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Oviposition-deterring effects of conspecific and heterospecific larval tracks on *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae)

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Abstract. The oviposition deterring effects of fresh larval tracks of *Cheilomenes sexmaculata* (F.), *Ceratomegilla undecimnotata* (Schneider), *Cycloneda limbifer* Casey, and *Harmonia dimidiata* (F.) on *C. sexmaculata* females were compared in standard laboratory choice tests. Moreover, the persistence of intraspecific effects of *C. sexmaculata* larval tracks were investigated. Fresh tracks of *C. sexmaculata*, *C. limbifer* and *C. undecimnotata* larvae effectively deterred *C. sexmaculata* females from ovipositing. The effect of fresh larval tracks of *H. dimidiata* was not statistically significant. The oviposition-deterring effects of 10 d-old conspecific larval tracks were considerably lower than those of fresh tracks, but remained significant. Clutch sizes were smaller in the blank test without larval tracks than in choice tests with fresh tracks of conspecific, *C. limbifer*, *C. undecimnotata*, *H. dimidiata* larvae and with 10 d-old tracks of conspecific larvae. The study indicates that semiochemicals in the tracks of conspecific and heterospecific coccinellid larvae can contribute considerably to the spacing of *C. sexmaculata* offspring among prey resources of differing quality and that conspecific as well as heterospecific larval tracks can influence clutch size.

INTRODUCTION

Excessive oviposition in an aphid colony can lead to intense competition among coccinellid larvae. Cannibalism by conspecifics and intraguild predation by other species threaten eggs and larvae, especially when prey are scarce (Hodek, 1973 p. 129; Mills, 1982; Osawa, 1989; Agarwala, 1991). Hungry larvae also attack conspecific prepupae and pupae (Schellhorn & Andow, 1999). Hence, females should not lay eggs in aphid colonies with conspecific or heterospecific larvae as they endanger the successful development of their progeny. Selection should favour the use of mechanisms that effectively deter oviposition at sites where prey shortage is imminent, or where other coccinellids are foraging.

The data presented by Kuchlein (1966) for different aphidophagous predators showed that the density of predatory larvae often declined independently of prey density once the density of predators reached a certain level. Pschorn-Walcher & Zwölfer (1956) had also observed this apparently strange response in aphidophagous coccinellids, but the spacing effects of coccinellid semiochemicals remained obscure for many years.

Individual spacing based on semiochemical cues, independent of physical encounter, was first reported in aphidophagous chrysopids (Růžička, 1994). Females of *Chrysopa oculata* Say largely avoided ovipositing on substrates that have been previously traversed by conspecific first instars, and on substrates treated with a chloroform extract of the oviposition-deterring semiochemicals (ODS) deposited by larvae. Although *C. oculata* also laid fewer eggs on substrates previously exposed to gravid females, and on those from which unhatched eggs had been removed, their deterrent effects were much lower than the tracks of first instar larvae.

The tracks of larval conspecifics also deter oviposition by females of various aphidophagous coccinellids (Růžička, 1997b; Doumbia et al., 1998; Yasuda et al., 2000; Růžička, 2001a; Fréchette et al., 2003; Oliver et al., 2006). Similarly, oviposition-deterring effects of heterospecific larval tracks have been reported (Růžička, 2001a, b, 2003), and effects on the searching behaviour of females have been described (Růžička & Zemek, 2003; Oliver et al., 2006). If coccinellid females generally avoid ovipositing on sites with tracks of competing heterospecific larvae, semiochemicals could be even more important in mediating the between-patch distribution of various species. For example, females of the coccinellid *Harmonia axyridis* Pallas reduced rates of oviposition and feeding when exposed to faeces of conspecifics, but not in response to faeces of *Propylea japonica* Mulsant. In contrast, faeces of both species deterred *P. japonica* from ovipositing and feeding (Agarwala et al., 2003b).

Since site contamination with ODS increases with the density of larval tracks, it follows that the oviposition of chrysopids and coccinellids can be observed to decrease with increasing density of conspecific larval tracks (Růžička, 1997a; Oliver et al., 2006). Low prey density stimulated searching behaviour and increased the mobility of aphidophagous larvae. Coccinellid larvae search thoroughly the area surrounding the site of an aphid encounter (Banks, 1957). Thus, the density of the larval tracks increases with both the number of larvae present, and their satiation. It is evident that larval tracks are a potentially useful cue for females because they can be expected to correlate reliably with risks of intraguild predation and/or cannibalism of progeny.

Clutch size varies among coccinellid species (Stewart et al., 1991) and among individual females within species, depending on factors such as body size (Dixon & Guo, 1993), age (Smith, 1966), food abundance (Dixon & Guo, 1993; Agarwala & Bardhanroy, 1999), and last, but not least, on the presence of conspecific larval tracks (Růžička, 2003). In the field, a significant positive relationship was found also between the clutch size of *H. axyridis* and its distance from the nearest aphid colony. In the laboratory, clutch size was significantly affected by the oviposition time interval (Osawa, 2003).

This study was undertaken to increase our knowledge of the oviposition-deterring effects of conspecific and heterospecific larval tracks in the exotic aphidophagous coccinellid *Cheilomenes sexmaculata* F., a frequent predator of several aphid species in parts of Africa and tropical Asia (Jha et al., 1991; Bind & Bind, 1993; Sugiura & Takada, 1998; Agarwala & Bardhanroy, 1999; Ulrichs et al., 2001; Omkar, 2004). This species is an effective predator of *Aphis craccivora* Koch and *Myzus persicae* (Sulzer), being better adapted to feed on *A. craccivora* than several other coccinellids (Pervez & Omkar, 2005; Omkar et al., 2005). Agarwala et al. (2003a) showed that *C. sexmaculata* females reduced oviposition in the presence of immobilised conspecific or *Coccinella transversalis* F. larvae or adults, but not when larvae or adults of another coccinellid, *Scymnus pyrocheilus* Mulsant (Coleoptera: Coccinellidae), or larvae of the syrphid *Ischiodon scutellaris* (F.) (Diptera: Syrphidae) were present. Possible effects of conspecific and heterospecific tracks of larvae on the size of clutches laid by *C. sexmaculata* females were also investigated in the present study.

MATERIAL AND METHODS

Insects

Cheilomenes sexmaculata (F.) (from Arab Emirates), *Cycloneda limbifer* Casey (from Cuba), *Ceratomegilla undecimnotata* (Schneider) [= *Semiadalia undecimnotata* (Schneider)] (from North Bohemia, Czech Republic) and *Harmonia dimidiata* (F.) [= *Leis dimidiata* (F.)] (from south-eastern China) were reared for experiments in laboratory cultures. *C. sexmaculata* was reared prior to the tests in the laboratory for 2–5 generations, *C. limbifer* > 80 generations, *C. undecimnotata* > 60 and *H. dimidiata* > 50 generations. *C. sexmaculata* and *C. limbifer* were reared on a mixture of *Aphis craccivora* Koch and *Aphis fabae* Scopoli whereas *C. undecimnotata* and *H. dimidiata* were reared on *Acyrthosiphon pisum* Harris. All aphid species were reared on *Vicia faba* L. as a host plant.

Substrate contamination

Two strips of paper, each 20 cm long and 4 cm wide and transversally folded to a length of 13 cm, were exposed to 40 unfed first-instars of one coccinellid species in the bottom of a Petri dish, 18.5 cm in diameter. The contamination period was four hours. Fluon on the inner rim of the dish confined the larvae within the arena. Strips were used in choice tests either immediately, or ten days after the contamination treatment.

Oviposition choice test

The choice test design was similar to earlier studies (Růžička, 1997b; 2001a; 2002). Each experimental unit consisted of 10 females of *C. sexmaculata* confined in a cylindrical cage 10 cm high and 19 cm in diameter for 20 h. The age of females used in experiments was 15–25 days. Prior to the experiments, these females were reared in 500 ml jars on a surfeit of *A. fabae*, 12 females with 12 males per unit, and had already laid fertile eggs. One clean and one contaminated strip of paper were provided simultaneously for oviposition. Strips were spaced symmetrically on the glass bottom, 5 cm apart. A surfeit of *A. fabae* was provided on cut shoots of the host plant and water soaked in swabs of bleached cellulose was provided in a small plastic dish. Tests were conducted at 24 ± 2°C, under fluorescent lighting. The photoperiod was 18L : 6D and each test had ten replicates. Two clean strips of paper were provided for oviposition in the blank test.

Statistical analysis

To analyse oviposition in the different choice tests, the total numbers of eggs in 10 replicates of each test (eggs laid in a cage by females on both paper strips and outside the strips) were compared. Differences between the intensity of oviposition in different tests were compared with one-way ANOVA. When significant the ANOVA was followed by a Dunnett multiple comparison test. In all other tests, eggs laid outside strips, including eggs on the glass below the paper strips, were excluded from the statistical analysis.

The numbers of eggs laid on the two substrates in each test were compared using a Wilcoxon paired-sample test (two-tailed P value). Differences in the size of clutches on the two substrates in each tests were compared with a Mann-Whitney test. Differences between the size of clutches in different tests were compared with a Kruskal-Wallis one-way ANOVA, and when significant followed by a Dunn's test.

RESULTS

In each test, females of *C. sexmaculata* in cages laid most eggs on the paper substrates provided for oviposition (Table 1). Eggs were exceptionally on the upper side of substrates (21 eggs in four clutches in the test with tracks of *C. undecimnotata*). One-way ANOVA showed that the variation among total numbers of eggs laid between the tests was highly significant ($F = 3.948$, $P = 0.004$). A Dunnett multiple comparison test showed that the total number of eggs laid by *C. sexmaculata* females in the control was significantly higher than with fresh conspecific tracks ($P < 0.01$), but similar to the numbers of eggs laid with 10 days old conspecific tracks and all tests with tracks of heterospecific larvae ($P > 0.05$).

Females of *C. sexmaculata* laid similar numbers of eggs on the two clean paper substrates in the blank test ($Z = -0.917$, $P = 0.359$), but significantly fewer eggs were laid on the substrate in the choice test that was contaminated with fresh tracks of conspecific larvae than on the clean substrate ($Z = -2.803$, $P = 0.005$). The difference between egg numbers on clean substrates and substrates with 10 d-old tracks of conspecific larvae was also significant ($Z = -2.803$, $P = 0.005$). While fresh tracks of first instars of *C. undecimnotata* and *C. limbifer* reduced oviposition by *C. sexmaculata* females ($Z = -2.803$, $P = 0.005$ and $Z = -2.701$, $P = 0.007$), fresh tracks of *H. dimidiata* had no

TABLE 1. Oviposition and clutch size of *Cheilomenes sexmaculata* on paper substrates in choice tests with tracks of conspecific or heterospecific coccinellid first instars and in the blank test.

Larval tracks of species	Tracks old (days)	Percentage of eggs ± SE on substrates	Clutch size eggs ± SE	Dunn's Multiple comparison test
C. sexmaculata	0	64.6 ± 4.9	9.0 ± 0.5	P < 0.001
C. sexmaculata	10	64.9 ± 4.2	7.1 ± 0.2	P < 0.001
C. undecimnotata	0	60.6 ± 3.0	8.5 ± 0.3	P < 0.001
C. limbifer	0	65.2 ± 4.1	8.0 ± 0.2	P < 0.001
H. dimidiata	0	72.6 ± 5.0	7.8 ± 0.2	P < 0.001
Clean substrates (blank test)	–	83.6 ± 2.8	6.7 ± 0.2	compared with

significant effect on the oviposition site selection (Z = –1.478, P = 0.139) (Fig. 1).

In the blank test, the average clutch size did not differ between the two clean substrates (U = 15945, P = 0.832). Although clutch sizes tended to be smaller on clean substrates than on those with larval tracks in all choice tests, the difference was not statistically significant in any comparison (U = 160.50, P = 0.234 for fresh conspecific tracks, U = 6511.5, P = 0.486 for 10 d-old conspecific tracks, U = 2027.5, P = 0.425 for *C. undecimnotata* tracks, U = 4108.5, P = 0.626 for *C. limbifer* tracks and U = 5088.5, P = 0.096 for tracks of *H. dimidiata* larvae).

Kruskal-Wallis nonparametric ANOVA showed that the effect of various tracks and/or age of tracks on the size of clutches was highly statistically significant F = 9.402, P < 0.0001. Dunn's multiple comparison test showed that all treatments were significantly different from the control (Table 1).

DISCUSSION

Responses to conspecific tracks – consequences for intraspecific competition and cannibalism

In experiments with the same design, effects of fresh conspecific larval tracks on *C. sexmaculata* oviposition were comparatively as strong as those reported for *C. undecimnotata* and *C. limbifer* (Růžička, 2001a). The comparison of intraspecific oviposition-deterring effects of fresh and ten d-old tracks in *C. sexmaculata* revealed substantial persistence of the ODS. It is obvious that substrates with tracks of first instar *C. sexmaculata* can effectively deter conspecific females from ovipositing for a period equivalent to that required for complete larval development. A similarly long persistence of oviposition-deterrence in conspecific tracks of first instars has only been recorded in the coccinellid *C. limbifer* from Cuba (Růžička, 2002).

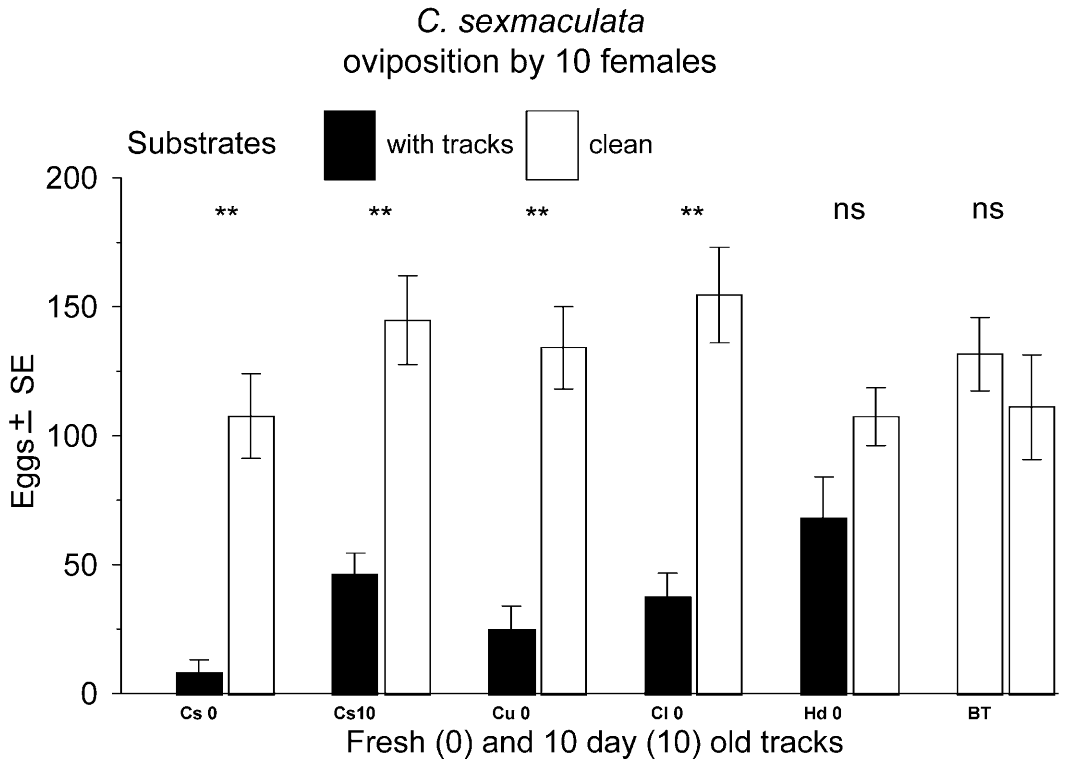

Fig. 1. Mean numbers of eggs (± SEM) laid by 10 *Cheilomenes sexmaculata* females on substrates with and without larval tracks in choice tests with conspecific (Cs), *Ceratomegilla undecimnotata* (Cu), *Cycloneda limbifer* (Cl) and *Harmonia dimidiata* (Hd) tracks of first instar larvae, and in a blank test (BT). Data were compared by a Wilcoxon paired-sample test (**, P < 0.01).

If prey availability is limited, competition and cannibalism can represent a considerable threat to conspecific developmental stages. ODS enable *C. sexmaculata* females to recognise potential danger sites and avoid or reduce oviposition where tracks of conspecific larvae are already present.

In the field, females occasionally encounter other conspecific females. Nevertheless, groups of 10 females in each replicate could obscure or influence some effects of larval tracks that might be observable if females were tested individually. A comparison of the deterrent effects of larval tracks on single and grouped conspecific females in each replicate will be evaluated in the following study of different coccinellids (Růžička, in prep.).

Responses to heterospecific tracks – consequences for interspecific competition and intraguild predation

Interspecific effects of larval tracks invariably occurred in chrysopids (Růžička, 1998). The absence of interspecific oviposition deterrence was reported for the aphidophagous coccinellids *Harmonia axyridis* and *Coccinella septempunctata* when females encountered larval tracks of the other species (Yasuda et al., 2000). However, a strong oviposition-deterring effect of heterospecific larval tracks was observed in two relatively small species, *C. limbifer* and *C. undecimnotata* (Růžička, 2001a). *C. sexmaculata* females reduced their oviposition after direct physical contact with immobilised conspecific or *Coccinella transversalis* larvae or adults (Agarwala et al., 2003a), but the effects of larval tracks were not investigated.

The study showed that females of *C. sexmaculata* which avoid ovipositing on substrates with fresh tracks of conspecific larvae are also deterred from ovipositing on substrates with larval tracks of *C. undecimnotata* and *C. limbifer.* With respect to the results with tracks of conspecific and heterospecific larvae in this study, tracks of *C. transversalis* are also likely to deter females of *C. sexmaculata* from ovipositing. Thus, the interspecific effects of larval tracks in deterring oviposition among aphidophagous coccinellids might be quite common, and sometimes extremely strong, even between species that are not currently sympatric. The spacing of individuals that comes about through direct physical encounter (Hemptinne et al., 1992; Agarwala et al., 2003a) might be generally less important because tracks of larvae are encountered by females more frequently than are actual larvae.

Interspecific effects of ODS inhibit oviposition and increase the dispersal of prey competing species away from patches with heterospecific larvae. This may apparently result in lower intraguild competition and more even and favourable distribution of the predators between prey patches of different qualities. Thus, the semiochemicals involved could play an important role in the distribution of the guild of aphidophagous coccinellids among prey patches.

Since track density is likely to correspond to the number and degree of starvation of the coccinellid larvae present, the density of larval tracks could be an important indicator of patch quality or the degree of development of an aphid colony. If females fail to find suitable sites for their eggs, they can either withhold oviposition, or lay eggs on plants without aphids. This may be especially advantageous for species which successfully develop on alternative prey or pollen. The habit to lay eggs apart from colonies of aphids may reduce non-sibling cannibalism among aphidophagous larvae (Osawa, 1992).

The odours of mites (Colburn & Asquith, 1970), aphids and honeydew (Evans & Dixon, 1986; Obata, 1986; Vohland, 1996) are known to attract coccinellid females and stimulate their oviposition, sometimes enabling the manipulation of these predators in the field with artificial honeydews (Evans & Richards, 1997). The presence of larval tracks could hamper the effectiveness of predators attracted in this manner. Larval tracks may also deter females from ovipositing on honeydew-contaminated sites where aphids have already been destroyed by other predators or parasitoids.

Larval tracks and clutch size

In the laboratory, conspecific larval tracks influenced clutch sizes, but the effect was not consistent among species, clutch size was increased in *C. limbifer*, but decreased in *C. undecimnotata* (Růžička, 2003). Although clutches of *C. sexmaculata* on clean and contaminated substrates in individual choice tests did not differ significantly, females always laid significantly larger clutches in choice tests with tracks of conspecific or heterospecific larvae than in the blank test with two clean substrates.

Semiochemical spacing and optimal foraging strategy

Coccinellids use visual and chemical cues to reach the habitat and find the prey (Carter & Dixon, 1982, 1984; Obata, 1986). Although the response to prey is weak, aphidophagous coccinellids effectively aggregate in areas of high aphid density (Ives et al., 1993). Since coccinellid females lay most eggs in clutches, the density of their larvae can easily increase. High arrival and oviposition may occasionally cause a considerable mortality rate among the progeny (Osawa, 1993). If finite aggregates of prey are prematurely depleted, overcrowded larvae suffer from cannibalism (Michaud & Grant, 2003; Snyder et al., 2004) and attack prepupae and pupae (Takahashi, 1989). Along with cannibalism, interspecific predation occurred in the field and in the laboratory (Dimetry, 1976a, b; Agarwala & Dixon, 1992). Nevertheless, the peak of arrival and oviposition in *H. axyridis* tends to occur before the peak of aphid density (Osawa, 2000). In order to optimize the exploitation of aggregates and patches of prey, aphidophagous predators likely evolved a reliable spacing mechanism that ensures adequate distribution of adults and larvae among prey resources of various sizes and quality. The avoidance of aphid colonies already exploited by predators is consistent with the optimal foraging theory that assumes a range of possible behaviours (Ferran & Dixon, 1993). Both, larvae and adults may avoid aggregating with competitors. Coccinellid larvae are generally less mobile than adults (Hattingh & Samways, 1995) and their movement decreases considerably after feeding (Ferran et al., 1994). This keeps the larvae in the primary colony of prey or close to oviposition sites.

Marks (1977) described an interesting repellent effect of own tracks in individual coccinellid larvae, but subsequent attempts to confirm semiochemical effects of larval tracks on larvae have not been successful (Ferran & Dixon, 1993). Naturally, the distribution of the progeny among prey resources of different quality by mobile females is likely to reduce the exposure of larvae to detrimental factors. If females assess the suitability of aphid colonies before ovipositing, and consequently reduce oviposition and feeding in low quality resources, the competition for food could decline and the fitness of the predators increase. As with other insects, the suitability of a resource depends on the amount of food available and the possible detrimental effects of competitors on the development of offspring.

A number of factors can influence the rating of generally unstable resources by females. Dixon (1959) reported that there is a lower critical threshold of young aphids for the survival of first instar coccinellid larvae. Assumed “inefficiency” of aphidophagous coccinellids as biological control agents was associated with their ability to exploit unstable food resources (Hemptinne & Dixon, 1991). The original presumption of laying only few eggs at the beginning of the development of aphid colonies resulted in a simple “egg window” model (Hemptinne et al., 1992). According to this theory, females should refrain from laying many eggs very early in the development of short-lived aphid colonies as well as from oviposition in large colonies that are shortly to decline, and so avoid prey shortage and competing with potentially dangerous conspecifics. Deterrent effects of physical encounters between conspecifics on oviposition seem plain enough and have been studied in detail. Coccinellid females confined with either conspecific females or larvae laid fewer eggs than females kept on their own (Hemptinne et al., 1992), however, while encounters with conspecific larvae decreased oviposition in *A. bipunctata*, encounters with conspecific females, but not larvae, inhibited egg laying in *C. septempunctata* (Hemptinne et al., 1993). The effects of volatile conspecific semiochemicals on oviposition were also investigated but, surprisingly, odour of conspecific larvae slightly increased the eggs laying of conspecific females (Hemptinne et al., 1992). Thus, the extent of inhibition of egg laying due to the presence of conspecifics was related solely to the rate of direct encounters between conspecifics.

Interestingly, the effects of larval tracks on females have not been taken into consideration until the incidental discovery of ODS in tracks of chrysopid larvae (Růžička, 1994). With an excess of aphids, substrates with larval tracks strongly deterred females from ovipositing. Soon afterwards, similar ODS were found in larval tracks of coccinellids and other aphidophagous predators (Růžička, 1997b; Růžička & Havelka, 1998). Strong intraspecific effects of larval tracks were observed in *C. septempunctata* and *A. bipunctata* (Růžička, 1997b; Doumbia et al., 1998), and a very low track density effectively deterred conspecific females of chrysopids and coccinellids from ovipositing (Růžička, 1994; 1997a, b; Oliver et al., 2006). ODS were present in tracks of all instars of chrysopids and coccinellids associated with different types of habitat. Coccinellid females reduced oviposition on plants with larval tracks both in (Yasuda et al., 2000) and outside (Fréchette et al., 2003) of the laboratory. Moreover, the oviposition of coccinellids and other predators frequently declined on sites with tracks of heterospecific larvae (Růžička, 1996, 1998, 2001a; Růžička & Havelka, 1998).

This study with *C. sexmaculata* further extended the still limited notion of the oviposition-deterring effects of conspecific and heterospecific tracks in coccinellids. In some species, the persistence of tracks of first instars was long enough to deter females throughout the larval development (Růžička, 2002). Undoubtedly, the network of oviposition-deterring tracks of coccinellid larvae can optimize the distribution of eggs in accordance with the quality of resources more effectively than less frequent encounters with conspecifics. This spacing factor is probably more important than the hypothetical preference for certain size or age structure of aphid colonies. Hence, ODS of larval tracks may be considered either the main, or at least one, of the dominant factors of oviposition-deterrence causing more even distribution of aphidophagous predators between prey patches (Růžička, 1998; Oliver et al., 2006). Likewise, Hemptinne et al. (2000) indicated that the predators use cues associated with conspecific larvae rather than those associated with the aphids and/or plants when assessing patch quality. Interactive effects of aphid density and conspecific larval track density on oviposition of *Aphidecta obliterata* (L.) was investigated in detail by Oliver et al., (2006). Increasing the degree of conspecific larval tracks significantly inhibited oviposition and, simultaneously, increasing the density of aphids increased the oviposition rate. This means a trade-of between prey density and ODS concentration in the network of larval tracks may determine the readiness of females to lay eggs.

Encounters of females with larval tracks enable reliable detection of temporarily hidden larvae and small instars. The repulsion of females by semiochemicals present in adhesive secretion that originally had served to fix the abdominal disc of larvae to the plant surface is also an extremely economic way of defending prey resources. The better females assess the degree of suitability of resources for ovipositing the higher survival of the progeny can be expected. If females adapt the time of stay to the quality of patches appropriately, the effect of larval tracks may be even more pronounced. In the absence of aphids, satiated *C. limbifer* females spent a significantly shorter time on substrates with heterospecific tracks and significantly longer time on substrates with conspecific tracks of first instars than on simultaneously presented substrates without tracks (Růžička & Zemek, 2003). *A. obliterata* was observed to search less frequently on filter paper previously exposed to conspecific third instar larvae than on simultaneously provided clean filter paper

(Oliver et al., 2006). Larval tracks are likely to stimulate or promote intense wandering and prey searching in coccinellid females on plants. This increases the predation of single aphids and the elimination of tiny colonies on neighbouring plants and hence reduces a potential spread of aphids.

To some extent, the future development of a prey resource can be predicted from the age of the predatory larvae. Young coccinellid larvae are likely to reduce the prey population more dramatically before they pupate than larvae close to pupation and the amounts of ODS secretions may differ accordingly. Unpublished data on the effects of extracts of first and last coccinellid instars are in accord with this statement.

Unfortunately, the effects of physical encounters and semiochemicals on the spacing of the progeny have not been reliably compared and the information on semiochemical spacing of different aphidophagous predators is still rather fragmentary for an optimal foraging model. With respect to species-specific behaviour, currently available data only enable this preliminary evaluation of the role of larval tracks in the distribution of aphidophagous coccinellids among prey resources.

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REFERENCES

Agarwala B.K. 1991: Why do ladybirds (Coleoptera: Coccinellidae) cannibalize. *J. Biosciences* **16**: 103–109.

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. 1992: Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecol. Entomol.* **17**: 303–309.

Agarwala B.K., Bardhanroy P., Yasuda H. & Takizawa T. 2003a: Effects of conspecific and heterospecific competitors on feeding and oviposition of a predatory ladybird: a laboratory study. *Entomol. Exp. Appl.* **106**: 219–226.

Agarwala B.K., Yasuda H. & Kajita Y. 2003b: Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: Role of fecal cues in predator avoidance. *J. Chem. Ecol.* **29**: 357–376.

Banks C.J. 1957: The behaviour of individual coccinellid larvae on plants. *Br. J. Anim. Behav.* **5**: 12–24.

Bind O. & Bind R.B. 1993: Record of aphid natural enemies complex of Uttar-Pradesh. 2. The coccinellids*. J. Adw. Zool.* **14**: 96–99.

Carter M.C. & Dixon A.F.G. 1982: Habitat quality and foraging behaviour of coccinellid larvae. *J. Anim. Ecol.* **51**: 865–878.

Carter M.C. & Dixon A.F.G. 1984: Honeydew: an arrestant stimulus for coccinellids. *Ecol. Entomol*. **9**: 383–387.

Colburn R. & Asquith D. 1970: A cage used to study the finding of a host by the ladybird beetle, Stethorus punctum. *J. Econ. Entomol.* **63**: 1376–1377.

Dimetry N.Z. 1976a: Studies on the cannibalism behaviour of the predatory larvae of Adalia bipunctata L. (Col., Coccinellidae). *Z. Angew. Entomol.* **81**: 156–163.

Dimetry N.Z. 1976b: The role of predator and prey density as factors affecting behavioural and biological aspects of Adalia bipunctata (L.) larvae. *Z. Angew. Entomol.* **81**: 386–392.

Dixon A.F.G. 1959: An experimental study of the searching behaviour of the predatory coccinellid beetle Adalia decempunctata (L.). *J. Anim. Ecol*. **28**: 259–281.

Dixon A.F.G. & Guo Y.Q. 1993: Egg and cluster size in ladybird beetles (Coleoptera, Coccinellidae) – The direct and indirect effects of aphid abundance. *Eur. J. Entomol.* **90**: 457–463.

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

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

Evans E.W. & Richards D.R. 1997: Managing the dispersal of ladybird beetles (Col.: Coccinellidae): Use of artificial honeydew to manipulate spatial distributions. *Entomophaga* **42**: 93–102.

Ferran A. & Dixon A.F.G. 1993: Foraging behaviour of ladybird larvae. *Eur. J. Entomol.* **90**: 383–402.

Ferran A., Ettifouri M., Clement P. & Bell W.J. 1994: Sources of variability in the transition from extensive to intensive search in coccinellid predators (Homoptera, Coccinellidae). *J. Insect Behav*. **7**: 633–647.

Fréchette B., Alauzet C. & Hemptinne J.-L. 2003: Oviposition behaviour of the two-spot ladybird beetle Adalia bipunctata (L.) (Coleoptera: Coccinellidae) on plants with conspecific larval tracks. In Soares A.O., Ventura M.A., Garcia V. & Hemptinne J.-L. (eds): *Biology, Ecology and Behaviour of Aphidophagous Insects*. Proc. 8th Int. Symp. Ecology of Aphidophaga. *Arquipélago. Life and Marine Sciences*. *Supplement* **5**, pp. 73–77.

Hattingh V. & Samways M.J. 1995: Visual and olfactory location of biotopes, prey patches, and individual prey by the ladybeetle Chilocorus nigritus*. Entomol. Exp. Appl*. **75**: 87–98.

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.

Hemptinne J.-L., Dixon A.F.G., Doucet J.-L. & Peterson J.-E. 1993: Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms. *Eur. J. Entomol.* **90**: 451–455.

Hemptinne J.-L., Doumbia M. & Dixon A.F.G. 2000: Assessmant of patch quality by ladybirds: Role of aphids and plant phenology. *J. Insect Behav*. **13**: 353–359.

Hodek I. 1973: *Biology of Coccinellidae*. Academia, Prague, 260 pp.

Ives A.R., Kareiva P. & Perry R. 1993: Response of a predator to variation in prey density at 3 hierarchical scales – lady beetles feeding on aphids. *Ecology* **74**: 1929–1938.

JhaV., Kargupta A.N., Dutta R.N., Jha U.N., Mishra R.K. & Saraswati K.C. 1991: Utilization and conservation of Euryale ferox Salisbury in Mithila (North Bihar), India. *Aquatic Botany* **39**: 295–314.

Kuchlein J.H. 1966: Some aspects of the prey-predator relation. In Hodek I. (ed.): *Ecology of Aphidophagous Insects.* Academia, Prague, pp. 237–242.

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

Michaud J.P. & Grant A.K. 2003: Intraguild predation among ladybeetles and a green lacewing: do the larval spines of Curinus coeruleus (Coleoptera: Coccinellidae) serve a defensive function? *Bull. Entomol. Res*. **93**: 499–505.

Mills N.J. 1982: Voracity, cannibalism and coccinellid predation. *Ann. Appl. Biol.* **101**: 144–148.

Obata S. 1986: Mechanisms of prey finding in the aphidophagous ladybird beetle, Harmonia axyridis (Col.: Coccinellidae). *Entomophaga* **31**: 301–311.

Oliver T.H., Timms J.E.L., Taylor A. & Leather S.R. 2006: Oviposition responses to patch quality in larch ladybird Aphidecta obliterata (Coleoptera: Coccinellidae): effects of aphid density, con- and heterospecific tracks. *Bull. Entomol. Res*. **96**: 25–34.

Omkar 2004: Prey quality dependent growth, development and reproduction of a biocontrol agent, Cheilomenes sexmaculata (Fabricius) (Coleoptera: Coccinellidae). *Biocontrol Sci. Tech.* **14**: 665–673.

Omkar, Mishra G., Srivastava S., Gupta A.K. & Singh S.K. 2005: Reproductive performance of four aphidophagous ladybirds on cowpeas aphid, Aphis craccivora Koch. *J. Appl. Entomol.* **129**: 217–220.

Osawa N. 1989: Sibling and nonsibling cannibalism by larvae of a lady beetle Harmonia axyridis Pallas (Coleoptera: Coccinellidae) in the field. *Res. Popul. Ecol.* **31**: 153–160.

Osawa N. 1992: A life table of the ladybird beetle Harmonia axyridis Pallas (Coleoptera, Coccinellidae) in relation to the aphid abundance. *Jap. J. Entomol*. **60**: 575–579.

Osawa N. 1993: Population field studies on the aphidophagous ladybird beetle Harmonia axyridis (Coleoptera, Coccinellidae): life tables and key factor analysis. *Res. Popul. Ecol.* **35**: 335–348.

Osawa N. 2000: Population field studies on the aphidophagous ladybird beetle Harmonia axyridis (Coleoptera: Coccinellidae): resource tracking and population characteristics. *Popul. Ecol.* **42**: 115–127.

Osawa N. 2003: The influence of female oviposition strategy on sibling cannibalism in the ladybird beetle Harmonia axyridis (Coleoptera: Coccinellidae). *Eur. J. Entomol*. **100**: 43–48.

Pervez A. & Omkar 2005: Functional responses of coccinellid predators: An illustration of a logistic approach. *J. Insect Sci.* **5**: Art. No. 5.

Pschorn-Walcher H. & Zwölfer H. 1956: The predator complex of the white-fir woolly aphids (Genus Dreyfusia, Adelgidae). *Z. Angew. Entomol*. **39**: 63–75.

Růžička Z. 1994: Oviposition-deterring pheromone in Chrysopa oculata (Neuroptera: Chrysopidae). *Eur. J. Entomol.* **91**: 361–370.

Růžička Z. 1996: Oviposition-deterring pheromone in Chrysopidae (Neuroptera): Intra- and interspecific effects. *Eur. J. Entomol.* **93**: 161–166.

Růžička Z. 1997a: Persistence of the oviposition deterring pheromone in Chrysopa oculata (Neur.: Chrysopidae). *Entomophaga* **42**: 107–112.

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

Růžička Z. 1998: Further evidence of oviposition-deterring allomone in chrysopids (Neuroptera: Chrysopidae). *Eur. J. Entomol.* **95**: 35–39.

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

Růžička Z. 2001b: Response of chrysopids (Neuroptera) to larval tracks of aphidophagous coccinellids (Coleoptera). *Eur. J. Entomol*. **98**: 283–285.

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. 2003: Perception of oviposition-deterring larval tracks in aphidophagous coccinellids Cycloneda limbifer and Ceratomegilla undecimnotata (Coleoptera: Coccinellidae). *Eur. J. Entomol*. **100**: 345–350.

Růžička Z. & Havelka J. 1998: Effects of oviposition-deterring pheromone and allomones on Aphidoletes aphidimyza (Diptera: Cecidomyiidae). *Eur. J. Entomol*. **95**: 211–216.

Růžička Z. & Zemek R. 2003: Effect of conspecific and heterospecific larval tracks on mobility and searching patterns of Cycloneda limbifer Say (Coleoptera: Coccinellidae) females. In Soares A.O., Ventura M.A., Garcia V. & Hemptinne J.-L. (eds): *Biology, Ecology and Behaviour of Aphidophagous Insects*. Proc. 8th Int. Symp. Ecology of Aphidophaga. *Arquipélago. Life and Marine Sciences. Supplement 5*, pp. 85–93.

Schellhorn N.A. & Andow D.A. 1999: Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. *Environ. Entomol*. **28**: 1092–1100.

Smith B.D. 1966: Effects of parasites and predators on a natural population of the aphid Acyrthosiphon spartii Koch on broom (Sarothamnus scoparius L.). *J. Anim. Ecol.* **35**: 255–267.

Snyder W.E., Clevenger G.M. & Eigenbrode S.D. 2004: Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* **140**: 559–565.

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

Sugiura K. & Takada H. 1998: Suitability of seven aphid species as prey of Cheilomenes sexmaculata (F.) (Coleoptera: Coccinellidae). *Jap. J. Appl. Entomol. Zool.* **42**: 7–14.

Takahashi K. 1989: Intra- and inter-specific predations by lady beetles in spring alfalfa fields. *Jap. J. Entomol*. **57**: 199–203.

Ulrichs C., Mewis I. & Schnitzler W.H. 2001: Efficacy of neem and diatomaceous earth against cowpea aphids and their deleterious effects on predating Coccinellidae. *J. Appl. Entomol.* **125**: 9–10.

Vohland K. 1996: The influence of plant structure on searching behaviour in the ladybird, Scymnus nigrinus (Coleoptera: Coccinellidae). *Eur. J. Entomol.* **93**: 151–160.

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.

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