Eur. J. Entomol. **91**: 361–370, 1994
ISSN 1210–5759

Oviposition-deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae)

ZDENĚK RŮŽIČKA

Institute of Entomology, Czech Academy of Sciences, Branišovská 31,
370 05 České Budějovice, Czech Republic

***Chrysopa oculata*, predator dispersion, oviposition spacing, oviposition pheromone**

Abstract. Larvae of *Chrysopa oculata* Say mark, chemically, the substrate with a substance secreted from the tip of their abdomen. The effect of paper substrates contaminated with this secretion on the oviposition of *C. oculata* females was assessed in laboratory choice experiments. The active substance(s) were soluble in chloroform and in water but not in methanol, ethylether or petroleum ether. Paper substrates treated with extracts of the substance remained active at room temperature for up to three weeks. The effectiveness, in terms of the amount of active secretion produced per unit of larval body weight, was greater for first rather than for third instar larvae. These results indicate the presence of a chemical factor or pheromone that serves to deter females of *C. oculata* from ovipositing near where larvae of this species are already present.

INTRODUCTION

Insect orientation and communication by means of pheromones is a very sophisticated system. Most recent investigations have concentrated on agricultural, forest and store product pests. Substances with pheromone activity have been used for sampling, mass trapping and for mating disruption in pest species (Ridgway et al., 1990). In addition to studies on attractants, attention has also been paid to pheromones that act as repellents. For example, females of certain species of phytophagous insects, whose larvae develop inside fruit, secrete a pheromone that deters conspecific females from ovipositing on the same fruit. Pheromones marking previously-occupied food sources have been studied thoroughly in tephritid flies (Prokopy, 1972, 1981). Furthermore, females of Lepidoptera, such as *Pieris brassicae*, mark egg batches and the host-plant with a spacing pheromone (Rothschild & Schoonhoven, 1977).

Pheromonal communication in predatory insects has been little studied in comparison with phytophagous, social and parasitoid species (Kerkut & Gilbert, 1985). Predatory insects often leave an area after encountering another conspecific individual (Hassell et al., 1976). Laboratory trials with *Adalia bipunctata* indicate that the presence of larvae can retard oviposition dramatically (Hemptinne & Dixon, 1991, Hemptinne et al., 1992). The inhibition of oviposition is correlated positively with the number of larvae also in *Cryptolaemus montrouzieri* (Lemaitre, 1992). These effects were not associated with the presence of repellent pheromones. Larvae of *Coccinella septempunctata* are, generally, thought to be unable to recognize and avoid searching the areas previously visited by other conspecific larvae. However, a larva was reported to recognize its own marker, secreted from its anal disc, and avoid the areas examined earlier (Marks, 1977). Despite of several attempts, this observation has not been confirmed (Ferran & Dixon, 1993).

The Nearctic golden-eyed lacewing, *Chrysopa oculata* Say, is one of the most common chrysopids in the mid-western United States and Canada. This common species occurs on trees as well as on field crops. Both larval and adult stages of *C. oculata* feed on a number of aphid species as well as on other insects and mites (Greve, 1984; New, 1984). Females lay eggs singly, placing most on the lower surface of a horizontal structure.

While developing techniques for the mass-rearing of *C. oculata*, it was observed that the presence of hatched eggs in the rearing cages deterred adults from ovipositing much more than the presence of unhatched eggs. Assessment of this effect and its mode of action are described in this paper.

MATERIAL AND METHODS

The experiments were performed on laboratory-reared *C. oculata*, collected in Kentville, Nova Scotia, Canada in 1987. Adult chrysopids were fed on the pea aphid, *Acyrthosiphon pisum* Harris, a liquid yeast hydrolysate diet with sucrose and drinking water.

The oviposition choice experiments were made in 40 × 40 × 40 cm nylon net-covered cages, with 200–400 adults of *C. oculata* per cage. The experiments were conducted at room temperature (21–26 °C), 40 ± 10% relative humidity. The experimental cages were illuminated by two 40W, white light fluorescent tubes, 1 and 1.3 m to the side and 0.4 m above the oviposition substrate. The light regime was maintained constantly at 16L : 8D. The oviposition assays consisted of 15 squares of dark blue paper, 50 × 50 mm each, evenly spaced in five rows. They were fixed to the underside of a 207 × 295 mm plastic sheet of orange-brown colour, held in a horizontal position 25 cm above the bottom of the cage. There was sufficient plastic material around each paper square to prevent a female present on one square from depositing eggs on a neighbouring square (Fig. 1). One of the shorter sides of the plastic sheet was in contact with the nylon wall nearest and parallel with the lateral light source. The adults reached the oviposition substrate either from the wall, or they climbed up the six 3 mm thick steel sticks which held the oviposition substrate in position. The number of eggs deposited on each paper square was determined at intervals of 20 hr. The number of eggs laid on each of the 15 clean paper squares in the control experiment was assessed at five observations.

Selection of an oviposition substrate by the females was studied in choice experiments. Substrates 1, 2 and 3, each in five replicates, were randomly placed in a 5 × 3 pattern using Latin square design as indicated in Fig. 1.

In order to identify the source of the oviposition-deterring effect the following experiments were performed:

Experiment A
- 1 – substrate from which hatched eggs of *C. oculata* (32–47/sq, $\bar{x}$ = 42) were removed 6 days after eclosion
- 2 – clean substrate
- 3 – substrate with hatched eggs of *C. oculata* (49–75/sq, $\bar{x}$ = 60) 6 days after eclosion

Experiment B
- 1 – clean substrate
- 2 – substrate with hatched eggs of *C. oculata* (43–49/sq, $\bar{x}$ = 46) 6 days after eclosion
- 3 – substrate from which hatched eggs of *C. oculata* (31–50/sq, $\bar{x}$ = 42) were removed 6 day after eclosion

Experiment C
- 1 – substrate from which unhatched eggs of *C. oculata* (80–110/sq, $\bar{x}$ = 98) were removed 1 day after oviposition
- 2 – clean substrate
- 3 – substrate with unhatched eggs of *C. oculata* (50/sq) 2 days after oviposition

Experiment D
- 1 – substrate from which unhatched eggs of *C. oculata* (49–113/sq, $\bar{x}$ = 71) were removed 2 days after oviposition

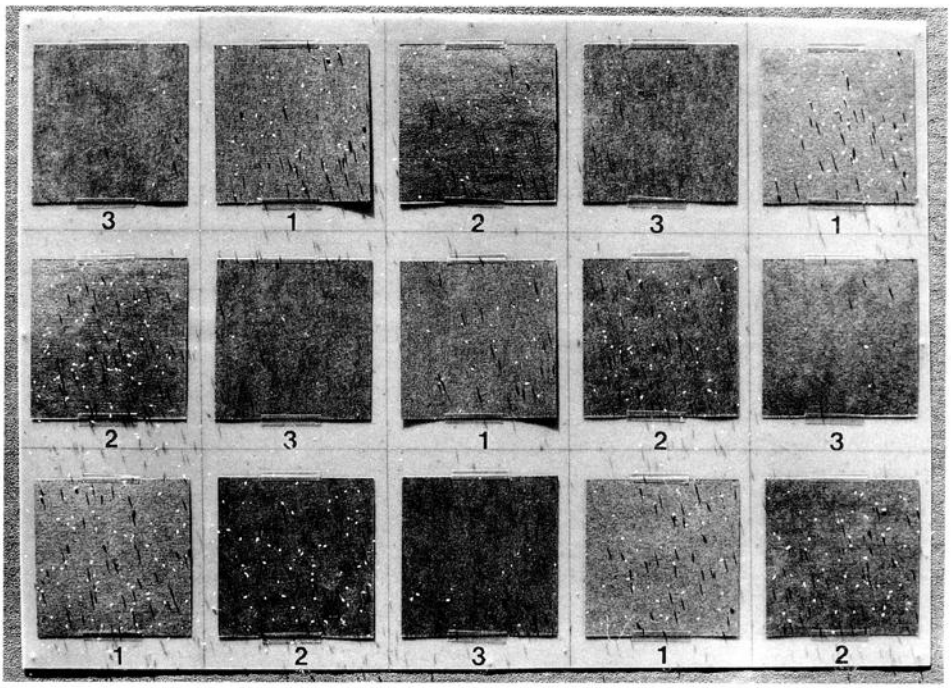

Fig. 1. Location of substrates 1, 2 and 3 on the plastic sheet. (A photograph of the distribution of the eggs laid by *C. oculata* in experiment O. Substrates 3 were sprayed with a chloroform extract of the pheromone.)

2 – substrate with unhatched eggs of *C. oculata* (58–77/sq, $\bar{x} = 66$) 2 days after oviposition
3 – clean substrate

Experiment E

1 – substrate from which hatched eggs of *C. oculata* (40–78/sq, $\bar{x} = 57$) were removed 2 days after eclosion
2 – substrate with fresh tracks of first instar larvae of *C. oculata* (10 larvae/sq)
3 – clean substrate

Experiment F

1 – clean substrate
2 – clean substrate
3 – substrate with fresh tracks of first instar larvae of *C. oculata* (10 larvae/sq)

Experiment G

1 – clean substrate
2 – substrate with fresh tracks of first instar larvae of *C. oculata* (10 larvae/sq)
3 – clean substrate

In experiments which used hatched eggs, paper squares with eggs were placed in Petri dishes. Three days after these eggs hatched, the squares with empty egg shells, or from which these had been removed, were offered in choice experiments. Eggs and pedicels were removed from the paper squares with the aid of a pair of fine steel forceps and a magnifying glass. First instar larvae given no food rarely survived in the Petri dishes for more than three days.

In experiments which used unhatched eggs, a fine pencil circle was drawn on the paper substrate around the pedicel of each egg. This enabled the identification of those eggs that were laid during the course of the experiment.

In order to obtain fresh "tracks" of larvae, larvae of *C. oculata* were transferred for 4 hours to a 9 cm diameter Petri dish, with a Fluon-painted inner wall and a square of paper on the bottom. First instars larvae were not fed before placing them in the Petri dish.

The following experiment was performed to assess whether older larvae could produce the oviposition-deterring substance(s) and to determine the place of the secretion:

Experiment H

1 – clean substrate

2 – substrate with 5 droplets/sq of abdominal secretion from third instar larvae of *C. oculata* (one droplet in each corner and the centre)

3 – substrate with fresh tracks of third instar larvae of *C. oculata* (3 larvae/sq)

In order to obtain paper contaminated with the anal secretion, a third instar larva was held with a pair of fine forceps, and the tip of its abdomen was brought into contact with the substrate. Droplets of secretion produced by the larvae were soaked up by the paper. Third instar larvae were fed on *A. pisum*. The average weight of first instar larvae was 0.16 ± 0.07 mg and of third instar larvae 17.4 ± 0.75 mg.

Various solvents of the active substance(s) were tested in the following experiments: Experiment I – ethylether, experiment J – methylalcohol, experiment K – petroleum ether, experiment L – chloroform (all solvents were of p.a. purity), experiment M and N – distilled water.

Experiments I–L

1 – clean substrate

2 – substrate sprayed with one of the solvents (1ml/5 sq)

3 – substrate sprayed with the solvent extract of first instar larvae of *C. oculata* (1ml/5sq)

Experiments M–N (performed 24 hrs after application)

1 – clean substrate

2 – substrate sprayed with water (1ml/5 sq)

3 – substrate sprayed with water extract of first instar larvae of *C. oculata* (1ml/sq)

In order to obtain extracts of first instar larvae, the larvae were anaesthetised with CO_2 and then placed on a plug of cotton wool in the spout of a glass funnel. The larvae were then rinsed briefly in 2.5 ml of solvent (10–30 sec).

To assess whether the substance retained its activity for several days, the following substrates were offered to females on the day of the treatment and then again after removal of eggs on 3, 9 and 19 days thereafter:

Experiment O

1 – clean substrate

2 – substrate sprayed with chloroform (1ml/5 sq)

3 – substrate sprayed with chloroform extract of glass walked over by larvae of *C. oculata* (1ml/5sq)

In order to obtain relatively uncontaminated pheromone for these experiments, 100 first instar larvae of *C. oculata* were placed in a 70 ml glass Erlenmayer flask. After four hours the larvae were anaesthetised with CO_2 and removed. The inner surface of the empty flask was rinsed briefly with 2.5 ml of the solvent.

Statistical analysis. Differences between numbers of eggs laid on substrates 1, 2 and 3 were analysed by ANOVA followed by SNK multiple comparisons test after log (x + 1) transformation.

RESULTS

C. oculata laid a similar number of eggs on each of the 15 clean paper substrates in the control experiment (Fig. 2). The differences in numbers of eggs laid on squares in positions 1, 2, and 3 were not statistically significant. There were no statistically significant interactions between days and positions. The number of eggs laid was dependent on the number of insects present in the cage, and the substrate treatment

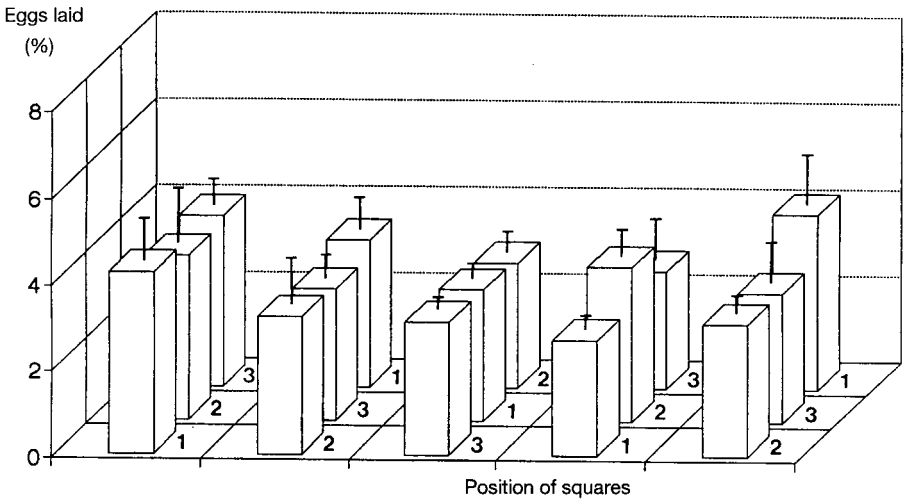

Fig. 2. Mean number (± SD) of eggs laid by females of *C. oculata* on each of the 15 clean substrates. (Means from five individual experiments. Total number of eggs laid on all 15 squares in each experiment = 100 %.)

provided. The lowest number of eggs laid on the 15 squares over a 20 hr period was 264, the highest 1545 eggs.

The females laid eggs, almost exclusively, on the clean substrate when this was offered simultaneously with substrates bearing hatched eggs and ones from which hatched eggs had been removed (Fig. 3 A and B, respectively). Differences between the numbers of eggs laid on the clean substrate and each of the two other substrates were statistically significant ($P < 0.01$). Similarly, females laid eggs mostly on the clean substrate when simultaneously offered substrates with unhatched eggs and previously cleaned from unhatched eggs, although differences were now considerably smaller (Fig. 3 C and D, respectively). Differences between the numbers of eggs laid on the clean substrate and the substrate previously cleaned from unhatched eggs were not statistically significant. A comparison of the results of experiments A and B with C and D indicate the existence of an effective oviposition deterring-pheromone on the substrates which had previously born hatched eggs.

Fewer eggs were laid on the substrate that was exposed to unfed first instar larvae of *C. oculata* prior to the test (Fig. 3 E). The repellent effect of this substrate is similar to that of the substrate from which the egg shells had been removed two days after hatching. The differences were statistically significant ($P < 0.01$).

A very strong repellent effect of the substrate marked with larval pheromone was also demonstrated in the following two experiments (Fig. 3 F, G). The difference was statistically significant ($P < 0.01$).

Ovipositing females of *C. oculata* showed little difference in their response to the substrate contaminated with droplets of the abdominal secretion of third instar larvae or previously walked on by third instar larvae (Fig. 3H). The difference was statistically

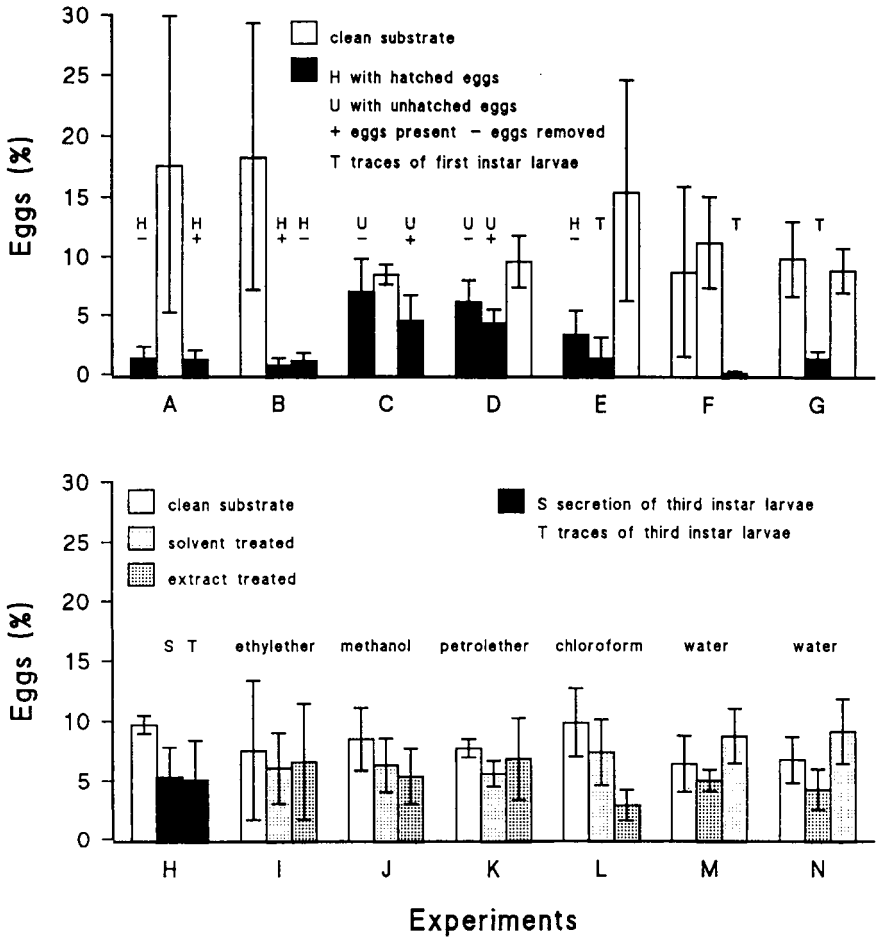

Fig. 3. Mean number (± SD) of eggs laid by females of *C. oculata* per square of substrates 1, 2 and 3 in experiments A–N. The sequence of columns in each experiment corresponds to the numerical order of substrates in Latin square design.

significant ($P < 0.05$) but much lower in comparison with substrates contaminated by first instar larvae. While ten first instar larvae left no visible stains on the paper substrate, three third instar larvae stained the substrate extensively with a brownish abdominal secretion. The third instar larvae were, on average, more than 100 times heavier than first instar larvae.

The oviposition-deterring substance(s) were not soluble in ethylether, methylalcohol and petroleum ether, (Fig. 3I,J and K) but were soluble in chloroform and water (Fig. 3L,M and N).

In the four replicates of experiment O (Fig. 4) the number of eggs laid on substrates treated with the solvent did not differ statistically ($P < 0.05$) from the number laid on clean

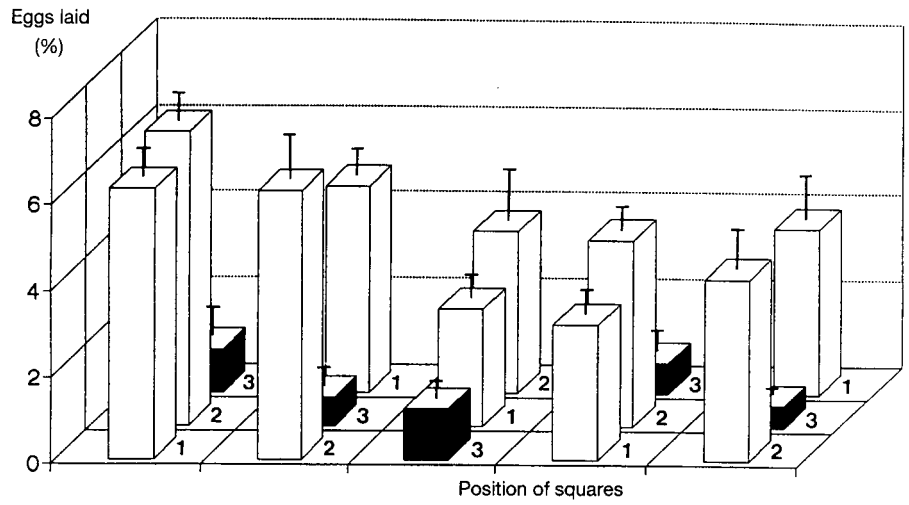

Fig. 4. Mean number (± SD) of eggs laid by females of *C. oculata* on the five clean substrates (1), the five substrates sprayed with chloroform (2), and the five substrates sprayed with the chloroform extract of the oviposition-deterring pheromone (3). (Means from four individual experiments. Total number of eggs laid on all 15 squares in each experiment = 100%.)

substrates. Females always laid significantly more eggs on these two substrates than on the substrate treated with the pheromone solution ($P < 0.001$).

DISCUSSION

Plant volatiles and semiochemicals in aphid honeydew are important cues for different kinds of aphid predators (for details see Evans & Dixon, 1986; Kesten, 1969; Meidari & Copland, 1992; Obata, 1986; Reid & Lampman, 1989). These compounds enable these predators to locate their prey, on which they feed, predominantly, in the larval and, sometimes, imaginal stages. Since adult chrysopids are most active at twilight or during the night (Duelli, 1984a), chemical orientation in these insects may be more important. Their positive response to chemical stimuli of plant origin (Flint et al., 1979) and to the scent of honeydew of a number of homopteran species (Ickert, 1968; Hagen et al., 1976) has been described. While honeydew feeders tend to oviposit near places where this food is present, species with predatory adults are more specific (Duelli, 1984b). Orientation to chemicals has also been described in larvae of these predators. Kairomones associated with lepidopteran scales or a hexane extract of these scales stimulate searching for prey, e.g. in larvae of *Chrysoperla carnea* (Lewis et al., 1977; Nordlund et al., 1977).

The results presented here suggest that *C. oculata* females, by responding to the pheromone left by larvae, can avoid laying eggs in areas either already occupied or previously searched by larvae. In such a case their progeny would have a low probability of finding prey. An oviposition-deterring pheromone would decrease cannibalism of eggs by chrysopid larvae and competition between conspecific larvae. This might account for the rare incidence of cannibalism in the field (Canard & Duelli, 1984).

Parasitoids also use different types of pheromone marking to reduce the incidence of superparasitism. The capability of insect parasitoids to discriminate between parasitized and non-parasitized hosts has been known for a long time (Salt, 1934). Host marking is especially important for parasitoids of mobile hosts (Vinson, 1985). Females of the aphid parasitoid *Ephedrus cerasicola* can, through antennal contact, discriminate between parasitized and non-parasitized aphids (Hofsvang & Hagvar, 1986). Females of the aphid hyperparasitoid *Alloxysta victrix* are repelled by the odour of conspecifics. The active chemical is produced by both virgin and mated females of this species and is attractive to males. This spacing pheromone elicits a dispersal response in hyperparasitoids and presumably makes biological control of aphids by primary parasitoids less effective (Micha et al., 1993). Females of several pupal parasitoids avoid searching in areas previously visited by conspecifics or females of related species (Price, 1970). The evolution of egg spacing behaviour in chrysopids is complex and has some similarity to territorial marking in mammalian predators.

The secretions of adult chrysopids, which offer them protection against certain predators, e.g. ants, contains scatole and tridecene (Blum et al., 1973). Protective substances are also employed by the larvae, which in *Chrysopa californica* Coq. curve their abdomen towards a predator and release a droplet of a repellent liquid from the anus, which can paralyse some antagonists, including congeneric species (Kennett, 1948). A similar defense mechanism is also used by larvae of *C. oculata*.

The results presented show that an oviposition-deterring substance was present in the tracks of unfed first instar larvae and third instar larvae of *C. oculata*. Relatively more of the pheromone was produced by first instar larvae than late third instar larvae. This accords with the best strategy of females searching for safe oviposition sites, since larvae at the end of their development are unlikely to be present when their eggs begin to hatch. The anal secretion of chrysopid larvae also contained the pheromone. The source of pheromone has not been identified. It is possible that it is produced somewhere on or near the abdominal tip. A secretion from the apex of the abdomen enables larvae to adhere to smooth surfaces (Spiegler, 1962). It is possible that the oviposition-deterring pheromone is present in this secretion.

Oviposition-deterring pheromones produced by larvae are not unknown in insects. The mandibular glands of larvae of *Ephestia kuehniella* produce an oviposition-deterring pheromone, which is released on encountering conspecifics (Corbet, 1971). The pheromone acts as a repellent at high concentrations and stimulates oviposition at low concentrations (Corbet, 1973). Further experiments with single chrysopid larvae are needed to assess whether the pheromone is released continuously or only on encountering other conspecific larvae and whether the quantity of pheromone secreted is influenced by the nature and frequency of encounters.

Phytophagous insects are likely to fly away if they repeatedly encounter an oviposition-deterring pheromone (Prokopy, 1981). Such a response in chrysopids would reduce the number of eggs laid on plants where chrysopid larvae are already present. This would enhance the chance of the larvae completing their pre-imaginal development. Since the pheromone may result in a more even dispersal of chrysopids in nature, it might play an important role in their life cycle strategies. Any tendency of females to disperse from areas of high predator population density would seriously counter the attempts to enhance

artificially chrysopid populations in the field. A search for similar oviposition-deterring pheromones in other species of chrysopids and other insect predators should be examined further and, finally, the possibility of employing the spacing pheromones in the mass rearing of chrysopids should be explored.

In conclusion, these results indicate that a repellent substance produced by chrysopid larvae can affect the selection of oviposition sites by the females of these predators. This is the first instance in which the existence of an oviposition-deterring pheromone has been described for a predatory insect.

ACKNOWLEDGEMENTS. I would like to thank K. Sláma for helpful suggestions and P. Kindlmann, I. Dostálková and J. Šula for statistical analyses and drawing the graphs. I am grateful to A.F.G. Dixon, C. Löfstedt and A.K. Minks for reading and comments on the manuscript.

REFERENCES

BLUM M.S., WALLACE J.B. & FALES H.M. 1973: Skatole and tridecene: Identification and possible role in a chrysopid secretion. *Insect Biochem.* **3**: 353–357.

CANARD M. & DUELLI P. 1984: Predatory behavior of larvae and cannibalism. In Canard M., Séméria Y. & New T.R. (eds): *Biology of Chrysopidae.* W. Junk, The Hague, pp. 92–100.

CORBET S.A. 1971: Mandibular gland secretion of larvae of the flour moth, Anagasta kuehniella, contains an epideictic pheromone and elicits oviposition movements in a hymenopteran parasite. *Nature* **232**: 481–484.

CORBET S.A. 1973: Oviposition pheromone in larval mandibular glands of Ephestia kuehniella. *Nature* **243**: 537–538.

DUELLI P. 1984a: Flight, dispersal, migration. In Canard M., Séméria Y. & New T.R. (eds): *Biology of Chrysopidae.* W. Junk, The Hague, pp. 110–116.

DUELLI P. 1984b: Oviposition. In Canard M., Séméria Y. & New T.R. (eds): *Biology of Chrysopidae.* W. Junk, The Hague, pp. 129–133.

EVANS E.W. & DIXON A.F.G. 1986: Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *J. Anim. Ecol.* **55**: 1027–1034.

FERRAN A. & DIXON A.F.G. 1993: Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *Eur. J. Entomol.* **90**: 383–402.

FLINT H.M., SALTER S.S. & WALTERS S. 1979: Caryophyllene: an attractant for the green lacewing. *Environ. Entomol.* **8**: 1123–1125.

GREVE L. 1984: Chrysopid distribution in northern latitudes. In Canard M., Séméria Y. & New T.R. (eds): *Biology of Chrysopidae.* W. Junk, The Hague, pp. 180–186.

HAGEN K.S., GREANY P., SAWALL E.F. & TASSAN R.L. 1976: Tryptophan in artificial honeydew as a source of an attractant for adult Chrysopa carnea. *Environ. Entomol.* **5**: 458–468.

HASSELL M.P., LAWTON J.H. & BEDDINGTON J.R. 1976: The components of arthropods predation. I. The prey death-rate. *J. Anim. Ecol.* **45**: 135–164.

HEMPTINNE J.-L., DIXON A.F.G. 1991: Why ladybirds have generally been so ineffective in biological control? In Polgár L., Chambers R.J., Dixon A.F.G. & Hodek I. (eds): *Behaviour and Impact of Aphidophaga.* SPB Academic Publishing, The Hague, pp. 149–157.

HEMPTINNE J.-L., DIXON A.F.G. & COFFIN J. 1992: Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* **90**: 238–245.

HOFSVANG T. & HAGVAR E.B. 1986: Oviposition behaviour of Ephedrus cerasicola (Hym. Aphidiidae) parasitizing different instars of its aphid host. *Entomophaga* **31**: 261–267.

ICKERT G. 1968: Beiträge zur Biologie einheimischer Chrysopiden (Planipennia, Chrysopidae). *Entomol. Abh. Mus. Tierk. Dresden* **36**: 123–192.

KENNETT C.E. 1948: Defense mechanism exhibited by larvae of Chrysopa californica Coq. (Neuroptera, Chrysopidae). *Pan-Pacif. Entomol.* **24**: 209–211.

KERKUT G.A. & GILBERT L.I (eds). 1985: *Comprehensive Insect Physiology Biochemistry and Pharmacology. Vol. 9. Behavior.* Pergamon Press, Oxford, 735 pp.

KESTEN U. 1969: Zur Morphologie and Biologie of Anatis ocellata (Col., Coccinellidae). *Z. Angew. Entomol.* **63**: 412–436.

LEMAITRE O. 1992: *Stimulation et Régulation de la Ponte de la Coccinelle Coccidiphage Cryptolaemus montrouzieri Mulsant.* Mémoire de Licence, Université libre de Bruxelles, 70 pp.

LEWIS W.J., JONES R.L., GROSS H.R. & HAGEN K.S. 1977: Kairomones and their use for management of entomophagous insects. VI. An examination of the kairomones for the predator of Chrysopa carnea Stephens at the oviposition sites of Heliothis zea (Boddie). *J. Chem. Ecol.* **3**: 507–511.

MARKS R.J. 1977: Laboratory studies of plant searching behaviour by Coccinella septempunctata L. larvae. *Bull. Entomol. Res.* **67**: 235–241.

MEIDARI M. & COPLAND M.J.W. 1992: Host finding by Cryptolaemus montrouzieri (Col., Cocinellidae) a predator of mealybugs (Hom., Pseudococcidae). *Entomophaga* **37**: 621–625.

MICHA S.G., STAMMEL J. & HOLLER C. 1993: 6-methyl-5-heptene-2-one, a putative sex and spacing pheromone of the aphid hyperparasitoid, Alloxysta victrix (Hymenoptera: Alloxystidae). *Eur. J. Entomol.* **90**: 439–442.

NEW T.R 1984: Chrysopidae: Ecology on field crops. In Canard M., Séméria Y. & New T.R. (eds): *Biology of Chrysopidae.* W. Junk, The Hague, pp. 160–167.

NORDLUND D.A., LEWIS W.J., JONES R.L., GROSS H.R. & HAGEN K.S. 1977: Kairomones and their use for management of entomophagous insects. 6. An examination of the kairomones for the predator Chrysopa carnea Steph. at the oviposition sites of Heliothis zea (Boddie). *J. Chem. Ecol.* **3**: 507–511.

OBATA S. 1986: Mechanisms of prey finding in the aphidophagous ladybird beetle, Harmonia axyridis (Col.: Coccinellidae). *Entomophaga* **31**: 303–311.

PRICE P.W. 1970: Trail odors: recognition by insects parasitic on cocoons. *Science* **179**: 546–547.

PROKOPY R.J. 1972: Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. *Environ. Entomol.* **1**: 326–332.

PROKOPY R.J. 1981: Epideictic pheromones that influence spacing patterns of phytophagous insects. In Nordlund D.A., Jones R.L. & Lewis W.J. (eds): *Semiochemicals.* John Willey & Sons, New York, pp. 181–213.

REID C.D. & LAMPMAN R.L. 1989: Olfactory responses of Orius insidiosus (Hemiptera, Anthocoridae) to volatiles of corn silk. *J. Chem. Ecol.* **15**: 1109–1115.

RIDGWAY R.L., SILVERSTEIN R.M. & INSCOE M.N. 1990: *Behavior Modifying Chemicals for Insect Pest Management: Applications of Pheromones and Other Attractants.* Dekker, New York, 761 pp.

ROTHSCHILD M. & SCHOONHOVEN L. 1977: Assessment of egg load by Pieris brassicae. *Nature* **266**: 352–355.

SALT G. 1934: Experimental studies in insect parasitism. II Superparasitism. *Proc. R. Soc. Lond. (Ser. B)* **114**: 455–476.

SPIEGLER P.E. 1962: The origin and the nature of the adhesive substance in larvae of the genus Chrysopa (Neuroptera, Chrysopidae). *Ann. Entomol. Soc. Am.* **55**: 69–77.

VINSON S.B. 1985: 9. Behaviour of parasitoids. In Kerkut G.A. & Gilbert L.I. (eds): *Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol. 9. Behavior.* Pergamon Press, Oxford, pp. 417–469.

Received February 24, 1994; accepted July 13, 1994