evolutionarily meaningful, such comparative studies require a strong phylogenetic basis. Indeed, phylogenetic relationships among taxa provide the pattern from which explanations of evolutionary processes are derived (e.g., Ridley 1983, Huey and Bennett 1986, Coddington 1988, Brooks and McLennan 1991). Within this context, comparative studies of recently evolved sister-species constitute a very powerful evolutionary tool because they involve the minimum number of uncontrolled variables that stem from separate evolutionary histories, and thus differences between such taxa provide strong support for inferences regarding the pathways involved in evolutionary change.

Our investigation uses a comparative experimental approach in examining the role of larval behavior in the evolution of prey specificity. In doing so, it focuses on a pair of predacious sister-species, *Chrysopa quadripunctata* (a generalist) and *Chrysopa slossonae* (a specialist) (*Insecta: Neuroptera: Chrysopidae*) that possess...
a number of characteristics that make them especially appropriate for a comparative study of predator–prey associations: (a) The two species differ markedly in their prey and natural enemies/competitors. The specialist feeds on an ant-tended species of aphid, whereas the generalist feeds on a variety of aphids and other arthropods. (b) The specialist’s geographic distribution occurs completely within the generalist’s range, and most if not all known differences between the species are related to their different food associations (Tauber and Tauber 1987). (c) The sister-species status of the generalist and specialist has been independently established in a systematic revision of the genus *Chrysopa* (phylogeny based on larval and adult morphology, with related chrysopine genera as outgroups) (C. A. Tauber, unpublished data). The close relationship of the two species is supported further by the ease with which the species hybridize in the laboratory (although no hybrids are found in nature) (Tauber and Tauber 1987). Thus interspecific differences between the species can be used to derive evolutionary pathways. Finally, (d) the morphologically based cladogram of *Chrysopa* identifies *C. quadripunctata* and *C. slossonae* as derived taxa within a clade of general feeders (C. A. Tauber, unpublished data). Thus we can infer with considerable confidence the direction of evolution, from general feeding to specialization.

**Natural History**

*C. slossonae* (the specialist) is an arboreal lacewing from eastern United States. Eggs and larvae have only been recorded from alder (*Alnus incana* ssp. *rugosa*) infested with the woolly alder aphid, *Prociphilus teselatus*. Although other aphid species occur on alder and other trees nearby, this aphid appears to constitute *C. slossonae’s* primary or only prey (Patch 1908, Pergande 1912, Eisner et al. 1978, Tauber and Tauber 1987).

Woolly alder aphids are commonly associated with several species of formicine ants: *Camponotus neverborensis*, *C. pennsylvanicus*, *Formica exsectoides*, *F. subsericea* (or a species near *subsericea*), and *F. sp*. near *schaufussi*. At least three of these (*C. neverborensis*, *C. pennsylvanicus*, and *F. subsericea*) tend the aphids. *Chrysopa slossonae* larvae circumvent the ants by covering themselves with the aphids’ waxy secretions and by hiding within the aphid colony (Patch 1908, Pergande 1912). The waxy covering, which serves as camouflage and perhaps as a physical barrier to the ants, protects the larvae from attack (Eisner et al. 1978). The high priority that hungry *C. slossonae* larvae give to covering themselves with the waxy secretions (vs. feeding) is indicative of their adaptation to the ant-tended prey (Eisner et al. 1978).

In contrast to its sister-species, *C. quadripunctata* (the generalist) occurs on a variety of trees, shrubs, and annual plants, including oak, maple, hickory, alder, apple, elm, rose, and various field crops throughout the United States and southern Canada (e.g., Banks 1903, Smith 1922, Agnew et al. 1981, Tauber and Tauber 1987). Its range of prey is broad and includes various species of aphids and other soft-bodied insects which may or may not be tended by ants (Smith 1926, Throne 1971). Occasionally *C. quadripunctata* larvae carry plant or animal debris on their dorsa (e.g., exuviae or waxy secretions from aphids), but generally they are naked (Smith 1922, 1926; L. R. Milbrath, M. J. Tauber, and C. A. Tauber, personal observation). As a defensive behavior, larvae remain motionless on leaves or twigs (Smith 1922).

A suite of developmental, reproductive, morphological, behavioral, and phenological traits differentiate the two sister-species and adapt them to their disparate prey (Tauber and Tauber 1987, Tauber et al. 1991). Although both larval and adult behavior are major determinants of *C. slossonae’s* specialized feeding, larval activity plays a crucial role in the specialist’s use of its prey, and it is reasonable to assume that larval defense against the aggressive aphid-tending ants occurred early in the evolution of predation on the woolly alder aphid. Thus, we began our analysis of prey specialization by focusing on larval defense and feeding behavior.

**Materials and Methods**

**Sources of larvae and rearing procedures**

We collected adults of *C. quadripunctata* from hickory (*Carya sp.* ) and oak (*Quercus sp.* ) in Tompkins County, New York, and *C. slossonae* from alder (*Alnus incana* ssp. *rugosa*) in Tompkins and Schuyler counties, New York. Specimens of both species are deposited in the Cornell University Insect Collection, Lot No. 1205.

We reared and maintained the insects at 24° ± 1°C and L : D 16:8. Adults received water, a diet of carbohydrate and protein (a 1:1:1:1 volumetric mixture of Wheat, sugar, honey, and protein hydrolyzate of yeast), and prey (green peach aphids, *Myzus persicae*, and/or pea aphids, *Acrithosiphon pismum*). *C. slossonae* adults also received woolly alder aphids. We reared larvae individually with a surplus of green peach aphids and/or pea aphids. All tests involved first- or second-generation laboratory-reared larvae.

**Experimental design**

To quantify the species-specific patterns of feeding and defensive behavior, our experimental bioassay consisted of observations of larval responses to prey (*M. persicae*) and two types of camouflage material in a 2 × 2 factorial design. The two species (*C. quadripunctata* and *C. slossonae*) and two types of aphid-derived camouflage material (waxy secretions from woolly alder aphids and exuviae from green peach aphids) were completely crossed to yield four primary treatments. We observed each individual larva twice.
during the first instar (early- and late-first instar) and twice during the third (early- and late-third instar). There were 10 larvae per treatment. All tests with a larva employed the same type of aphid-derived material (either exuviae or waxy secretions). We chose the green peach aphid rather than the woolly alder aphid as the experimental prey because: (1) woolly alder aphids constitute an inappropriate prey for use in the bioassay because they simultaneously serve as both food and a source of camouflaging material (i.e., the waxy wool they secrete), and (2) the woolly alder aphid is very difficult to handle experimentally, whereas the green peach aphid is not. The experimental arena consisted of a 60 × 15 mm petri dish into which was fitted a circular piece of a Chinese cabbage leaf infested with green peach aphids. We adjusted the density of aphids on the leaf to ≈265 aphids/dish (the large majority were first and second instars). Waxy secretions or exuviae were then dropped from a brush over the surface of the leaf. Our preliminary observations indicated that larvae in the experimental arena were as likely to encounter aphids as camouflaging material (exuviae or waxy secretions). Preliminary observations of larval behavior identified five distinct activities: (1) Feeding: initiated with the insertion of one or both mandibles into the prey and terminated with the withdrawal of the mandibles; food consisted of living aphids and very rarely moribund aphids or honeydew; (2) Cleaning: wiping of the mandibles against the substrate or against each other; (3) Loading (i.e., camouflaging): placing or rearranging material on the larva’s dorsum; the usual material was waxy secretions from woolly alder aphids or exuviae from green peach aphids; (4) Immobile: nonmovement of the larva in the absence of feeding; (5) Mobile: movement of the larva (head, body, or legs), but excluding loading, feeding, and cleaning.

Each observation period lasted 45 min and it began with the introduction of a larva into the center of the petri dish. We used a dissecting microscope and a stopwatch to measure the duration of each activity (in seconds), and we recorded all activities in sequence. Individual occurrences of an activity comprised events. A series of similar events in rapid succession (separated by other events) constituted a bout. Newly hatched larvae (early-first instars) ranged from 4 h to 20 h old at observation; the early-third instars were from 6 h to 21 h old (post molt) when they were observed; and all were held without food from hatch or molt to observation. Following an observation, early-first and early-third instars were returned to their vials and allowed to feed for ≈12 h. Subsequently, we removed any debris from their dorsa and held them without food (in clean vials containing a water-saturated cotton ball wrapped in perforated Parafilm) for 12 h prior to the next observation. Thus, when tested, late-first and late-third instars were 28–45 h old (posthatch or molt). Withholding food and camouflaging material for the above periods prior to observation ensured that larvae would be active but without excessive stress (e.g., Tauber et al. 1991).

We made additional observations (10 larvae per condition) to increase the sample size for the analysis of the first activity in which larvae engaged when faced with a choice between feeding and camouflaging behavior. We treated these larvae as above, except that each observation lasted only until the larva initiated feeding or loading, or until 5 min had elapsed, whichever came first.

Ethograms

We constructed ethograms (see Fig. 1) to provide a pictorial representation of larval time–activity budgets (relative sizes of circles) during the 45-min observation period, as well as the sequence of larval activities (relative widths of arrows between circles). All larval activities are included in the ethograms except “mobile”; the proportion of time spent in the “mobile” state is represented in the pie-shaped figure above each ethogram.

Statistics

We analyzed the data (the number of events per activity and the proportion of time spent on each activity [except “mobile”]) with a four-factor, repeated-measures ANOVA; species, type of aphid-derived material, instar, and age within instar were the factors, with repeated measures on instar and age within instar (SAS Institute 1985). The behavioral category referred to as “mobile” included several different activities such as searching, walking, and running. Because these activities often could not be distinguished from one another, we excluded the “mobile” category from analysis. Neither the untransformed data nor transformed data (log[number events + 1] and arcsine square-root [proportion of time]) displayed equal variances. However, the analysis with untransformed data did not present a problem because inequality of variances has little effect in a balanced design (see Scheffé 1959).

We used G tests with the simultaneous test procedure (Sokal and Rohlf 1981: 728–730) to assess the independence of the initial activity (feeding or loading) from treatment (each combination of species and the type of aphid-derived material). Because of the repeated-measures design, we tested each instar and age separately. We assessed the consistency in the initial activity across developmental stages with Cochran’s Q test on data within each treatment (Sokal and Rohlf 1981). Preliminary tests showed that the presence or absence of waxy secretions did not significantly influence the duration of feeding. Therefore, to analyze the time required for larvae to consume individual aphids, we combined data from the two treatments, and we assessed the effects of the remaining factors (species, instar, age) on the log-transformed data with ANOVA (SAS Institute 1985).
Fig. 1. Examples of ethograms of larval behavior during 45-min observation periods (N = 10 larvae/ethogram). A. Early-first instar Chrysopa quadripunctata with exuviae. B. Early-first instar C. quadripunctata with waxy secretions. C. Early-first instar C. slossonae with waxy secretions. D. Late-first instar C. slossonae with waxy secretions. E. Late-third instar C. quadripunctata with exuviae. F. Late-third instar C. quadripunctata with waxy secretions. The pie diagram in the upper right of each ethogram represents the total 45-min observation period. The white section depicts the average proportion of time spent on the four main activities: camouflaging (i.e., loading of aphid material, L), feeding (F), cleaning (C), and immobility (I). Whereas the black portion is the proportion of time spent walking. The area of each circle labeled L, F, C, or I represents the average proportion of time spent on a particular activity based on the equation πr² = average proportion of time. The start arrows indicate the initial activities (loading of aphid material or feeding only). The width of each of the arrows radiating from start and from each circle represents the average probability of changing from one activity to the other. The combined probabilities of all arrows radiating from a single circle equals 1.0. The W-arrow refers to transitions between loading events separated by >5 s of walking.

RESULTS

Initial activity (feeding vs. camouflaging behavior)

The woolly alder aphid’s waxy secretions had a large and significant influence on larval behavior. For example, in the presence of the secretions, 47–87% of the C. quadripunctata and C. slossonae larvae initiated camouflaging behavior prior to feeding, whereas larvae provided with exuviae usually fed first (Table 1, e.g., Fig. 1A and B). In the presence or absence of waxy secretions C. slossonae larvae showed a greater tendency than C. quadripunctata to load initially (Table 1). Although significant in only one case, this interspecific difference prevailed in three of the four age classes. The early-first instars of both C. quadripunctata and C. slossonae gave similar priority to camouflaging behavior.

In general, the numbers of C. slossonae larvae that loaded prior to feeding remained consistent throughout larval development regardless of the type of aphid-derived material they encountered. C. quadripunctata larvae that were provided with waxy secretions also were consistent in the incidence of loading prior to feeding. However, C. quadripunctata that had access to exuviae showed a significant change in behavioral priorities with maturation (Q = 11.33, P < .025, Table 1). That is, a substantial proportion (29%) of C. quadripunctata early-first instars placed exuviae on their
Table 1. Incidence of camouflaging behavior (loading*) before feeding, when Chrysopa larvae were given access to prey and one of two types of aphid-derived material†

| Species                  | Type of aphid-derived material | Larvae engaging in behavior |  |  |  |  |  |  |  |
|--------------------------|--------------------------------|----------------------------|---|---|---|---|---|---|
|                          |                                | First instar                             |  |  |  |  |  |  |  |
|                          |                                | Early | Late | Early | Late | Early | Late |
| Chrysopa quadripunctata  | exuviae                        | %     | No.  | %     | No.  | %     | No.  |
|                          | waxy secretions                |       |      |       |      |       |      |
| Chrysopa slossonae       | exuviae                        | %     | No.  | %     | No.  | %     | No.  |
|                          | waxy secretions                |       |      |       |      |       |      |

* Loading = placing of aphid-derived camouflaging material onto dorsum.
† Percentages within columns followed by the same superscript letter are not significantly different (G tests with simultaneous test procedure. \( P = .05 \)).

Dorsa prior to feeding, whereas no late-first instars and only 0–5% of the early and late-third instars did so.

Sequence of activities

The sequence of larval behavior was influenced greatly by the type of aphid-derived material in the experimental arena. For example, when waxy secretions were present, the initial loading behavior was usually followed by additional loading (a loading bout). Subsequently, larvae fed and then generally resumed loading (Fig. 1B, C, D, and F). In contrast, when exuviae were present, larvae normally engaged in protracted feeding (first instar, Fig. 1A) or bouts of feeding and cleaning (Fig. 1E).

For both species, loading bouts were more likely to occur when wax was available (\( P = .27 \pm .07, N = 160 \)) than when exuviae were present (\( P = .12 \pm .10, N = 160; \) e.g., Fig. 1E and F). Larvae usually cleaned after feeding (\( P = .45 \pm .15, N = 160 \)).

Feeding

Both C. quadripunctata and C. slossonae larvae showed similar patterns of movement when attacking, manipulating, and feeding on M. persicae. The larvae lunged at and impaled the aphids with their jaws, often lifting them from the substrate. They ingested the aphids’ body fluid by pumping it through feeding tubes formed by the elongate mandibles and maxillae. Usually only one jaw was inserted into the prey, whereas the other jaw served to hold and turn the prey while the inserted jaw continued draining the prey’s body fluid. After the fluid had been largely removed, the larva usually twirled and shifted the carcass between the two jaws, apparently to exhaust its contents. Larvae of both species usually fed until the aphid’s exoskeleton collapsed fully.

Under all conditions C. slossonae had a higher predation rate during the 45-min observation period than C. quadripunctata (Table 2). They ate approximately twice as many aphids (of equivalent size) as C. quadripunctata, and they did so during an equal or shorter period (Table 2, Fig. 2). The interspecific differences in feeding disappeared by the third instar.

First instars spent proportionately more time feeding than third instars (Table 2, Fig. 1B and F). Within the first instar, older (late) larvae fed faster than younger (early) larvae; this difference disappeared by the third instar (Table 2, Figs. 1C, D and 2). The presence or absence of waxy secretions did not influence the time spent feeding or the number of aphids eaten (Table 2).

Cleaning

After feeding, the larvae of both species frequently removed the aphid carcass and any aphid-produced fluids from the mouthparts by wiping the jaws against each other or on the substrate. As measured by the number of events and the proportion of time, C. slossonae larvae cleaned significantly more than C. quadripunctata larvae (Table 3, Fig. 1B and C). By the same measures, the third instars generally cleaned more than the first instars (Table 3, Fig. 1A and E) and, within each instar, the older larvae cleaned more than the younger ones (Table 3, Fig. 1C and D). The kind of aphid-derived material (wax or exuviae) that was available did not influence the amount of time spent cleaning or the number of cleaning events (Table 3).

Camouflaging behavior

Larvae of both species displayed similar behavioral patterns when camouflaging themselves. Camouflaging (i.e., loading) consisted of grasping and lifting aphid-derived material with the jaws, arching the head and abdomen dorsally, and embedding the material among the long, curved setae that cover the dorsum of the abdomen and thorax (see also Eisner et al. 1978, re: C. slossonae). However, the two species differed significantly in the quantitative expression of this behav-
ior. *C. slossonae* larvae were generally more prone to load (either waxy secretions or exuviae) than larvae of *C. quadripunctata* (Table 4, Fig. 1B and C). A notable exception occurred when third instars had access to waxy secretions. Under these circumstances interspecific differences in the number of loading events and in the proportion of time spent loading were small.

The type of aphid-derived material that we provided had a large and significant effect on larval camouflaging behavior. In the presence of waxy secretions larvae of both species engaged in camouflaging behavior more often and spent more time loading than when exuviae were available (Table 4, Fig. 1A, B, E, and F). Furthermore, all (100%) of the larvae that had access to waxy secretions loaded at least once during the 45-min observation period, whereas in the presence of exuviae only some of the *C. quadripunctata* (57%) and most (95%) of the *C. slossonae* larvae loaded.

When waxy secretions were available, third instars of both species loaded much more often than first instars; however, the reverse was true when exuviae were present (Table 4). Furthermore, first instars generally spent proportionately more time loading than third instars (Table 4, Fig. 1A and E).

**Immobility**

Under all conditions *C. quadripunctata* were immobile a greater proportion of time than *C. slossonae* (Table 5, Fig. 1B and C). In the presence of exuviae,
first instar and early-third instar *Chrysopa quadripunctata* spent significantly more time immobile than when waxy secretions were available (Table 5, Fig. 1A and B). Within each instar, younger larvae generally spent proportionately more time in an immobile state than older larvae (Table 5, Fig. 1C and D).

**DISCUSSION**

The evolution of food specificity in insects comprises a variety of processes involving the entire life cycle: (a) establishment on a specific food, (b) adaptation to the food, and (c) maintenance of host fidelity through reproductive isolation. Our comparative experiments here reveal a pattern of species-specific, ontogenetic, and environmentally induced variation that elucidates the role of larval behavior in the first two of these processes. First, our results implicate phenotypic plasticity in larval defensive behavior as a major component in the initial adoption of the woolly alder aphid as prey. And second, they illustrate the types of changes in larval behavior that comprise adaptation to the woolly alder aphid. We discuss each of these findings in turn.

**Phenotypic plasticity in larval behavior**

*C. quadripunctata*‘s responsiveness to the woolly alder aphid’s waxy secretions leads us to suggest that plasticity in camouflaging behavior constituted a significant preadaptation in *C. slossonae*‘s progenitor for the evolution of prey specificity. *C. slossonae* larvae circumvent the aggressive ants that tend the woolly alder aphid by disguising themselves with the aphids’ waxy secretions (Eisner et al. 1978). Our results here show that camouflaging is not unique to the specialist; in the presence of waxy secretions, larvae of the generalist (especially the third instars) express a level of camouflaging behavior that rivals the specialist’s. Thus, if *C. quadripunctata* larvae were to encounter woolly alder aphid colonies, their ability to recognize and use the aphids’ waxy secretions as camouflage would provide considerable protection against ants. Given that generalist larvae can feed and develop on woolly alder aphids (Tauber and Tauber 1987), such behavioral plasticity in defensive behavior could have been a key factor in the generalist progenitor’s adoption of the woolly alder aphid as prey.

**Table 5.** Proportion of time that *Chrysopa* larvae were immobile when prey and one of two types of aphid-derived camouflaging material were present (means ± 1 sd; *N* = 10 larvae per cell).

<table>
<thead>
<tr>
<th>Species</th>
<th>Type of aphid-derived material</th>
<th>First instar</th>
<th>Third instar</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Early</td>
<td>Late</td>
</tr>
<tr>
<td><em>Chrysopa quadripunctata</em></td>
<td>exuviae</td>
<td>0.2510 ± 0.1698</td>
<td>0.2470 ± 0.1321</td>
</tr>
<tr>
<td></td>
<td>waxy secretions</td>
<td>0.1706 ± 0.2160</td>
<td>0.1402 ± 0.1568</td>
</tr>
<tr>
<td><em>Chrysopa slossonae</em></td>
<td>exuviae</td>
<td>0.2155 ± 0.2535</td>
<td>0.0184 ± 0.0173</td>
</tr>
<tr>
<td></td>
<td>waxy secretions</td>
<td>0.0763 ± 0.1054</td>
<td>0.0227 ± 0.0233</td>
</tr>
</tbody>
</table>

* Species (*P* = .0001), aphid-derived material (*P* = .0250), age (*P* = .0001), aphid-derived material × instar (*P* = .0001), species × instar × age (*P* = .0178), species × aphid-derived material × instar × age (*P* = .0101) were significant terms in the repeated-measures ANOVA. Instar was not significant, nor were any interactions other than those listed.
**LARVAL INSTAR (AGE)**

![Graph](image)

**Fig. 2.** Time required for *Chrysopa* larvae to consume one aphid (first or second instar aphids; time from insertion to withdrawal of mandibles = handling time). Species (*P* = .0103), instar (*P* = .0001), age (*P* = .0002), species × instar (*P* = .0064), and instar × age (*P* = .0492) were significant terms (ANOVA with log-transformed data).

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**Larval adaptation to the woolly alder aphid**

The pattern of interspecific differences between the generalist and specialist sister-species illustrates that adaptation to the woolly alder aphid involved quantitative changes in larval defensive and feeding behavior. Given that the generalist’s repertoire of larval behavior contains the major elements of the specialist’s behavior, we conclude that the evolution of *C. slossonae*’s specialization did not require the progenitor’s acquisition of novel behavioral traits. Larvae of both species attack and feed on prey in a similar manner, they display similar patterns of movement when covering themselves with camouflaging material, and the wax from woolly alder aphids influences the camouflaging behavior of the two species similarly. The species differ only in the amount of time and the degree of priority given to the various types of behavior. That is, the main species-specific differences are quantitative. Thus, larval adaptation to the ant-tended woolly alder aphid probably involved selection on quantitative variation in behavioral traits that existed in the generalist progenitor.

**Evolution of feeding behavior.** —Quantitative differences in feeding behavior differentiate *C. slossonae* and *C. quadripunctata*. Each age class of *C. slossonae* that we tested consumed an equal or greater number of prey in a shorter period of time than did *C. quadripunctata* (Table 2, Fig. 2). Moreover, the species-specific differences in feeding were unaltered by the type of aphid-derived material that the larvae encountered. That is, the waxy secretions from the woolly alder aphid did not influence either the number of prey eaten, the rate of feeding, or the amount of cleaning. Given this consistency, we propose that *C. slossonae*’s greater attack and ingestion rates arose in conjunction with morphological changes associated with feeding on large, robust prey. Woolly alder aphids are much larger than the aphids that *C. quadripunctata* attacks (Pergande 1912), and *C. slossonae* larvae have broader head capsules and larger, more widely spaced mouthparts than *C. quadripunctata* (C. A. Tauber, M. J. Tauber, and J. R. Ruberson, unpublished manuscript). These interspecific differences in size are polygenically based, and presumably a large feeding apparatus provides the specialist with ample power to seize and subdue robust aphids, as well as strong pumping action to drain body fluid quickly.

The species-specific differences in feeding rates were particularly evident in the first instars (Table 2, Fig. 2). Because these instars are small relative to the green peach aphid, it is likely that our behavioral bioassay challenged their feeding capacity and thus was a sensitive measure of feeding rates. In contrast, the third instars of both species are large relative to green peach aphids, and our bioassay did not reveal interspecific differences in feeding behavior. Nevertheless, in nature, where the larva prey on the robust woolly alder aphids, *C. slossonae*’s larger head and mouthparts may be advantageous throughout larval life.

**Evolution of larval defensive behavior.** —The larvae of both *Chrysopa* species display two forms of defence (crypsis and immobility) that are generally perceived as effective mechanisms for protection from natural enemies (see Endler 1986), but they differ in the degree to which they express the two types of behavior. The pattern of interspecific variation in the laboratory study appears to reflect the species’ different interactions with natural enemies in the field. *C. slossonae* commonly encounter aphid-tending ants, and this species places high priority on crypsis (i.e., camouflaging behavior, as measured by the tendency to load prior to feeding, the number of loading events, as well as the proportion of time allocated to loading; Tables 1 and 4; see also Eisner et al. 1978). In contrast, *C. quadripunctata*, whose association with ants is less evident, has a greater tendency to use immobility as a defense.

It is noteworthy that both the interspecific and intraspecific patterns of variation in defensive behavior support the notion that the evolution of a high propensity for camouflaging behavior may involve a trade-off with immobility. That is, *C. quadripunctata* spent more time motionless but less time loading than *C. slossonae*. Furthermore, in the presence of exuviae, *C. quadripunctata* loaded very little but spent considerable time immobile, whereas the reverse was true when wax was available.

The ontogenetic pattern of interspecific differences in responsiveness to the aphid secretions leads us to suggest that *C. slossonae*’s greater propensity to engage in camouflaging behavior evolved, in part, as a general trait across instars. This conclusion originates in the observation that when less preferred camouflaging materials (e.g., aphid exuviae) were present both first and third instars of *C. slossonae* loaded more than *C. quadripunctata*. However, variation in the trait is not sim-
ple. For example, when larvae had access to waxy se-
cretions, third instars of the two species expressed
similar, very high levels of camouflaging behavior,
whereas under the same conditions, first instars showed
large interspecific differences. It appears that first (and
perhaps second) instars were the target of selection for
the specialist’s increased propensity for camouflaging
behavior in the presence of the waxy secretions. We
conclude therefore that the evolution of the specialist’s
camouflaging (defensive) behavior involved a complex
genotype-environment interaction that may vary
throughout larval development.

Implications for applied ecology
The stability of predator–prey associations consti-
tutes a significant issue for applied ecologists as well
as for evolutionary biologists. For example, the poten-
tial for biological control agents to adopt nontarget
organisms as prey, including rare, protected, or endan-
gered species, has given rise to serious questions con-
cerning the behavioral stability of biological control
agents and the ecologically sound use of biological con-
trol to suppress pests (e.g., Bernays 1986, Ehler 1990,
Howarth 1991). In this regard, our study emphasizes
that one of the most useful methods for assessing the
potential for change in natural enemy–host/prey asso-
ciations is to examine the behavior of closely related
species of natural enemies. For example, on the one
hand, our findings suggest that some traits, e.g., phe-
notypic plasticity in defensive behavior and prey ac-
ceptability, may favor prey shifts. On the other hand,
our findings also illustrate that quantitative differences
in larval behavior can differentiate a specialist from a
closely related generalist. Because this type of special-
ized prey association appears to be stable in field pop-
ulations of C. slossonae, we conclude that specializa-
tion based on quantitative traits should not exclude a
predator from evaluation for biological control.

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