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Use of odours by *Cycloneda sanguinea* to assess patch quality

Renato Almeida Sarmento[1,3]*, Madelaine Venzon[2], Angelo Pallini[3], Eugenio Eduardo Oliveira[4] & Arne Janssen[1]

[1]Institute for Biodiversity and Ecosystem Dynamics, Section Population Biology, University of Amsterdam, PO Box 94084, Amsterdam, The Netherlands, [2]EPAMIG (Agriculture and Livestock Research Enterprise of Minas Gerais), Minas Gerais, Viçosa, Brazil, [3]Department of Animal Biology/Entomology, Federal University of Viçosa, CEP: 36570-000, Viçosa-MG, Brazil, and [4]Zoological Institute, Department of Animal Physiology, University of Cologne, Weyertal 119, 50923 Cologne, Germany

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Abstract

Adult ladybirds are likely to encounter various species of prey when foraging for oviposition sites. Optimal oviposition theory predicts that females should lay eggs in those sites that are the most suitable for offspring development. Therefore, factors that directly affect offspring mortality, such as the presence of predators and food, are expected to play an important role in the assessment of patch profitability by ladybird predators. Using a Y-tube olfactometer, we tested whether the predatory ladybird *Cycloneda sanguinea* L. (Coleoptera: Coccinellidae) can use volatile cues to assess patch profitability and avoid predator-rich patches. We assessed the foraging behaviour of *C. sanguinea* in response to odours associated with tomato plants infested with a superior prey, *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae), and with an inferior prey, *Tetranychus evansi* Baker and Pritchard (Acari: Tetranychidae), in the presence or absence of the heterospecific predator *Eriopis connexa* Mulsant (Coleoptera: Coccinellidae). Females of *C. sanguinea* significantly preferred plants infested by *M. euphorbiae* to plants infested by *T. evansi* and avoided odours emanating from plants on which *E. connexa* females were present. Our results show that *C. sanguinea* use volatile cues to assess patch profitability and to avoid patches with heterospecific competitors or intraguild predators.

Introduction

The assessment of patch quality by female insects is assumed to be an important step in their foraging process (Dixon, 1959, 2000). Factors that directly affect offspring mortality (e.g., the presence of predators and food) are expected to play an important role in the assessment of patch suitability by insect females, and it is likely to drive the evolution of oviposition behaviour (Hemptinne et al., 1993; Rieger et al., 2004). Furthermore, foraging theory developed for invertebrate predators, and ladybirds in particular, indicates that if the females are to maximize their fitness, they should be reluctant to lay eggs close to those places that are less suitable for the development of their offspring (Mangel, 1987; Hodek, 1993; Kindlmann & Dixon, 1993; Fréchette et al., 2006), because neonates have a limited dispersion capacity and need to quickly find a meal (Kindlmann & Dixon, 1993; Tschanz et al., 2005).

However, enemy-free patches can be just as important as the presence and the quality of food in the patches (Mangel, 1987; Ruzicka, 2001a; Griffin & Yeargan, 2002a,b; Fréchette et al., 2006). The patch dynamics and enemy-free space hypotheses are not mutually exclusive, and may provide complementary explanations (Fréchette et al., 2006). Therefore, females are expected to assess the general quality of prey for choosing an optimal ovipositional site, and consequently to maximize their fitness (Stephens & Krebs, 1986; Hodek, 1993; Doumbia et al., 1998; Tschanz et al., 2005). However, when searching for a more suitable ovipositing patch, some predators are capable of assessing not only the presence and quality of prey, but also the

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*Correspondence: Renato Almeida Sarmento, Institute for Biodiversity and Ecosystem Dynamics, Section Population Biology, University of Amsterdam, PO Box 94084, Amsterdam, The Netherlands. E-mail: sarmento@science.uva.nl

presence of competitors and intraguild predators (Obata, 1986; Janssen et al., 1995a,b, 1997; Ruzicka, 1996, 2003, 2006; Li et al., 1997). This assessment occurs not only when they face a competitor or predator, but also when they detect cues associated with the presence of such competitors or predators (Janssen et al., 1997; Grostal & Dicke, 1999; Hemptinne & Dixon, 2000; Hemptinne et al., 2001; Ruzicka, 2001a; Pettersson et al., 2005).

The ladybird predator *Cycloneda sanguinea* L. (Coleoptera: Coccinellidae) has generalist feeding habits and is among the potential natural enemies studied as biocontrol agents of *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae) and *Tetranychus evansi* Baker and Pritchard (Acari: Tetranychidae), which are important pests of tomato plants in Brazil (Eichler & Reis, 1976; Sarmento et al., 2007). Although *C. sanguinea* can consume different prey types, there are indications that the predator has higher fitness when fed with aphids (Vandenberg & Gordon, 1988; Isikber & Copland, 2002). It is able to complete its biological cycle when fed only on *M. euphorbiae*, but not when fed only on *T. evansi* mites (Oliveira et al., 2005).

The co-occurrence of *C. sanguinea* and other coccinellid predators such as *Eriopis connexa* Mulsant (Coleoptera: Coccinellidae) in various crops, including tomato, has been described (Gassen, 1986; Grutzmacher & Link, 2000). Moreover, *E. connexa* was shown to efficiently prey on *T. evansi* and on *M. euphorbiae* (Sarmento et al., 2007). The simultaneous occurrence of predators, such as *C. sanguinea* and *E. connexa*, on a patch may impose oviposition of one or both species in a non-optimal patch (Yasuda & Ohnuma, 1999; Griffin & Yeargan, 2002a,b). Besides competition for prey-rich patch, predators may therefore also face intraguild predation (Magalhães et al., 2005; Ruzicka, 2006).

In this study, we investigated whether *C. sanguinea* can use volatile cues to assess patch suitability and to avoid patches that contain heterospecific predators. Previous experiments showed that *C. sanguinea* prefer odours of tomato plants infested either by *M. euphorbiae* or *T. evansi*, when clean plants were offered as an alternative. The predators avoided odours from clean plants when tested vs. clean air (Sarmento, 2003). For this reason, we first assessed the preference of *C. sanguinea* to odours of tomato plants infested with *T. evansi* vs. clean air. This experiment focused on determining if the preference of *C. sanguinea* to plants infested by these herbivores is because of the avoidance of clean tomato plants or because plants infested by herbivores are more attractive to *C. sanguinea*. Subsequently, we investigated the preference of *C. sanguinea* for odours from tomato plants infested with *T. evansi* or with *M. euphorbiae*. Lastly, we assessed the capacity of *C. sanguinea* to use odours to detect the presence of the heterospecific predator *E. connexa*. We also tested whether the prey preference of *C. sanguinea* would change in the presence of *E. connexa*.

Materials and methods

Arthropod rearing and plant material

Spider mites (*T. evansi*) were obtained in 2002 from a natural infestation of tomato plants under experimental greenhouse conditions. Predators (*C. sanguinea* and *E. connexa*) and aphids (*M. euphorbiae*) were collected from tomato plants cultivated in experimental fields. Each species of predator (*C. sanguinea* and *E. connexa*) was reared separately in the laboratory in transparent plastic tubes (10 cm in height × 2 cm in diameter) containing a piece of wet cotton wool as water source, and they were fed with both diets (*M. euphorbiae* and *T. evansi*) on tomato leaves. The eggs deposited on the walls of the tubes were collected daily and transferred to Petri dishes (5.0 cm in diameter × 1.5 cm in height), where they were kept until the larvae eclosed. Subsequently, larvae were kept individually in Petri dishes and fed with *M. euphorbiae* and *T. evansi* until adulthood. Cultures were kept inside a climate box at 25 ± 1 °C, 70 ± 10% r.h., and L12:D12.

Tomato seeds [(*Lycopersicon esculentum* Mill variety Santa Clara I-5300 [Solanaceae])] were sown in trays in a commercial substrate composed of vermiculite and organic fertilizer and kept in mite-proof screen cages in a greenhouse. Plants of 21 days old were transplanted to plastic pots (2-l) that contained a mixture of soil and bovine manure (3:1 vol/vol), and fertilizer (4-14-8 N-P-K). Tomato plants were further grown in mite-proof screen cages in a greenhouse until they were 45 days old and had at least four completely developed leaves. Herbivores were reared in the greenhouse on tomato plants placed in mite-proof screen cages (1.0 × 1.0 × 0.5 m) with a wooden frame. Tomato plants infested by *T. evansi* were obtained by placing four small infested leaves on each plant, which were placed inside a mite-proof screen cage in a greenhouse. To obtain aphid-infested plants, four small tomato leaves infested with *M. euphorbiae* were put on each plant. The plants were incubated in this way for 1 week, resulting in 300–400 adult mites or 150–180 aphids per plant.

Olfactometer experiments

The response of *C. sanguinea* to odour sources was determined in two-choice tests, using a Y-tube olfactometer (Sabelis & van de Baan, 1983; Janssen et al., 1999). The olfactometer consisted of a glass tube in the form of a Y (27 cm in length × 3.5 cm in diameter). The base of the tube was connected to an air pump that produced an airflow from the arms of the tube to the base. The airflow through both arms of the Y-tube was measured with hot-wire anemometers, and calibrated with valves between the air outlet of the containers of the odour sources and the arms of the olfactometer. When wind speeds in both arms are equal, the odours form two neatly separated fields in the base of the Y-tube (Sabelis & van de Baan, 1983). Pilot experiments showed that the best wind speed to assess the foraging behaviour of *C. sanguinea* in a Y-tube olfactometer is 0.45 m s^{-1}. Therefore, the wind speed in each arm of the Y-tube was calibrated to ca. 0.45 m s^{-1}. Each odour source consisted of three tomato plants either with or without herbivores or heterospecific predators. The odour sources were placed in a tray (30 × 20 × 8 cm) that was placed inside a second water-containing tray (60 × 39 × 6 cm). A Plexiglas container (50 × 36 × 43 cm) was placed over the plants so that it rested in the water-containing outer tray. In this way, a water barrier was created to prevent the escape of arthropods, and the water served as an air-tight seal for the container at the same time. The containers had an air inlet and outlet (1 cm in diameter) in opposite walls. The inlet and outlet were covered with mite-proof gauze.

Adult females of *C. sanguinea* were used in the experiments because this stage is responsible for finding suitable food and oviposition sites for the development of their offspring (Kindlmann & Dixon, 1993). Two-day-old mated females of *C. sanguinea* were starved for 24 h before the experiments. They were tested individually in the olfactometer by introducing them one at a time at the base of the tube after disconnecting the pump. After the pump was reconnected, the female started moving upwind to the junction of the tube, where it had to choose one of the two arms. It was observed that each female spent some time walking in circles inside each arm of the tube, perceiving each of the odour sources and subsequently making a choice. Each female was observed from the time that it left the tube until it either reached the end of one arm or for a maximum of 5 min. When the female spent more than 5 min without reaching the end of an arm, it was scored as having made no choice. The percentage of predators that did not make a choice in each replicate was very low (1–2%), and these predators were not included in the analysis. Each replicate experiment was continued until 20 females had responded to either of the odour sources. After five responses, the Y-tube was cleaned with alcohol (70%) and left to dry for 5 min. Subsequently, the odour sources were switched to the opposite arm of the olfactometer to correct for any unforeseen asymmetry in the experimental set-up.

Three replicate experiments were done using different sets of plants and insects for each experiment. The following comparisons were tested: (i) clean air vs. tomato plants infested by *T. evansi*; (ii) tomato plants infested by *M. euphorbiae* vs. tomato plants infested by *T. evansi*; (iii) tomato plants infested by *M. euphorbiae* vs. tomato plants infested by *M. euphorbiae* + *E. connexa* (five adult females per plant); and (iv) tomato plants infested by T. *evansi* vs. tomato plants infested by *M. euphorbiae* + *E. connexa* (five adult females per plant). Differences in numbers of *C. sanguinea* females choosing the odour sources were tested using a G-test with expected fractions of 0.5 for each odour source. Pooled results were tested with a replicated goodness-of-fit test (Sokal & Rohlf, 1995).

Results

Identification of host plants

In one replicate, *C. sanguinea* females showed a significant preference to odours from plants infested by *T. evansi* when clean air was given as alternative (P = 0.02) (Figure 1A). The other two replicates showed the same trend, but the preference was not significant (Figure 1A). However, the replicates were not heterogeneous (G_H = 0.47, d.f. = 2, P = 0.787) and the pooled results showed a significant preference of *C. sanguinea* towards odours from plants infested with *T. evansi* (G_P = 9.87, d.f. = 1, P<0.001; Figure 1A). The same phenomenon was observed in previous experiments, where *C. sanguinea* females were more attracted to odours of tomato plants infested by *M. euphorbiae* when offered clean air as alternative (Sarmento, 2003).

Suitability of patches

Cycloneda sanguinea significantly preferred odours from plants infested with *M. euphorbiae* to plants infested by *T. evansi* (Figure 1B). There were no significant differences between replicates (G_H = 1.63, d.f. = 2, P = 0.436). There was significant preference for plants infested by *M. euphorbiae* in all replicates, resulting in a highly significant overall preference of *C. sanguinea* towards odours from those plants (G_P = 26, d.f. = 1, P<0.001; Figure 1B).

When given a choice between odours from plants infested with *M. euphorbiae* vs. plants infested with *M. euphorbiae* plus the heterospecific predator *E. connexa*, *C. sanguinea* preferred odours of plants without *E. connexa* (Figure 1C). The overall results showed a significant preference of *C. sanguinea* toward odours from plants infested with *M. euphorbiae* alone (G_P = 29.11, d.f. = 1, P<0.001; Figure 1C), and all replicates were similar (G_H = 0.23, d.f. = 2, P = 0.889).

When *C. sanguinea* was offered a choice between odours from plants infested with *T. evansi* vs. plants infested with *M. euphorbiae* + *E. connexa*, *C. sanguinea* had a clear and significant preference for odours of plants infested with *T. evansi* in all replicates (Figure 1D). Overall, a highly significant preference was found (G_P = 26, d.f. = 1, P<0.001;

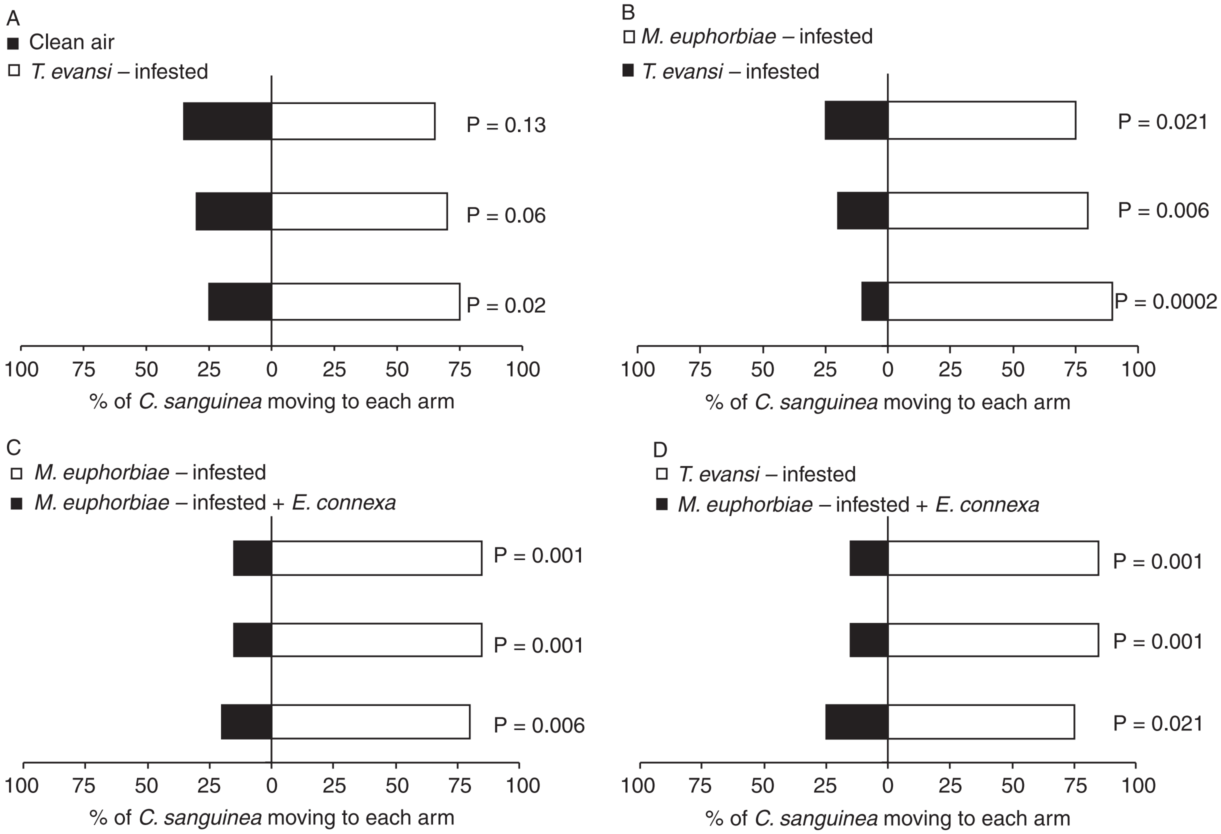

Figure 1 Choice of *Cycloneda sanguinea* females when offered odours of (A) tomato plants infested by *Tetranychus evansi* vs. clean air, (B) tomato plants infested by *Macrosiphum euphorbiae* vs. plants infested by *T. evansi*, (C) tomato plants infested by *M. euphorbiae* vs. volatiles of tomato plants infested by *M. euphorbiae* + *Eriopis connexa*, and (D) volatiles of tomato plants infested by *T. evansi* vs. volatiles of tomato plants infested by *M. euphorbiae* + *E. connexa*. Each bar represents the result of one replicate, in which 20 insects were tested. Pooled results were tested with a replicated goodness-of-fit test.

Figure 1D), and the trend was similar in all three replicates ($G_H = 0.85$, d.f. = 2, P = 0.651).

Discussion

Our results indicate that *C. sanguinea* can use volatile cues to assess patch quality. Olfactory choice experiments showed that females of *C. sanguinea* were attracted to volatiles of tomato plants that were attacked by *T. evansi*. This is in accordance with some previous results with other predator species that are likely to use volatile cues to locate prey habitats (Tumlinson et al., 1992; Zhu et al., 1999). We also show that *C. sanguinea* was capable of discriminating between odours of plants with different prey types and significantly preferred plants infested by its superior prey *M. euphorbiae* to plants infested by its inferior prey *T. evansi*. According to Oliveira et al. (2005), *C. sanguinea* females were not able to complete their biological cycle when fed only on a *T. evansi* diet, but successfully completed its biological cycle when fed only on a *M. euphorbiae* diet. Experiments carried out with *E. connexa* females showed that the predator had many more reserve metabolites in their fat body cells when fed with *Myzus persicae* (Sulzer) (Homoptera: Aphididae) than when fed with *T. evansi* (Sarmento et al., 2004). Besides the inferior nutritional quality of *T. evansi*, the presence of the web produced by *T. evansi* on the plants may diminish predation rate of ladybirds in patches consisting of only these mites (Oliveira et al., 2005; Sarmento et al., 2007).

Cycloneda sanguinea avoided odours emanating from plants infested by *M. euphorbiae* containing the heterospecific predator *E. connexa* and preferred plants with the aphid only. Furthermore, *C. sanguinea* significantly preferred plants infested by the inferior prey *T. evansi* to plants with the superior prey *M. euphorbiae* + *E. connexa*. Thus, not only does food quality orchestrate the assessment of patches by *C. sanguinea*, but the presence of heterospecific predators does so as well. Intraguild predation is a widespread feeding behaviour frequently observed in aphidophagous guilds and may play a role in patch choice of ladybirds (Polis et al., 1989; Yasuda & Ohnuma, 1999; Burgio et al., 2002; De Clercq et al., 2003; Arim & Marquet, 2004).

It is not clear from our experiments what the nature is of the volatiles used by *C. sanguinea* to perceive the presence of *E. connexa* on infested plants. Janssen et al. (1997) showed that the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) avoided odours emanating from bean plants infested by its prey, the spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae), plus conspecific predators. These authors suggested that *P. persimilis* can use volatiles (alarm pheromones) produced by adult prey in response to the presence of conspecific predators to avoid such places. Results from Zhu et al. (1999) suggest that some ladybirds are attracted to (*E*)-β-farnesene, an aphid alarm pheromone. Therefore, it is possible that the presence of *E. connexa* on the plants and its feeding on aphids could have elicited the production of alarm pheromones by the aphids, and *C. sanguinea* may have used such volatiles to avoid plants hosting *E. connexa*.

The avoidance of patches occupied by conspecific/heterospecific competitors/predators has been widely observed in many aphidophagous species (Ruzicka, 1996, 2001a). Furthermore, the enemy-free space hypothesis suggests that the presence of natural enemies may be as important (or more important) as food quality in shaping oviposition behaviour (Hodek, 1993; Fréchette et al., 2006). Natural selection could thus have favoured the preference for oviposition sites that are free of enemies over those of high food quality. This hypothesis was originally developed to account for oviposition preferences of phytophagous insects, but as Sadeghi & Gilbert (1999) pointed out, selection pressures affecting oviposition in predators and phytophagous insects are likely to be similar. We therefore favour the possibility that *C. sanguinea* can use volatile cues to assess patch profitability and avoid patches with *E. connexa*, probably to avoid competition for food and/or intraguild predation. Further experiments are underway to investigate this.

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