

Selection of Molting and Pupation Sites by *Coleomegilla maculata* (Coleoptera: Coccinellidae): Avoidance of Intraguild Predation

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ABSTRACT Molting and pupating insects are especially vulnerable to natural enemies and one possible component of their defensive strategy is the selection of suitable microhabitats. We hypothesized that larvae of the lady beetle *Coleomegilla maculata lengi* Timberlake select molting and pupation sites that effectively reduce their susceptibility to intraguild predation. We characterized microsites on potato plants and evaluated their associated risk of predation by the lacewing *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae), a common intraguild predator. The majority of molts (>60%) occurred on potato plants in sites similar to those used by mobile coccinellid larvae. In contrast, 90% of the larvae left the plant to pupate. Second, third, and fourth instars selected artificial shelters for both molting and pupation when these were available. Vulnerability of pupae and newly molted larvae to lacewing larvae depended on plant microsite, with leaves supporting an aphid colony as the most risky sites. Molting and pupating microhabitat selection by coccinellid larvae appears to be a trade-off between the advantages of remaining close to the aphid resource, and the costs of being exposed to intraguild predators.

KEY WORDS *Coleomegilla maculata*, habitat selection, molt, pupation, intraguild predation, defense

ONTOGENIC TRANSFORMATION PHASES like shedding (amphibians, reptilians, birds) or molting and metamorphosis (arthropods) may disrupt physiological, morphological, and behavioral patterns of animals. Such disruptions temporarily handicap normal reproductive, foraging, and defensive functions (Soluk 1990). For instance, shedding and molting individuals are usually more vulnerable to intraspecific (Polis 1981, Crump 1992), intraguild (Dick et al. 1990) and extraguild predation (Soluk 1990) than foraging individuals. One of the main detrimental effects associated with shedding and molting is reduced locomotion (Wassersug and Sperry 1977). Consequently, sessile stages cannot display escape or aggressive behaviors normally displayed by mobile individuals.

Holometabolous insects are immobile (or sessile) as eggs and pupae as well as during molting. Molting, a periodic process of shedding the exoskeleton, is divided into two phases: exuviation, the shedding of the old cuticle, and postexuviation, the sclerification of new teguments. The insect usually remains immobile during the first phase, whereas it can move during the second. Few studies have evaluated the vulnerability of molting insects to natural enemies. However, it has been shown that molting individuals may reduce mortality through avoidance of parasitoids and predators by selecting a less exposed site or by delaying molting. Larvae of the mayfly *Ephemera subvaria* McDun-

nough (Ephemeroptera: Ephemerellidae) molt more frequently during the daytime when predatory stoneflies are less active (Soluk 1990). The springtail *Isoptoma carpenteri* Börner (Collembola: Isotomidae) delays molting when predation risk by pseudoscorpions is high (Witt and Dill 1996).

Pupation is a more complex process than molting, and involves thorough physiological and morphological transformations, such as genesis of sexual organs and wings. Pupae are usually sessile and protected by morphological (Hinton 1955, Völkl 1995), chemical (Edmunds 1974, Bowers 1992, Attygalle et al. 1993), and behavioral defenses (Hinton 1955). Prepupation stages have been shown to select pupation sites that lower the probability of predation or of hyperparasitism. For example, Brodeur and McNeil (1989, 1992) showed that the aphid parasitoid *Aphidius nigripes* Ashmead (Hymenoptera: Braconidae) has the ability to induce its host to leave the aphid colony and mummify in microhabitats where the incidence of pupal hyperparasitism is reduced. Tschinkel (1981) observed that tenebrionid larvae tend to disperse just before pupation, to presumably reduce cannibalism. Also, aquatic larvae of *Toxorhynchites* sp. (Diptera: Culicidae) enter a phase of "frenzy killing" at the end of their larval development and eliminate, without feeding on them, all invertebrate predators they encounter in the habitat (Corbet and Griffiths 1963).

In this study we assessed the susceptibility to predation of molting and pupating of the lady beetle *Coleomegilla maculata lengi* Timberlake to the lacewing *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae). Both species are common predators of

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potato aphids (Burke and Martin 1956, Mack and Smilowitz 1980, Legaspi et al. 1994) and occur simultaneously in potato fields (Obrycki et al. 1983). The immature coccinellid goes through four larval instars, therefore three molts, before pupating (Warren and Tadic 1967). Just before molting and pupating, the larva stops feeding and attaches itself to the substrate by the anal pseudopod (Majerus 1994). As shown by Lucas et al. (1997, 1998), larvae and pupae of *C. maculata* are highly vulnerable to intraguild predation. In this article, we tested the hypothesis that coccinellid larvae select molting and pupating sites that lower their mortality by natural enemies. We first characterized and compared the within plant distribution of molting, pupating, and mobile *C. maculata* larvae. Next, we determined how molting and pupation site selection might reduce the probability of attack by the intraguild predator *C. rufilabris*.

Materials and Methods

Chrysoperla rufilabris and *C. maculata* were purchased from Groupe Biocontrôle (Sainte-Foy, Canada) and reared on the potato aphid *Macrosiphum euphorbiae* Thomas at $23 \pm 2^\circ\text{C}$ and a photoperiod of 16:8 (L:D) h. All experiments were carried out under the same environmental conditions.

Distribution of Molting Larvae, Pupae, and Mobile Larvae. A potato plant with 4–6 leaves was placed in a plastic container (15 cm high by 12 cm diameter), with a muslin covered lid that prevented insects from escaping. The stem of the plant passed through a hole in the cage floor into a second container filled with water. Leaves were identified as follows: the lowest leaf: F1, the second leaf: F2, and so on. An aphid colony was established, using clip-cages, on the second leaf (F2), 24 h before the test. The aphid density was fixed at 20, 30, 40, and 50 aphids (second instar) for *C. maculata* L1, L2, L3, and L4, respectively, and maintained every day. A trial started by introducing a coccinellid larva at the base of the plant, a minimum of 24 h before molting and terminated once molting or pupation occurred. As exuviae remained attached on the plant, their position was an accurate indication of transformation sites. Exuviae were recorded as being found on or off the plant, and for those on the plant, the precise location (F1, F2, F3–6, terminal, stem) was determined. For mobile larvae, their position on the plant was recorded every hour over a 24-h period. A minimum of 15 replicates were carried out for each larval instar. A distance-index was attributed for each exuvia, based on its position compared with the aphid colony position: (1) exuvia on the same leaf, same leaflet and same surface as the colony; (2) exuvia on the same leaf, same leaflet, but on the surface opposite to the colony; (3) exuvia on the same leaf, but on a leaflet other than the colony; (4) exuvia on a leaf other than the colony; (5) exuvia off the plant.

Distribution of molting and pupation sites were compared according to their position (likelihood ratio *G* test). The average occurrence of mobile larvae on each part of the plant or outside of the plant was

established. It was then compared with the position of the following molting larva or pupa on the plant (likelihood ratio *G* test). The distance-indexes (exuvia-colony) of the molting larvae and of the pupa were compared by a Mann–Whitney *U* test.

Selection of an Artificial Shelter. Tests were performed to evaluate the utilization of an artificial shelter (refuge) by molting and pupating coccinellid larvae. A *C. maculata* larva was placed in a petri dish (5 by 1 cm) covered with muslin. Each petri dish contained a moist cotton wick (1.5 by 0.5 cm), pollen as a food source and a packing clear plastic bubble as a shelter (3 by 3 cm). Because the plastic shelter was transparent, light intensity should not be a significant factor in site selection. Four stages (*C. maculata* L1, first molt; L2, second molt; L3, third molt; L4, pupation) were tested and the position of exuviae found on the petri dish, cotton wick, pollen, or plastic shelter was recorded. Twenty replicates were carried out per treatment. A theoretical randomized distribution of exuviae on the four sites was calculated based on their relative surface (petri dish, 77% of total surface; cotton wick, 2.5%; pollen, 1.6%; and plastic shelter, 18.9%). The theoretical and observed distributions of each coccinellid instar for molting/pupating sites were compared using a *G* test.

Vulnerability of Mobile and Molting Larvae. Vulnerability of mobile and molting *C. maculata* larvae to *C. rufilabris* was evaluated on a potato stem (10–13 cm), bearing one leaf (6 by 5 cm) at a height of 3–5 cm. Molting larvae were collected from rearing units after they had attached to the substrate but before exuviation. A mobile (L1, L2, L3, or L4) or a molting larva (first, second, or third) of *C. maculata* was placed in the center of the upper surface of the leaf. A third-instar *C. rufilabris*, starved for 24 h before the test, was introduced on the stem with its head facing the leaf. The experiment ended after the chrysopid killed the coccinellid, the coccinellid left the leaf, or 30 min had elapsed. A replicate was considered valid when the lacewing came in contact (face on) with the coccinellid. The occurrence of predation during the exuviation and postexuviation phases were recorded. The proportion of fatal contacts was calculated by dividing the number of contacts from the chrysopid that caused the death of the coccinellid by the total number of contacts between the two predators. Fifteen trials were conducted per treatment. Mortality of mobile larvae and molting larvae, as well as the proportion of fatal contacts during the exuviation and postexuviation phases were compared using likelihood ratio *G* tests.

Risk Associated to Molting Site. Coccinellid vulnerability to *C. rufilabris* during the molting process was evaluated at different sites on the potato plant. Given the difficulty in synchronizing coccinellid molts, we used second-instar *C. maculata* larvae pinned by their last abdominal segment to the plant and considered these to be “pseudomolting larvae.” Pseudomolting larvae did not have a superior defensive capacity than molting larvae because they were not able to escape and because *C. maculata* second-instar larvae did not have efficient aggressive defenses against *C. rufilabris*

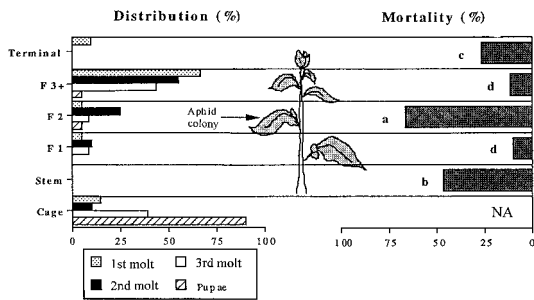


Fig. 1. Distribution of molting and pupation sites selected by *C. maculata* larvae on a potato plant (on the left). Corresponding mortality of *C. maculata* pinned larvae in the presence of a *C. rufilabris* third-instar larva (on the right). Different letters indicate a significant difference in *C. maculata* mortality between sites (*G* test, $P < 0.05$). NA, nonapplicable.

third-instar larvae (Lucas et al. 1997). In addition, >90% of nonattacked pseudomolting larvae were alive after 24 h. Pseudomolting larvae were fixed in 14 different sites on the plant: on the stem, on the terminal portion and on both surfaces, and on the edge and the center of leaves F1, F2, and F3+. Forty *M. euphorbiae* second-instar aphid nymphs were introduced on the second leaf (F2) and kept in a clip-cage 24 h before the beginning of the experiment. The test started with the introduction of a third-instar *C. rufilabris* larva on the petiole of the second leaf. Fifteen replicates were conducted. After 24 h, the mortality of pseudomolting larvae by the lacewing was determined under a stereo microscope. Mortality of pseudomolting larvae was compared by likelihood ratio *G* tests according to the position on the plant (F1, F2, F3–6, terminal, stem), as well as the surface and the position (edge or center) on the leaf.

Results

Distribution of Molting Larvae, Pupae, and Mobile Larvae. Molting larvae occurred in microhabitats similar to those used by foraging mobile larvae (L1 versus first molting larva, $G = 10.83$, $df = 5$, $P > 0.050$; L2 versus second molting larva, $G = 8.94$, $df = 5$, $P > 0.100$; L3 versus third molting larva, $G = 10.48$, $df = 5$, $P > 0.050$). There was no significant difference among sites selected for first, second, and third molting ($G = 14.11$, $df = 10$, $P > 0.100$), most with molts occurring on the plant. All parts of the plant were used for molting except for the stem (Fig. 1, left). The terminal portion was used only by first instars.

Pupation sites differed significantly from molting sites ($G = 47.15$, $df = 15$, $P < 0.001$; Fig. 1, left), as 90% ($n = 20$) of fourth-instar larvae left the plant to pupate on the cage. Mobile fourth-instar larvae foraged in microhabitats different from sites selected for pupation ($G = 14.27$, $df = 5$, $P < 0.025$). The distance between the pupation site and the aphid colony was greater than the distance between the molting site and the aphid colony (Mann-Whitney *U*, first molt versus

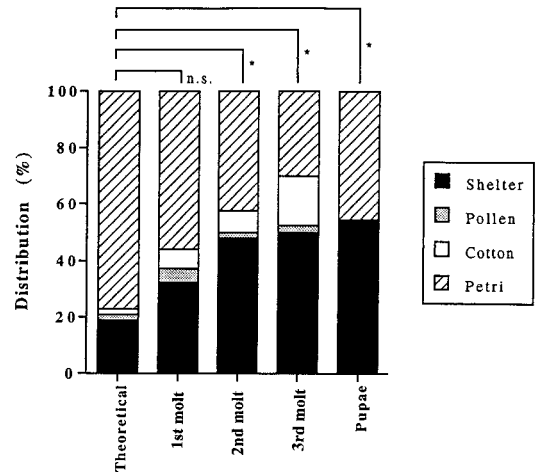


Fig. 2. Distribution of molting and pupation sites selected by *C. maculata* larvae in a petri dish. The asterisk indicates a significant difference between the two selected bars (*G* test, $P < 0.05$).

pupa, $P < 0.001$; second molt versus pupa, $P < 0.001$; and third molt versus pupa, $P < 0.001$). Different larval instars chose similar distances from the aphid colony for molting (Mann-Whitney *U*, first versus second molt, $P = 0.506$; first versus third molt, $P = 0.225$; second versus third molt, $P = 0.137$).

Selection of an Artificial Shelter. In petri dishes, molting and pupation sites were similar ($G = 16.04$, $df = 9$, $P > 0.050$; Fig. 2). Second molt ($G = 12.59$, $df = 3$, $P < 0.010$), third molt ($G = 20.81$, $df = 3$, $P < 0.005$), and pupation ($G = 9.27$, $df = 3$, $P < 0.050$) occurred more often in the shelter than was predicted based on its surface area (18.90%).

Vulnerability of Mobile and Molting Larvae. First molting larvae were no more susceptible to lacewing predation than mobile first and second instar larvae ($G = 1.23$, $df = 1$, $P > 0.250$; Fig. 3). However, older molting/pupating stages were more vulnerable to predation than mobile large coccinellid larvae (second molt versus second and third instar, $G = 12.02$, $df = 1$, $P < 0.005$; third molt versus third and fourth instar, $G = 15.50$, $df = 1$, $P < 0.005$). Mortality was similar for the three molting larvae ($G = 0.901$, $df = 2$, $P > 0.500$), but the proportion of fatal contacts was significantly higher during exuviation than during the postexuviation phase (first molt, $G = 33.67$, $df = 1$, $P < 0.005$; second molt, $G = 9.66$, $df = 1$, $P < 0.005$; third molt, $G = 35.05$, $df = 1$, $P < 0.005$; Fig. 4).

Risk Associated to Molting Site. Vulnerability of coccinellid pseudomolting larvae to lacewing predation differed greatly according to the site on the plant ($G = 66.49$, $df = 4$, $P < 0.005$; Fig. 1, right), the leaf bearing the aphid colony (F2) being the most risky site for molting/pupating. Leaves without aphids (F1 and F3+) were the safest microhabitats ($G = 4.45$, $df = 1$, $P < 0.050$). Susceptibility of pseudomolting larvae was similar on the different parts of the leaf ($G = 0.09$, $df = 1$, $P > 0.750$) and also on both surfaces ($G = 0.97$, $df = 1$, $P > 0.250$).

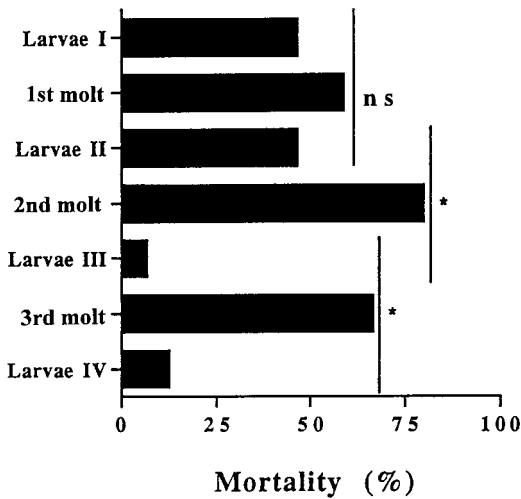


Fig. 3. Mortality of mobile and molting larvae of *C. maculata* in the presence of a *C. rufilabris* third-instar larva. The asterisk indicates a significant difference between molting and mobile larvae (*G* test, $P < 0.05$).

Discussion

In organisms with complex life cycles such as amphibians and holometabolous insects, frequent habitat shifts occur, either during or between larval, adult, and

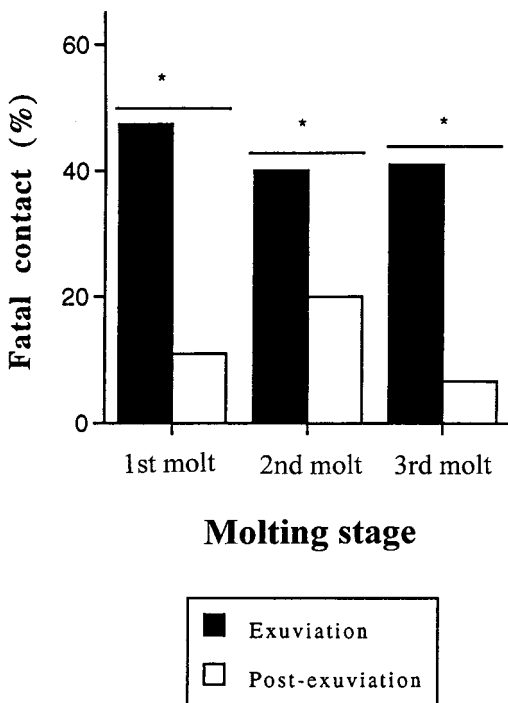


Fig. 4. Percentage of fatal contacts during exuviation and postexuviation of *C. maculata* in the presence of a *C. rufilabris* third-instar larva. The asterisk indicates a significant difference between open and solid bars (*G* test, $P < 0.05$).

metamorphosis stages (Wilbur 1980). Thus, for highly vulnerable transformation phases, the selection of a protected site could be an effective defensive strategy against predation. Our study revealed that microhabitat selection differed significantly for premolting and prepupating larvae of *C. maculata*. In fact, the majority of molts occurred on the plant, in sites used by mobile larvae, whereas 90% of fourth instar larvae left the plant to pupate.

Premolting and prepupating larvae face the same trade-off: maximizing growth rate versus minimizing mortality caused by natural enemies. Microhabitat selection might have evolved to counterbalance the risks of mortality during prospection for a suitable site (prospection risk), mortality during the molt/pupation stages (site predation risk), and losing the aphid resource (resource-dependency). The extent to which each of these risks modulate microhabitat selection appears to differ for premolting and prepupating larvae of *C. maculata*.

Molts occurred on the plants close to the aphid colony in sites used by mobile larvae. In this instance, premolting larvae secure their resource-dependency and reduce prospection risk. Starvation is a major factor of mortality for coccinellid larvae once aphid colonies had collapsed (Majerus 1994). Coccinellid larvae have poor prey detection capacities and it seems that they must come in contact with prey to detect them (New 1991). Prospecting for a safe molting site could be dangerous for larvae because it increases the probability of fatal encounters, especially if stems are used, as they frequently are, by foraging predators (at least apterous stages and ground-leaving predators) (Griffiths et al. 1985). When shelters were available near the aphid resource, they were preferred by second and third molting larvae, suggesting that premolting larvae actively search for and choose protected sites when prospection risks are low. Although the site-predation risk is expected to be high in the vicinity of aphid colonies, its relative importance to microhabitat selection by molting coccinellids might be lessened by a time component. The clumped distribution of aphids has been shown to result in an aggregative numerical response of predators in the vicinity of the aphid colony (Frazer 1988), and in a shift from random search to area restricted search patterns by predators (Dixon 1959, Hemptinne et al. 1996). These behaviors would favor encounters among aphidophagous predators (Hassell 1978), thereby increasing site-predation risks for molting coccinellid larvae. However, the period of vulnerability of molting *C. maculata* larvae is relatively short because the exuviation/postexuviation phase lasts for less than an hour (i.e., <1% of the total duration of the preimaginal development).

For prepupating larvae the selection of pupation sites off the host plant primarily reflects the site-predation risk constraint. Pupation of *C. maculata* lasts 3.8 d at 26.7°C, which represents 20% of its preimaginal developmental time (Warren and Tadic 1967). Pupae are therefore exposed to natural enemies for a longer period than molting individuals. Selection of a site

away from the aphid colony might therefore be an adaptive response to intraguild predation. However, further work is needed to evaluate the survival of coccinellid pupae in different microhabitats and to better understand if the observed pattern results from a search for enemy-free space (Berdegue et al. 1996, Hopkins and Dixon 1997). For instance, pupae located off the plants may be attacked by ground predators like carabid beetles (Winder 1990). Prepupating larvae are not as resource dependent as younger instars because alate imagos emerging from the pupa have a much greater capacity to disperse and find resources than larvae. Finally, prospection risks are lower for fourth-instar coccinellids than for younger instars. Large larvae are more mobile, stronger, and less vulnerable to predation than younger larvae (Sengonca and Frings 1985; Lucas et al. 1997, 1998).

Other factors, aside from intraguild predation, may influence the selection of a pupating site away from the host plant. Pupal parasitism by *Phalacrotophora* sp. (Diptera: Phoridae) of the coccinellid *Harmonia axyridis* Pallas occurred more intensely on plants infested by aphids than in other pupation sites (Osawa 1992). Similarly, the level of pupal cannibalism was higher close to the aphid colony. Extraguild predation may also induce the search for a protected pupation site. Some species of caterpillars select pupation sites based on their related vulnerability to predation (West and Hazel 1982, Hazel et al. 1998). The search for microclimatic conditions that reduce the duration of pupation, and thereby the period of exposure to natural enemies, can also affect site selection, as hypothesized for mummies of aphid parasitoids (Hymenoptera: Aphididae) Brodeur and McNeil 1992).

The simultaneous occurrence of various defensive strategies is common among animals (Edmunds 1974), and for instance, several defenses used against predators are not efficient against parasitoids (Gross 1993). In addition to the predator-avoidance strategy, *C. maculata* pupae may also reduce mortality as a result of natural enemies through flipping behavior, "gin-traps" (sclerotized toothed along junctions of movable abdominal segments; Eisner and Eisner 1992, Hinton 1955), warning coloration (Majerus 1994), and the synthesis of toxic alkaloids (Blum 1981).

The data reported here suggest that vulnerable stages, such as holometabolous pupae that are exposed for a long period and unable to flee, may chiefly adopt a primary defensive response (occurring regardless of predator presence); whereas, stages exposed for a short period, such as most insect molting larvae, may modify their response according to their immediate environment (refuge, presence of predators, and so on). Although it was not possible to evaluate the predation risk off the plant, based on several studies (parasitism and cannibalism, Osawa 1992; numerical response, Frazer 1988; area-restricted searching, Dixon 1959; absence of predation activity off the plant by chrysopids, M. Canard, personal communication), we can expect that the risk was lower off the plant than close to the extraguild prey. Therefore, we can conclude that the search for enemy free space by prepupating larvae could be the main defensive strategy of pupae.

ing pupae.

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