Recognition of oviposition-deterring allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae)

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Abstract. Females of Coccinella septempunctata L. were deterred from ovipositing at sites previously exposed to larvae of C. septempunctata or Chrysopa oculata Say. If aphidophagous predators can respond to one another's deterring allomone then they may avoid competing for prey. The deterrent effect from exposure to C. septempunctata or C. oculata larvae considerably decreased when contaminated sites were kept in open air for 24 h. Females of C. oculata avoided ovipositing at sites exposed to larvae of C. oculata, but the deterrent effect of sites exposed to larvae of C. septempunctata was negligible.

INTRODUCTION

Larvae of Chrysopa oculata Say and Chrysopa perla L. periodically mark the substrate with an oviposition-deterring allomone (ODA) which they secrete from the tip of their abdomen (Růžička, 1994, 1996). The ODA of C. oculata is chemically stable and although volatile, it actively deters females for several weeks (Růžička, 1997a). Wax filaments produced by the larvae deter oviposition of conspecific females in the coccidophagous coccinellid Cryptolaemus montrouzieri Mulsant (Merlin et al., 1996). This paper reports on the presence and persistence of an ODA in one of the most common aphidophagous coccinellid species, Coccinella septempunctata L., and on the response of ovipositing adults of C. oculata and C. septempunctata to one another's ODAs.

MATERIAL AND METHODS

Experiments were conducted on *Chrysopa oculata* Say from a laboratory culture reared for nine years from adults collected in Kentville, Nova Scotia, Canada and on P, F1 and F2 generations of *C. septempunctata* collected at Raná, near Louny, Czech Republic. The experiments were performed at $24 \pm 2^{\circ}$ C and a photoperiod of 18L:6D. The light source was white-light fluorescent tubes.

Oviposition choice tests with adults

The tests were carried out in cylindrical cages 18 cm in diameter and 10 cm high, in which 10 females were offered a surplus of aphids, *Acyrthosiphon pisum* Harris, and drinking water. In tests with *C. oculata*, liquid yeast hydrolysate with sucrose (Růžička, 1997b) was also supplied. Each test was repeated ten times.

In experiments on C, oculata, oviposition sites consisted of 4 dark blue paper squares (each 50×50 mm), 2 of which were contaminated with ODA and 2 of which were clean. The squares were symmetrically spaced 10 mm apart and attached to the top of the cage (Fig. 1A).

In experiments on *C. septempunctata*, oviposition sites consisted of 2 white paper strips placed 50 mm apart at the bottom of the cage. Each strip was 20 cm long by 4 cm wide and was transversally folded every 10 mm in order to provide suitable place for oviposition on the underside (Fig 1B).

Contamination of sites by larvae

In experiments on females of *C. oculata*, each paper square was exposed to either 10 first-instar larvae of *C. oculata* or 10 first-instar (or 10 second-instar) larvae of *C. septempunctata* for 4 h. A single square was placed on the bottom of a glass Petri dish, 9 cm in diameter, the inner wall of which was painted with Fluon to prevent escape of the larvae. Oviposition sites contaminated by conspecific or heterospecific larvae were used immediately.

In experiments on females of *C. septempunctata*, two "folded" paper strips were exposed to either 40 first-instar larvae of *C. oculata* or 40 first-instar (or 40 second-instar) larvae of *C. septempunctata* for 4 h. The stripes were placed on the bottom of a glass Petri dish, 18 cm diameter, the inner wall of which was painted with Fluon. Oviposition sites contaminated by conspecific or heterospecific larvae were used immediately or later, after 24 h exposure in open air.

Statistical analysis: Differences in numbers of eggs (%) laid on contaminated and uncontaminated sites in choice tests were analysed by Student's t-test.

RESULTS

Females of *C. oculata* laid eggs both on paper ovipositional sites and the walls of cages, whereas *C. septempunctata* laid egg batches almost exclusively on the undersides of folded papers.

The proportion of eggs laid by females of C. oculata on ovipositional sites contaminated by conspecific first-instar larvae was considerably lower than that on clean ovipositional sites (Fig. 2A). The difference was statistically significant (P < 0.0001). The proportions of eggs laid on ovipositional sites contaminated by first- or second-instar larvae of C. septempunctata were similar to those on clean sites. The difference was statistically significant (P < 0.001) for first-instar larvae. For second-instar larvae, the difference was not statistically significant at level $\alpha = 0.01$ (P = 0.207).

The proportion of eggs laid by females of *C. septempunctata* on sites recently contaminated by conspecific larvae was considerably lower than on clean sites (Fig. 2B). The dif-

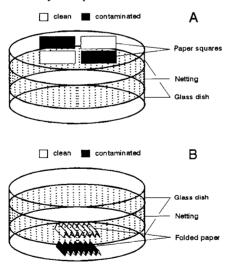
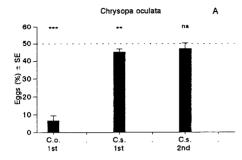


Fig. 1. Design of oviposition arena: A – used for experiments on C. oculata, and B – for C. septempunctata.

ference was statistically significant for both first- and second-instar larvae (P < 0.0001). After 24 h in the open air, contaminated sites deterred females from ovipositing considerably less. The difference was statistically significant for second-instar larvae (P < 0.0001) but it was not statistically significant at level $\alpha = 0.01$ (P = 0.019) for first-instar larvae. Females of C. septempunctata laid a significantly lower proportion of eggs on sites contaminated by larvae of C. oculata than on clean sites. The difference between contaminated sites provided for oviposition with no delay and clean sites was statistically significant (P < 0.0001). The proportion of eggs laid by females on contaminated sites kept for 24 h in open air was similar to that laid on clean sites. The difference was not statistically significant at level $\alpha = 0.01$ (P = 0.052).



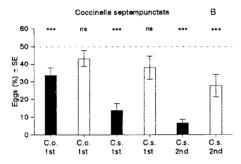


Fig. 2. Oviposition of *Chrysopa oculata* (A) and *Coccinella septempunctata* (B) on contaminated sites when given a choice between clean and contaminated sites. The latter were contaminated by conspecific or heterospecific first- and second-instar larvae and used immediately (black bars) or after a delay of 24 h (clear bars). Student's t-test: ns at 0.01 < P, ** at P < 0.001, *** at P < 0.0001. Each trial type n = 10.

DISCUSSION

As in chrysopids, the larvae of *C. septem-punctata* also secrete an ODA, which they apparently deposit on surfaces while searching for prey. Females of *C. septempunctata* were deterred from ovipositing at sites contaminated by first- and second-instar conspecific larvae. The secretion of an ODA might be a common phenomenon in aphid feeding coccinellids.

It has already been demonstrated in two congeneric chrysopid species, *C. oculata* and *C. perla*, that females respond similarly to ODAs of conspecific and heterospecific larvae (Růžička, 1996). Results here indicate that *C. septempunctata* females are able to recognize and respond to the ODA of the aphid feeding larvae of a species from another taxonomic order. Interestingly, the geographical distributions of *C. oculata* and *C. septempunctata* have only recently overlapped (Schaefer & Dysart, 1988).

Females of *C. oculata* responded similarly to sites contaminated by conspecific larvae immediately before testing and those kept for several days after the contamination in open air. Also one hour exposure of contaminated paper to high temperature of up to 140°C did not decrease the deterrent effect. Nevertheless, the ODA of chrysopid larvae

is volatile, as a clean site became contaminated when kept with a contaminated site in a closed container (Růžička, 1997a).

In contrast, here the responses of *C. septempunctata* females were considerably stronger to sites used immediately after contamination with ODA of *C. oculata* larvae than to those kept for 24 h in the open air before use. Similarly, the deterrent effects of sites contaminated with ODA of *C. septempunctata* first and second-instar larvae on conspecific females decreased significantly already after 24 h in open air at room temperature.

The response of *C. oculata* females to ODA of *C. septempunctata* is negligible. Differences between responses of chrysopid and coccinellid females to conspecific and heterospecific ODAs indicate that ODAs of larvae of these two predators differ. Stronger response to ODA of heterospecific larvae in *C. septempunctata* than in *C. oculata* females is in accordance with higher vulnerability of coccinellid larvae in potential competition (Sengonça & Frings, 1985).

Defence liquid of a predatory insect is sometimes a very complex mixture of irritant compounds (Eisner et al., 1996). Also ODAs of predatory species are likely to be mixtures

of deterrent compounds. Differences between response of *C. oculata* and *C. septempunctata* females (Fig. 2A) may also indicate that they respond with different intensity to particular compound(s) in larval ODAs.

The aphids were abundant both on clean and ODA contaminated sites of oviposition arena. This indicates that aphid colonies contaminated with a particular predator's ODA in the field may not be utilized for oviposition by visiting females of another species of predators. This would space out the various aphidophaga among prey patches and reduce the probability that larvae would have to search for another aphid colony in order to complete development. Not only can larval cannibalism be reduced by females responding to conspecific larval secretion, but also interspecific competition between very different predators can be reduced by responding to heterospecific larval secretions. Females of less aggressive or more specialized predator species, by responding to the ODAs of other predators, may avoid exposing their larval progeny to attack by more aggressive, less-specialized larvae of other predator species.

In both predatory species tested here, the deterrent effect of conspecific larval secretion was considerably stronger than that of heterospecific secretion.

In conclusion, results here show that females of *C. septempunctata* are deterred from ovipositing at sites contaminated with the secretion of conspecific larvae and/or larvae of *C. oculata*. Deterrent effects of conspecific secretion proved stronger than that of heterospecific secretion. In *C. septempunctata* females deterrent effects of sites with the ODAs considerably decreased after 24 h. Females of *C. oculata* were deterred by conspecific secretion, but laid only slightly less eggs on sites contaminated with ODA of *C. septempunctata* larvae.

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