Eur. J. Entomol. **100**: 345–350, 2003
ISSN 1210-5759

Perception of oviposition-deterring larval tracks in aphidophagous coccinellids *Cycloneda limbifer* and *Ceratomegilla undecimnotata* (Coleoptera: Coccinellidae)

Zdeněk RŮŽIČKA

Institute of Entomology, Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic; e-mail: ruzicka@entu.cas.cz

Key words. Oviposition-deterring semiochemicals, pheromone, larval tracks, aphidophagous coccinellids, *Cycloneda limbifer*, *Ceratomegilla undecimnotata*, *Leis dimidiata*, sense organs, perception, chemoreceptors, antennae, maxillary palpi, egg clusters, batches, oviposition strategy

Abstract. The ability of the aphidophagous coccinellids *Cycloneda limbifer* Casey and *Ceratomegilla undecimnotata* (Schneider) to discriminate between simultaneously provided clean paper strips and paper strips with oviposition-deterring larval tracks was studied after the ablation of different sense organs. Females oviposited similar numbers of eggs on paper strips with conspecific tracks and on clean paper strips only when deprived of both maxillary palpi. *C. undecimnotata* without maxillary palpi also did not differentiate between clean paper strips and paper strips with tracks of the coccinellid *Leis dimidiata* (F.). If both antennae and one maxillary palpus were simultaneously ablated, females of both species laid significantly more eggs on clean than contaminated paper strips. The results of this study indicate that females use contact chemoreceptors on maxillary palpi exclusively to detect oviposition deterring tracks of conspecific larvae.

Intact females of *C. limbifer* laid significantly larger batches of eggs on paper strips with conspecific larval tracks, than on clean paper strips in blank test. In contrast, intact females of *C. undecimnotata* laid significantly smaller batches on paper strips with conspecific tracks than on clean paper strips in blank test. This is the first evidence of an opposite effect of conspecific oviposition deterring larval tracks on egg clustering in aphidophagous coccinellids.

INTRODUCTION

Females of different phytophagous and parasitoid insects perceive oviposition deterring semiochemicals of conspecifics (ODS) through various kinds of sense organs. Contact and olfactory chemoreceptors on these organs serve for the detection of semiochemicals of varying chemical natures and physical properties. Non-specialised tarsal and antennal receptors of *Pieris brassicae* (L.) and *Pieris rapae* (L.) (Lepidoptera, Pieridae) perceive ODS, which contain both nonvolatile and volatile components (Schoonhoven, 1990). In addition, females of *P. brassicae* also perceived oviposition deterring pheromones via abdominal contact chemoreceptors (Klijustra & Roesingh, 1986). *Rhagoletis cerasi* (L.) (Diptera, Tephritidae) females detected the relatively stable oviposition-deterring pheromones of conspecific females (Hurter et al., 1976), by contact chemoreceptors on their tarsi (Städler et al., 1994). While females of *Ceutorhynchus assimilis* Payk. (Coleoptera, Curculionidae) sensed oviposition-deterring pheromones of conspecific females primarily via contact gustatory chemoreceptors on the antennae (Ferguson et al., 1999), *Monochamus alternatus* Hope (Coleoptera, Cerambycidae) perceived oviposition- deterring secretions of conspecific females by maxillary and labial palpi (Anbutsu & Togashi, 2000, 2001). Besides frequent antennal perception, parasitoids also detected spacing pheromones through sensillae on the ovipositor (Van Lenteren, 1972).

The location of various receptors on sense organs has been studied in many species of aphidophagous coccinellids. In *Coccinella septempunctata* L., chemoreceptors were described on the labial and maxillary palpi (Yan et al., 1982, 1987). In *Ceratomegilla undecimnotata* (Schneider), gustatory and mechanosensitive sensilla organs were reported along the entire length of the antennae, while olfactory sensillae were confined to two terminal segments of the antennae (Jourdan et al., 1995). On the maxillary palpi of aphidophagous coccinellids, olfactory chemoreceptors were more numerous than gustatory ones. The total number of both was always higher in polyphagous than in oligophagous or monophagous species, the numbers being even lower in coccidophagous coccinellids, which feed on immobile prey (Barbier et al., 1989, 1996). In addition, some mechanoreceptors were also described on the palpi. Obata (1986) suggested that the aphidophagous coccinellid *Harmonia axyridis* (Pallas) used olfactory stimuli to locate sites with aphids for the first time. Adult *C. septempunctata* respond to aphid alarm pheromone via olfactory cells (Al Abassi et al., 2000). This species was attracted to aphid odours in olfactometer trials and even differentiated between volatiles of different aphid species (Sengonca & Liu, 1994). Aphid released volatiles also attracted adults of *Hippodamia convergens* Guérin-Méneville (Acar et al., 2001), but adults without antennae or antennal tips did not respond to volatile cues (Hamilton et al., 1999).

Females of different aphidophagous coccinellids effectively avoided ovipositing on sites with tracks of conspecific larvae, *C. septempunctata* L. (Růžička, 1997b), *Adalia bipunctata* (L.) (Doumbia et al., 1998), *H. axyridis* (Yasuda et al., 2000), *C. undecimnotata*, *C. limbifer*

(Růžička, 2001), however, the sense organs through which coccinellid females detected oviposition-deterring semiochemicals were not defined.

Laboratory experiments showed that a volatile oviposition-deterring substance, which evaporated from larval tracks of the aphidophagous chrysopid *Chrysopa oculata* Say within a few days, can contaminate clean substrates. In contrast, sites with tracks of larvae preserved their deterrent effects on females for much longer time (Růžička, 1997a). Intraspecific oviposition-deterring effects of tracks of first instars of the coccinellid *C. septempunctata* disappeared after one day (Růžička, 1997b), whereas tracks of some other coccinellid species effectively deterred females from oviposition for many days (Růžička, 2002). However, unpublished results of laboratory experiments indicated the absence of a volatile spacing cue in the tracks of their larvae. Females of some coccinellids also avoided oviposition on sites with tracks of heterospecific coccinellid larvae (Růžička, 2001).

Experiments in this study were designed to identify organs with chemoreceptors for the perception of oviposition-deterring semiochemicals in females of *C. limbifer* and *C. undecimnotata*. Both species avoided ovipositing on sites with larval tracks of some heterospecific coccinellids, but the effect of tracks of *L. dimidiata* larvae on *C. undecimnotata* was the most intense. The ability to differentiate between simultaneously provided clean and ODS contaminated sites was studied in laboratory experiments with females deprived of different sense organs.

MATERIAL AND METHODS

Experiments were done on *Cycloneda limbifer* Casey, *Ceratomegilla undecimnotata* (Schneider) and *Leis dimidiata* (F.), from laboratory cultures. The oviposition behaviour of normal females in choice tests with clean and contaminated sites was compared with the oviposition behaviour of females after the ablation of different sense organs. The ability of females to avoid sites with conspecific tracks was studied in experiments with *C. limbifer* and *C. undecimnotata*. In addition, the ability of *C. undecimnotata* females to discriminate between clean sites and sites with tracks of *L. dimidiata* larvae after these ablations was investigated. Transversely folded paper strips, one clean and one previously exposed to larvae, were provided for ovipositing simultaneously. Each strip was 20 cm long and 4 cm wide, the length of folded paper strip was 13 cm. Ten females without males were present in the test simultaneously. Each test was terminated after 20 hours and had ten replicates.

Ablation experiments. Two tests were made with intact females, a control choice test (0) with one clean and one contaminated substrate, and a blank oviposition test (BT) with two clean substrates. Oviposition in these tests was compared with oviposition of females deprived of different organs, which may detect any oviposition deterring semiochemicals. Prior to the ablation, each coccinellid female was carefully fixed with narrow strips of scotch tape to small piece of paper. All segments of amputated organ(s) were then removed under binocular glass by means of fine surgical instruments. Either one or both sense organs of one kind, or different combinations of these organs, were eliminated: one antenna (1a), both antennae (2a), one leg of the second pair (1l), one antenna and one maxillary palpus (1a1p), two antennae and one maxillary palpus (2a1p), two maxillary palpi (2p), one antenna and two maxillary palpi (1a2p), two antennae and two maxillary palpi (2a2p).

Contamination of substrates by larvae. Two folded paper strips were exposed to 40 unfed first-instar larvae of one species for four hours on the bottom of a glass Petri dish, 18 cm in diameter. The inner wall of the dish was painted with Fluon (Polytetrafluoroethylene (PTFE) Dispersion; Imperial Chemical Industries Limited, Plastics Division, Welwyn Garden City, Herts, UK), to prevent dispersal of larvae from the bottom. Contaminated paper strips were offered for egg laying immediately after their exposure to larvae.

Oviposition choice test. The design of choice tests was adopted from previous studies on aphidophagous coccinellids (Růžička, 1997b; 2001). The cylindrical experimental cage, with substrates, was 10 cm high, 18 cm in diameter. The side of the cage was made from firm netting, the bottom and the top was made from glass. Two folded paper strips, one clean and one previously exposed to larvae, were provided for oviposition to 10 females for 20 hours. Symmetrically spaced strips were on the bottom, 50 mm apart. Drinking water and a surplus of suitable aphid prey, *Aphis fabae* Scopoli for *C. limbifer* and *Acyrthosiphum pisum* Harris for *C. undecimnotata,* were available to females during the tests. *A. fabae* was offered on shoots of the host plants, *Vicia faba*, *A. pisum* without the host plant. Each test had ten replicates. Experiments were carried out at 24 ± 2°C with a 18L : 6D photoperiod, using light from fluorescent tubes.

Statistical analysis. Differences between numbers of eggs on two paper strips in each test were compared using the Wilcoxon paired sample test. The same test was used to compare differences between numbers of eggs on and outside paper strips. Size differences between clusters of eggs on contaminated paper strips in choice tests and on clean paper strips in blank test were compared using the Student's t-test.

RESULTS

Effects of ablations on female discrimination between clean and contaminated paper strips

Intact females of *C. limbifer* and *C. undecimnotata* laid similar numbers of eggs on two clean paper strips in blank tests with conspecific larvae ($P = 1$ and $P = 0.4316$), and *C. undecimnotata* in blank test with larvae of *L. dimidiata* ($P = 0.5566$). Intact females of both species effectively avoided oviposition on sites with larval tracks in the choice test with conspecific larvae ($P < 0.01$ and $P < 0.01$), and *C. undecimnotata* in the choice test with tracks of heterospecific larvae ($P < 0.01$) (Fig. 1).

Females of *C. limbifer* also laid significantly lower numbers of eggs on paper strips with tracks of conspecific larvae than on clean paper strips after the ablation of one antenna ($P < 0.05$), both antennae ($P < 0.05$), one leg of the second pair ($P < 0.01$), one palpus maxillaris and one antenna ($P < 0.01$), one palpus maxillaris and both antennae ($P < 0.01$), or one palpus maxillaris ($P < 0.05$). Females without both maxillary palpi laid similar numbers of eggs on clean and contaminated paper strips ($P > 0.9999$), and also when one and both antennae were simultaneously ablated with maxillary palpi ($P = 0.1484$ and $P = 0.8438$) (Fig. 1).

Similarly, *C. undecimnotata* laid lower numbers of eggs on sites with the tracks of conspecific larvae (P-value in

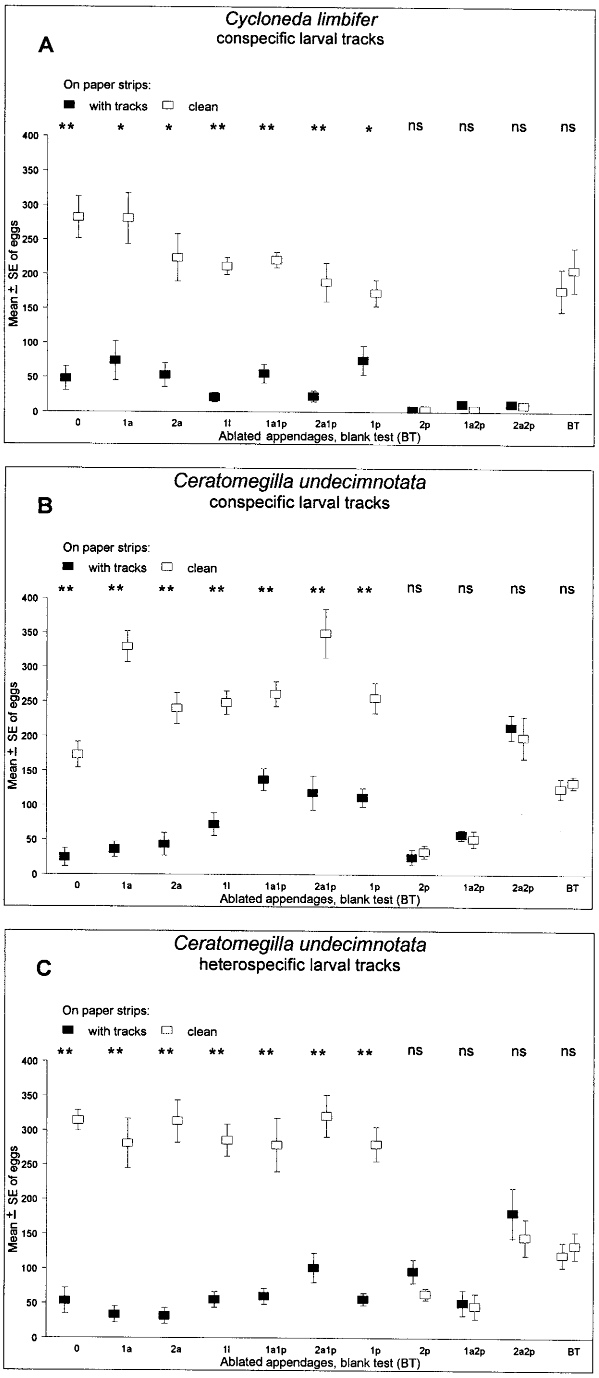


Fig. 1. Oviposition of coccinellid females on clean and contaminated paper strips in choice tests with tracks of conspecific larvae of *Cycloneda limbifer* (A), *Ceratomegilla undecimnotata* (B) and oviposition of *C. undecimnotata* in choice test with tracks of *Leis dimidiata* larvae (C). Choice tests with intact females (0), females without: one antenna (1a), both antennae (2a), one leg of the second pair (1l), one antenna and one maxillary palpus (1a1p), both antennae and one maxillary palpus (2a1p), one maxillary palpus (1p), both maxillary palpi (2p), one antenna and both maxillary palpi (1a2p) both antennae and both maxillary palpi (2a2p), and blank test with intact females (BT). Wilcoxon paired sample test, ** = P < 0.01; * = P < 0.05; ns = not significantly different (P ≥ 0.05).

parenthesis) or larvae of *L. dimidiata* (P-value in brackets), than on clean sites after the ablation of one antenna (P < 0.01) [P < 0.01], both antennae (P < 0.01) [P < 0.01], one leg of the second pair (P < 0.01) [P < 0.01], one maxillary palpus and one antenna (P < 0.01) [P < 0.01], one maxillary palpus and both antennae (P<0.01) [P < 0.01], or one maxillary palpus (P < 0.01) [P < 0.01], but laid similar numbers of eggs on both sites after the ablation of both maxillary palpi (P = 0.5566) [P = 0.1602], and when maxillary palpi with one antenna (P = 0.5566) [P = 0.3594], or both antennae (P = 0.8457) [P = 0.2324] were simultaneously ablated (Fig. 1).

Effects of ablations on oviposition outside paper strips

Coccinellid females avoided oviposition outside paper strips in the control and blank tests with conspecific and heterospecific larvae (P < 0.01 for each test control and blank test) (Fig. 2). Females of *C. limbifer* without maxillary palpi, or without maxillary palpi and one antenna, or maxillary palpi and both antennae, laid more eggs outside paper strips than on paper strips (P = 0.01 for each test). *C. undecimnotata* laid more eggs outside paper strips than on strips in tests with conspecific and heterospecific larval tracks when maxillary palpi (P < 0.01) [P < 0.01], or maxillary palpi and one antenna were ablated (P < 0.01) [P < 0.05], but females without maxillary palpi and both antennae laid their eggs almost exclusively on paper strips (P < 0.01) [P < 0.05] (Fig. 2).

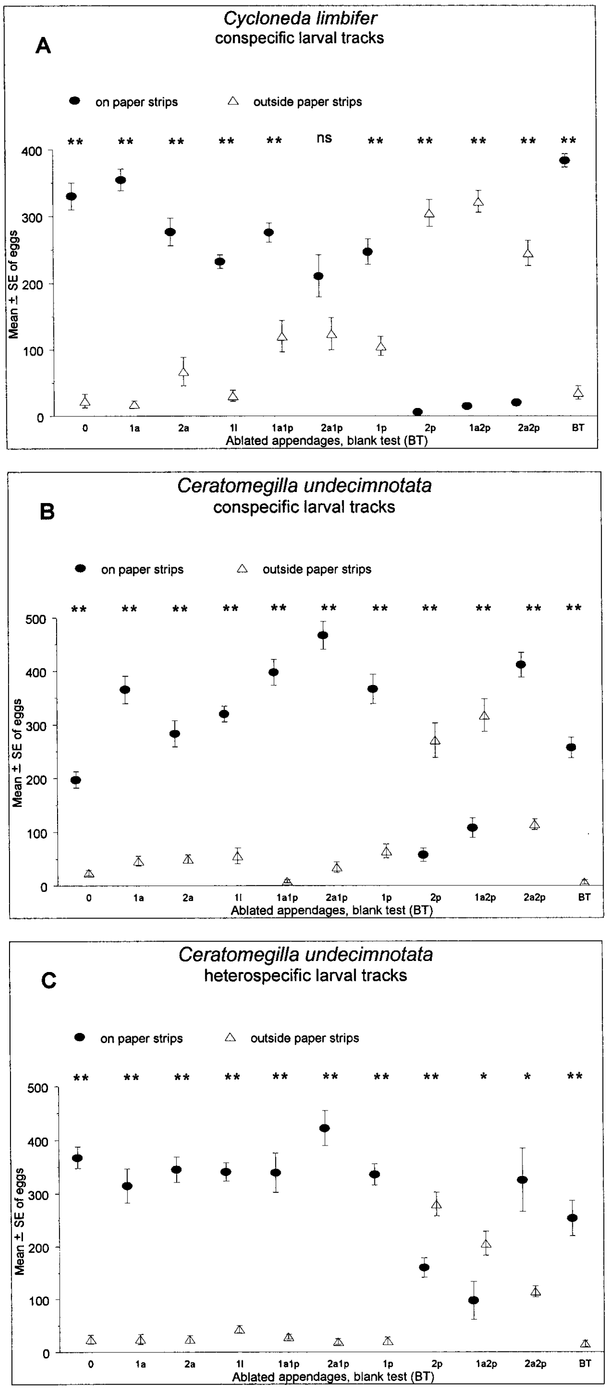
Effects of ablations on egg clustering

C. limbifer laid egg batches of similar size on the two clean paper strips in the blank test (P = 0.7994). In the control test, intact females of *C. limbifer* also laid batches of similar size on the clean and contaminated paper strips (P = 0.8229); however, the average cluster size on these paper strips was significantly larger than the average size of clusters on the paper strips in the blank test (P < 0.0001). Batches of eggs oviposited on contaminated paper strips were also larger than those laid on clean paper strips in the blank test when females were deprived of one antenna (P < 0.0001), both antennae (P < 0.0001), one palpus maxillaris (P < 0.0001), and one palpus maxillaris and both antennae simultaneously (P = 0.05).

C. undecimnotata also laid egg batches of similar size on the two clean paper strips in the blank tests in the experiments with conspecific and heterospecific larvae (P = 0.5156) [P = 0.2241]. However, *C. undecimnotata* females laid significantly smaller batches on paper strips with conspecific tracks in the control test than on clean paper strips in the blank test (P < 0.01). In the control test with larval tracks of *L. dimidiata,* the size of batches on the paper strips with tracks did not differ from the size of batches on clean paper strips in the blank test [P = 0.2041] (Fig. 3).

DISCUSSION

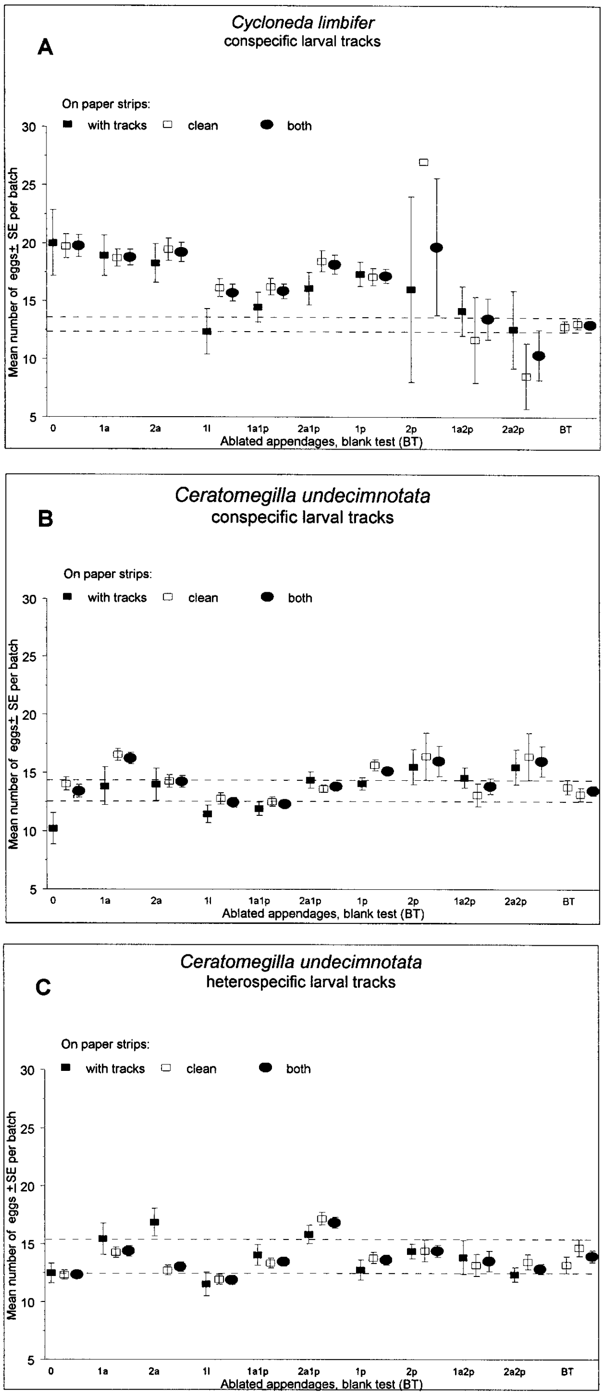
Coccinellid females are voracious and relatively mobile aphid predators. When searching for the prey and oviposition sites, they must frequently come across the oviposition deterring larval tracks of different competitors for the same prey species. Females are likely to detect these tracks through direct contact. This study showed that females of both coccinellid species, *C. limbifer* and *C.*


A *Cycloneda limbifer* conspecific larval tracks

B *Ceratomegilla undecimnotata* conspecific larval tracks

C *Ceratomegilla undecimnotata* heterospecific larval tracks

Fig. 2. Oviposition of coccinellid females on both paper strips (clean and contaminated) provided for oviposition and outside paper strips in choice tests with tracks of conspecific larvae of *Cycloneda limbifer* (A), *Ceratomegilla undecimnotata* (B) and oviposition of *C. undecimnotata* in choice test with tracks of *Leis dimidiata* larvae (C). Choice tests with intact females (0), females without: one antenna (1a), both antennae (2a), one leg of the second pair (1l), one antenna and one maxillary palpus (1a1p), both antennae and one maxillary palpus (2a1p), one maxillary palpus (1p), both maxillary palpi (2p), one antenna and both maxillary palpi (1a2p) both antennae and both maxillary palpi (2a2p), and blank test with intact females (BT). Wilcoxon paired sample test, ** = $P < 0.01$; * = $P < 0.05$; ns = not significantly different ($P \geq 0.05$).


A *Cycloneda limbifer* conspecific larval tracks

B *Ceratomegilla undecimnotata* conspecific larval tracks

C *Ceratomegilla undecimnotata* heterospecific larval tracks

Fig. 3. Size of egg batches on clean, contaminated and both (clean and contaminated) paper strips provided for oviposition in choice tests with tracks of conspecific larvae of *Cycloneda limbifer* (A), *Ceratomegilla undecimnotata* (B) and oviposition of *C. undecimnotata* in choice test with tracks of *Leis dimidiata* larvae (C). Choice tests with intact females (0), females without: one antenna (1a), both antennae (2a), one leg of the second pair (1l), one antenna and one maxillary palpus (1a1p), both antennae and one maxillary palpus (2a1p), one maxillary palpus (1p), both maxillary palpi (2p), one antenna and both maxillary palpi (1a2p) both antennae and both maxillary palpi (2a2p), and blank test with intact females (BT).

undecimnotata, effectively responded to oviposition-deterring tracks of conspecific larvae via their maxillary palpi. Without both maxillary palpi, females of each species were unable to discriminate clean paper strips from paper strips with oviposition-deterring larval tracks of conspecific larvae. After the ablation of maxillary palpi, *C. undecimnotata* females were unable to discriminate also between clean sites and sites with larval tracks of *L. dimidiata*. Females with one maxillary palpus effectively avoided oviposition on sites previously exposed to conspecific or heterospecific larvae. Both species successfully discriminated between clean and contaminated sites also when one maxillary palpus was ablated simultaneously with one or both antennae. This also indicated, that ablation injuries had generally small impact on female ability to avoid oviposition on the less suitable of two oviposition sites. Similarly, ablation of one leg of the second pair had little impact on the ability of females of both coccinellids to discriminate between sites with and without larval tracks.

Obata (1986, 1997) reported that adults of *Harmonia axyridis* (Pallas) used olfactory cues to find aphids. In *C. septempunctata*, Sengonca & Liu (1994) confirmed that coccinellid adults can be attracted by aphid odours. Zhu et al. (1999) recorded strong electroantennogram responses from antennae to a hexane extract of the volatile semiochemicals associated with the prey species and its host plant in *Coleomegilla maculata lengi* (Timberlake). Ablation of the antennae in adults showed that *H. convergens* perceives volatile semiochemicals associated with their prey through this organ (Hamilton et al., 1999). The contact perception of ODS by maxillary palpi alone in *C. limbifer* and *C. undecimnotata* could also explain why *A. bipunctata* did not inhibit their oviposition, when females were exposed to the odour of conspecific larvae, but had not access to the surface with larval tracks (Hemptinne et al., 1992).

Intact females of both species laid eggs mostly on the lower side of the clean paper strips provided for egg laying. Females with one maxillary palpus also strongly preferred oviposition on the paper substrate. *C. limbifer* laid almost all eggs outside the paper strips after the ablation of both maxillary palpi and when both palpi with one or both antennae were simultaneously removed. *C. undecimnotata* without maxillary palpi, or maxillary palpi and one antenna, preferred oviposition outside strips also, but laid a larger portion of eggs on paper strips than females of *C. limbifer*. In contrast to *C. limbifer*, *C. undecimnotata* laid most eggs on the paper strips than outside when both palpi and both antennae were ablated. Current knowledge does not explain why females changed their usual preference for paper strips, after the ablation of both maxillary palpi in three choice tests with *C. limbifer*, and in two out of three tests with *C. undecimnotata*. This change of oviposition behaviour, and the difference between species, might be associated with the location of mechanoreceptors on the ablated sense organs.

Comparison of intra- and interspecific oviposition deterring effects of larval tracks in aphidophagous coccinellids (Růžička, 2001) indicated the occurrence of different semiochemicals, or different ratios of active compounds, in larval tracks of different species. Although females of *C. limbifer* effectively avoided oviposition on sites with conspecific larval tracks and *C. undecimnotata* larval tracks, fresh tracks of conspecific larvae had a strong attractant effect on their searching behaviour, while heterospecific tracks strongly deterred females from searching (Růžička & Zemek, in press). Because only intact females were used in this study, sense organs which perceived cues modifying searching behaviour of females were not identified.

Many predatory arthropods lay eggs in clusters. The clutch size in coccinellids was positively correlated with the number of ovarioles (Stewart et al., 1991). Within a coccinellid species, the size of cluster seemed to be directly related to aphid density (Agarwala & Bardhanroy, 1999). Egg clustering in mites can be an adaptation to counter attack by prey (Faraji et al., 2002), in coccinellids to interspecific predation (Agarwala & Dixon, 1993; Agarwala & Yasuda, 2001). This study revealed a strong opposite effect of conspecific larval tracks on egg cluster size in studied species. Females of *C. limbifer* with all sense organs also laid significantly larger batches on clean and contaminated paper strips in the control test than on clean paper strips in the blank test. Females with both maxillary palpi also laid larger batches in the choice tests than in the blank test when deprived of one or both antennae. Similar behaviour was observed in females with one maxillary palpus or females with one maxillary palpus and without antennae. The increase of clutch size on sites with conspecific tracks in *C. limbifer* might be related to attractant effects of conspecific tracks on female searching behaviour described in the previous paragraph (Růžička & Zemek, in press). In contrast, intact females of *C. undecimnotata* laid significantly smaller egg batches on the paper strips with conspecific tracks than on clean paper strips in the blank test. This difference between the oviposition behaviour of *C. limbifer* and *C. undecimnotata* females on sites with oviposition-deterring tracks of conspecific larvae and on clean sites indicates opposite kinds of adaptation of these coccinellid species to the presence of conspecific competitors. This is an interesting phenomenon in oviposition strategies of closely related predators. Presumably, both tactics can successfully enhance progeny survival.

This study showed that aphidophagous coccinellids *C. limbifer* and *C. undecimnotata* used exclusively contact chemoreceptors on maxillary palpi to detect oviposition-deterring tracks of conspecific and heterospecific larvae. It also disclosed that sites with deterrent conspecific tracks effectively stimulate females of *C. limbifer* to lay larger clusters of eggs, while *C. undecimnotata* females tend to lay smaller egg clusters on sites with conspecific tracks than on sites without tracks. The opposite response of females to the presence of larval competitors is a new element among adaptations in oviposition strategies of aphidophagous predators.

ACKNOWLEDGEMENTS. This research was supported by the grant of the Grant Agency of the Czech Republic, No. 206/00/0809, from the Entomology Institute project Z5007907 (Acad. Sci. CR) and the grant project S5007102 (Grant Agency Acad. Sci. CR). I thank M. Červenská and R. Guttwirthová for their assistance with experiments and cultures of insect.

REFERENCES

Acar E.B., Medina J.C., Lee M.L. & Booth G.M. 2001: Olfactory behaviour of convergent lady beetle (Coleoptera: Coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: Aphididae). *Can. Entomol.* **133**: 389–397.

Agarwala B.K. & Bardhanroy P. 1999: Numerical response of ladybird beetles Col., Coccinellidae) to aphid prey (Hom.: Aphididae) in a field bean in north-east India. *J. Appl. Entomol.* **123**: 401–405.

Agarwala B.K. & Dixon A.F.G. 1993: Why ladybirds lay eggs in clusters. *Funct. Ecol.* **7**: 541–548.

Agarwala B.K. & Yasuda H. 2001: Overlapping oviposition and chemical defense of eggs in co-occurring species of ladybird predators of aphids. *J. Ethology* **19**: 47–53.

Al Abassi S., Birkett M.A., Petterson J., Pickett J.A. Wadhams L.J. & Woodcock C.M. 2000: Response of the seven-spot ladybird to an alarm pheromone inhibitor mediated by paired olfactory cells. *J. Chem. Ecol.* **26**: 1765–1771.

Anbutsu H. & Togashi K. 2000: Deterred oviposition response of Monochamus alternatus (Coleoptera, Cerambycidae) to oviposition scars occupied by eggs. *Agric. Forest Entomol.* **2**: 217–223.

Anbutsu H. & Togashi K. 2001: Oviposition deterrent by female reproductive gland secretion in the Japanese pine sawyer, Monochamus alternatus. *J. Chem. Ecol.* **27**: 1151–1161.

Barbier R., Ferran A., LeLannic J. & Lesrat A. 1989: The fine structure and function of the sensory organs on the maxillary palps of adults ladybird Semiadalia undecimnotata Schn. (Coleoptera: Coccinellidae). *Bull. Soc. Zool. France. Evol. Zool.* **114**: 119–128.

Barbier R., LeLannic J. & Brun J. 1996: Sensory receptors of maxillary palps of adult aphidophagous, coccidophagous and phytophagous coccinellids. *Bull. Soc. Zool. France. Evol. Zool.* **121**: 255–268.

Doumbia M., Hemptinne J.-L. & Dixon A.F.G. 1998: Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* **113**: 197–202.

Faraji F., Janssen A. & Sabelis M.W. 2002: The benefit of clustering eggs: the role of egg predation and larval cannibalism in a predatory mite. *Oecologia* **131**: 20–26.

Ferguson A.W., Ziesmann J., Blight M.M., Williams I.H., Wadhams L.J., Clark S.J., Woodcock C.M. & Mudd A. 1999: Perception of oviposition deterring pheromone by cabbage weevil (Ceutorhynchus assimilis). *J. Chem. Ecol.* **25**: 1655–1670.

Hamilton R.M., Dogan E.B., Schaalje G.B. & Booth G.M. 1999: Olfactory response of the lady beetle Hippodamia convergens (Coleoptera: Coccinellidae) to prey related odours, including a scanning electron microscopy study of the antennal sensilla. *Envir. Entomol.* **28**: 812–822.

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.

Hurter J., Katsoyannos B., Bollor E.F. & Wirz P. 1976: Beitrag zur Anreicherung und teilweisen Reinigung der eiablageverhindernden Pheromons der Kirschenfliege, Rhagoletis cerasi L. (Dipt.: Trypetidae). *Z. Angew. Entomol.* **80**: 50–56.

Jourdan H., Barbier R., Bernard J. & Ferran A. 1995: Antennal sensilla and sexualdimorphism of the adult ladybird beetle Semiadalia undecimnotata Schn. (Coleoptera, Coccinellidae). *Int. J. Insect Morph. Embryol.* **24**: 307–322.

Klijustra J.W. & Roesingh P. 1986: Perception of the oviposition-deterring pheromone by tarsal and abdominal contact chemoreceptors in Pieris brassicae. *Entomol. Exp. Appl.* **40**: 71–79.

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

Obata S. 1997: The influence of aphids on the behaviour of adults of the ladybird beetle, Harmonia axyridis (Coleoptera: Coccinellidae). *Entomophaga* **42**: 103–106.

Růžička Z. 1997a: Persistence of the oviposition-deterring pheromone in Chrysopa oculata (Neur.: Chrysopidae). *Entomophaga* **42**: 109–114.

Růžička Z. 1997b: Recognition of oviposition-deterring allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *Eur. J. Entomol.* **94**: 431–434.

Růžička Z. 2001: Oviposition responses of aphidophagous coccinellids to tracks of coccinellid (Coccinellidae) and chrysopid (Chrysopidae) larvae. *Eur. J. Entomol.* **98**: 183–188.

Růžička Z. 2002: Persistence of deterrent larval tracks in Coccinella septempunctata, Cycloneda limbifer and Semiadalia undecimnotata (Coleoptera: Coccinellidae). *Eur. J. Entomol.* **99**: 471–475.

Růžička Z. & Zemek R. in press: Effects of conspecific and heterospecific larval tracks on mobility and searching patterns of Cycloneda limbifer females (Coleoptera: Coccinellidae). *Proc. 8th Int. Symp. on Ecology of Aphidophaga.* Kluwer Acad. Publ., The Netherlands.

Schoonhoven L.M. 1990: Host marking pheromones in Lepidoptera with special reference to two Pieris spp. *J. Chem. Ecol.* **16**: 3043–3052.

Sengonca C. & Liu B. 1994: Responses of the different instar predator, Coccinella septempunctata L. (Coleoptera: Coccinellidae), to the kairomone produced by the prey and non-prey insects as well as the predator itself. *Z. Pflkrankh. Pflschutz* **101**: 173–177.

Städler E., Ernst B., Hurter J. & Boller E. 1994: Tarsal contact chemoreceptor for the host marking pheromone of the cherry fruit fly, Rhagoletis cerasi: responses to natural and synthetic compounds. *Physiol. Entomol.* **19**: 139–151.

Stewart L.A., Dixon A.F.G., Růžička Z. & Iperti G. 1991: Clutch and egg size in ladybird beetles. *Entomophaga* **36**: 329–333.

Van Lenteren J.C. 1972: Contact chemoreceptors on the ovipositor of Pseudocoila bochei Weld (Cynipidae). *Neth. J. Zool.* **22**: 347–350.

Yan F.S., Qin J.D. & Xiang F.S. 1982: The fine structure of the chemoreceptors on the labial palps of Coccinella septempunctata. *Acta Entomol. Sinica* **25**: 135–140.

Yan F.S., Qin J.D. & Xiang X.F. 1987: The chemoreceptors on the maxillary palps of the adult lady bird beetle Coccinella septempunctata. *Acta Entomol. Sinica* **30**: 146–150.

Yasuda H., Takagi T. & Kogi K. 2000: Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird Harmonia axyridis (Coleoptera: Coccinellidae). *Eur. J. Entomol.* **97**: 551–553.

Zhu J., Cossé A. A., Obrycki J.J., Boo K.S. & Baker T.C. 1999: Olfactory reactions of the twelve-spotted lady beetle Coleomegilla maculata and the green lacewing, Chrysoperla carnea to semiochemical released from their prey and host plant: electroantennogram and behavioral responses. *J. Chem. Ecol.* **25**: 1163–1177.

Received January 27, 2003; revised April 9, 2003; accepted June 25, 2003