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Further evidence of oviposition-deterring allomone in chrysopids (Neuroptera: Chrysopidae)

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Abstract. Females of species predatory as adults, *Chrysopa commata* Kis & Ujhelyi, *C. oculata* Say and *C. perla* (L.), and also species not predatory as adults, *Chrysoperla carnea* (Stephens), laid more eggs on clean substrates, than on those exposed previously to conspecific or heterospecific first-instar larvae. Substrates contaminated with oviposition-deterring allomones (ODAs) deterred females of *C. oculata* most. On the average the deterrent effects of substrates contaminated by larvae of *C. oculata* or *C. perla* were greater than those contaminated by *C. carnea* or *C. commata*. Results indicate that both intra- and interspecific responses to ODA occur in chrysopids and may enable them to distribute their larvae more uniformly between prey patches.

INTRODUCTION

Larvae of a eurytopic Nearctic species *Chrysopa oculata* Say (Neuroptera: Chrysopidae) mark substrates they walk over with an oviposition-deterring pheromone (ODP), which they secrete from the tip of their abdomen (Růžička, 1994). The ODP of this species and another eurytopic Palaearctic species, *Chrysopa perla* (L.), deter the females of both these species from ovipositing. *C. oculata* females show the stronger response to secretion of larvae of both species, but the intra- and interspecific responses are similar in each species (Růžička, 1996). Adults of these two chrysopids feed on aphids. The ODP of *C. oculata* is chemically stable as 1 h exposure to 140°C does not decrease its deterrent effect on conspecific females. Paper enclosed for several hours above glass walked on by unfed first instar larvae became contaminated with ODP. Although the ODP of *C. oculata* is volatile, it can retain its effectiveness even if kept in open air, at room temperature for several weeks (Růžička, 1997a).

Deterrent effect of larval secretion on females of other species should be considered as an oviposition-deterring allomone (ODA). The term allomone was proposed for a semiochemical that is adaptively favourable to the emitter, but not to the receiver, when it contacts an individual of another species (Nordlund & Lewis, 1976; Nordlund, 1981).

This study reports the presence of ODA in two other chrysopids, a European species, *Chrysopa commata* Kis & Ujhelyi, which is associated with low vegetation (Zelený, 1969) and a eurytopic cosmopolitan species, *Chrysoperla carnea* (Stephens) (Chrysopidae) sensu lato (Thierry et al., 1996). The adults of the latter species are not predatory. The 16 intra- and interspecific responses to ODA shown by the four chrysopid species, *C. carnea*, *C. commata*, *C. oculata* and *C. perla* are also reported.

MATERIAL AND METHODS

Adults of *C. commata*, *C. oculata* and *C. perla* were from laboratory stock cultures, and those of *C. carnea* were collected at hibernation sites in the spring. The *C. oculata* were originally collected in Kentville, Nova Scotia, Canada in 1987, *C. perla* in České Budějovice in 1992, *C. commata* in Velký Osek in 1993 and *C. carnea* in Prague in 1996 and 1997. In the laboratory larvae were reared on the pea aphid, *Acyrthosiphon pisum* Harris (Homoptera: Aphididae) and adults were supplied with a liquid yeast hydrolysate diet (Růžička, 1997b), drinking water and aphids (*A. pisum*) except for *C. carnea*, which was not supplied with aphids.

The duration of each test was 4 h and consisted of offering 10 females of a species clean or ODA-contaminated blue paper substrate on which to oviposit. The oviposition arena consisted of two contaminated and two clean squares of paper, each 50 x 50 mm. They were spaced symmetrically 10 mm apart and fixed to the underside of the glass top of 100 mm high nylon cylindrical cage, 18 cm in diameter (details in: Růžička, 1997c). Prior to a test, each "contaminated" square was exposed to 10 unfed first instar larvae of a particular species on the bottom of a 9 cm glass Petri dish, for 4 h. Each test was repeated 10 times. The response of females of each species to clean substrates and those contaminated by conspecific and heterospecific larvae were compared. The control oviposition arena consisted of four clean paper squares.

Statistical analysis: differences in numbers of eggs (%) laid per contaminated and uncontaminated substrates in choice tests were analysed by Student's t-test (arcsin transformation). Differences in numbers of eggs laid by females on substrates contaminated by larvae of different species were analysed by ANOVA followed by SNK multiple comparison test (arcsin transformation). Similarly, the test was used to analyse differences in numbers of eggs laid by females of different species to contaminated substrates.

RESULTS

Females of all four species laid eggs on the test substrates as well as on the walls of the cages. In each species, proportions of eggs laid on two pairs of substrates in the control were similar (Fig. 1). The total numbers of eggs laid varied with the species, with the highest by *C. oculata*, and the lowest by *C. carnea*.

In each species, the proportion of eggs laid on substrates contaminated by larvae of all four species was lower than on clean substrates (Fig. 1). The average response of females was more marked to substrates contaminated by larvae of *C. oculata* or *C. perla* than to those contaminated by *C. carnea* or *C. commata* (Table 1A). On average the response of the females to contaminated substrates was strongest in *C. oculata*. The average response of *C. carnea* and *C. commata* females were lower and did not differ. The average response to contaminated substrates was lowest for females of *C. perla* (Table 1B).

TABLE 1. (A) Average oviposition by females of all four species on substrates contaminated by larvae in choice tests. (B) Average deterrent effect on females of substrates contaminated by larvae of all four species in choice tests.

A			B		
Larvae	Eggs (%) per contaminated substrates		Females	Eggs (%) per contaminated substrates	
	Mean ± SE	*		Mean ± SE	*
C. oculata	25.1 ± 2.0	a	*C. oculata*	25.6 ± 2.3	a
C. perla	24.6 ± 2.0	a	*C. carnea*	32.9 ± 2.0	b
C. carnea	35.5 ± 2.0	b	*C. commata*	36.5 ± 2.1	b
C. commata	35.6 ± 1.9	b	*C. perla*	42.2 ± 1.3	c

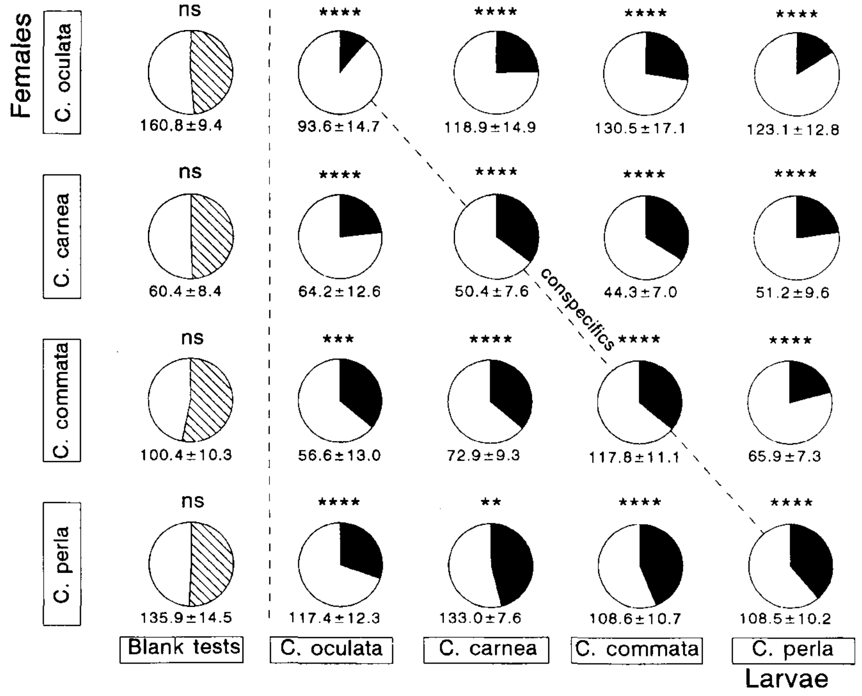

Fig. 1. Pie diagrams indicating the percentage of eggs laid by *Chrysopa* and *Chrysoperla* spp. on clean (white and striped sectors) and larval contaminated (black sectors) substrates in choice tests. Student's t-test: P > 0.05 ns, 0.001 < P < 0.01 **, 0.0001 < P < 0.001 ***, P < 0.0001 ****. Mean ± SE total number of eggs laid per test is given below each diagram.

The variation in the total numbers of eggs (Fig. 1) laid in the four choice tests was not significantly greater than expected by chance (ANOVA) for *C. oculata*: (P = 0.3431), *C. carnea*: (P = 0.5119) and *C. perla*: (P = 0.3060), but was significantly greater for *C. commata*: (P < 0.001).

DISCUSSION

Deterrent effects of substrates contaminated with the ODA of *C. oculata*, or *C. perla*, on oviposition by females of four species were generally stronger than those contaminated by larvae of *C. carnea* or *C. commata*. This may be due to different amounts of ODA being secreted, and/or different frequency of marking by the abdominal tip, or different kinds of ODA. The first instar larvae of *C. perla* and also those of *C. oculata* are slightly larger than those of *C. carnea* and *C. commata*. Differences in the size or mobility of unfed first instar larvae may result in different degrees of substrate contamination.

Substrates contaminated by conspecific larvae did not deter females from ovipositing more than substrates contaminated by larvae of the other chrysopid species. Although the strongest response was shown by *C. oculata* to substrates contaminated by conspecific larvae, the deterrent effects of substrates contaminated by conspecific larvae in *C. carnea*, *C. commata* and *C. perla* were relatively weak.

There was very little difference between the average response of eurytopic *C. carnea* and *C. commata*, which are associated with herbaceous plants and grasses. The response of *C. carnea* was weaker than that of eurytopic *C. oculata* but stronger than that of eurytopic *C. perla*. There is no indication of a relationship between habitat preference and their response to ODA.

C. carnea and *C. commata* are similar in size. The similar average response of the non-predatory females of *C. carnea* and the predatory females of *C. commata* to contaminated substrates indicates that adult diet does not influence the degree of a female's response to ODAs. For the cosmopolitan species *C. carnea*, however, it might be interesting to compare the intensity of response of individuals from geographically different populations.

The average response to ODA was lowest in *C. perla*, the largest of the four species, and that with the longest egg stalks. In addition to ODA, egg stalks also protect eggs and newly hatched larvae of *C. oculata* from cannibalism by conspecific adults and first instar larvae (Duelli & Johnson, 1992; Růžička, 1997b).

Females of the three species: the cosmopolitan *C. carnea*, the European *C. commata* and the Palaearctic *C. perla*, responded to the ODAs of the other species less than the Nearctic *C. oculata*. In contrast with all other chrysopid species, *C. oculata* frequently lays its eggs in short rows with the distance between eggs usually only a few milimetres. A relationship may exist between whether chrysopids lay eggs singly or in rows and their response to ODA. A strong response to conspecific larval ODA occurs also in the coccinellid *Coccinella septempunctata*, which lays its eggs in large batches (Růžička, 1997c).

Comparison of these results with those of a former study on *C. oculata* and *C. perla* (Růžička, 1996), reveals no change in the level of response to ODA even though 2 years have expired (corresponding to approximately 20 generations in the laboratory). Similarly, the percentages of eggs laid on the two substrates, one of which was contaminated by conspecific larvae, by *C. oculata* in these experiments did not differ from those laid in the previous study ($P = 0.9471$), but there was a small difference in the case of *C. perla* ($P = 0.0407$). In addition, interspecific responses to ODA by these two species were also similar ($P = 0.3422$ for *C. oculata* and $P = 0.9438$ for *C. perla* females).

While in the former study tests were performed with 50–200 females, equal numbers of males present in 0.06 m^3 cube cages with an oviposition arena consisting of 5 contaminated and 10 clean paper squares (50 × 50 mm), the current tests involved 10 females without males, in 0.0023 m^3 cylindrical cages, ovipositing in an arena of 2 contaminated and 2 clean paper squares of equal size. Both gave similar results, therefore, these designs are equally suitable for studying ODA in chrysopids.

In summary, ODAs are secreted by the larvae of 4 species of chrysopids independently of whether the adults are predatory or not. Intra- and interspecific responses to larval ODA(s) possibly promote a more even distribution of the pre-imaginal stages of these predators between patches of prey in the field.

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