Foraging behaviour of *Coccinella septempunctata* (L.): volatiles and allelobiosis

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Introduction

Sevenspotted ladybird, *Coccinella septempunctata* (L.), has a pronounced seasonal migration rhythm, and is a very mobile species in the landscape. Adults hibernate in well recognisable sites such as ridges, hills, mountains, water towers etc. The distribution of ladybirds within such a hibernating site is patchy, and the number of ladybirds in an aggregation can be high, sometimes exceeding 200 individuals per m^2 (Majerus 1994; Hodek and Honek 1996). This aggregated distribution may be mediated by a putative aggregation pheromone, pyrazine (Al abassi et al 1998). The seasonal migrations to and from hibernating sites are important traits in the population biology of the sevenspotted ladybird, and the mobility and dynamic redistribution of adults in the landscape has inspired investigations of both the principles and mechanistic aspects of foraging behaviour.

In a recent review, the general principle for the foraging behaviour of *C. septempunctata* is described as a ‘journey through the landscape’, during which food sources such as aphids are used when found. This strict dependence on aphid availability is modified by an oviposition-deterring pheromone and a level of mobility to meet the dynamic nature of the food resource – aphid colonies (Evans 2003). Later in this paper we refer to this strategy as the ‘tramp hypothesis’, and use this as a platform for discussion and speculation.

To be successful, the *C. septempunctata* searching strategy presupposes a high capacity to meet variation in food, plus a capacity for learning, as suggested by Vet and Dicke (1992). Hodek and Honek (1996) discuss the potential advantage for some ladybird species with mixed feeding i.e. a diet that contains aphids as well as pollen. A valuable contribution to this discussion is given by Rana et al. (2002) showing laboratory evidence that habituation to one aphid species leads to a diminished capacity to use another as optimal food.

This invites comparisons of the relative importance of behavioural cues for different polyphagous insects such as *C. septempunctata* and others with a more limited i.e. oligo- monophagous food choice. It may be hypothesized that cues specifically connected with prey/food presence would have a higher relative behavioural value for mobile and specialised third trophic level insects. From the same perspective, polyphagous insects would tend to be less mobile and more dependent on cues related to favourable habitats which can be more thoroughly searched. Thus it is interesting to compare these guilds with respect to the importance of cues representing habitat preferences and those directly related to food/prey presence. If the minimum searching time investment and optimised food/prey finding probability represents efficiency, then food/prey specialisation and a strong dependency on stimuli indicating the source should be important for ecological fitness.

A polyphagous predator can survive on a suboptimal food source, and a well developed behavioural system to identify high quality habitats that may offer several potential food sources is to be expected. So far cues characterising favourable habitats are usually described in terms of physical parameters such as microclimate, light, humidity, temperature etc. However, few investigations have been devoted to discovering how the plant chemosphere affects the behaviour both of herbivores and their enemies. The chemical characterisation of a favourable habitat for a polyphagous insect, such as the adult *C. septempunctata,* would mean information on plant status as well as presence of prey. From a chemical point of view, most of the active substances may be ubiquitous, and it is still an open question how the message is formulated (Pettersson et al 2005).

The aim of this paper is to discuss foraging behaviour of the polyphagous adults of *C. septempunctata* and make some comparisons with more prey-specific third trophic representatives (ladybirds and parasitoids). Special reference will be given to effects of volatile stimuli, habitat choice and tritrophic effects of plant/plant communication mediated by chemicals – allelobiosis (*sensu* Pettersson et al. 2003; Ninkovic et al. in press).

Different spatial scales in searching – habitat choice and finding food sources

In terms of spatial scale, different stages can be recognised in foraging behaviour. The first step is to find high quality habitats likely to contain food, and the second is to locate prey/food over a closer range. To some extent these two steps may share mechanistic traits, such as cues and stimuli, but from a behavioural point of view the insect responses may be quite different. For close range responses, factors such as functional response, habituation, learning and handling time may be important whereas for high quality habitat choice, cues may have more importance in behavioural priming, release of arresting responses, conditioning and preparation for close range responses (Dixon 2000). To distinguish between habitat choice and food search it might be useful to view stimuli supporting habitat choice as priming stimuli that prepare the individual to respond to stimuli directly related to food source.

Identifying high quality habitats

Availability of preferred food and an acceptable microclimate are key factors for habitat preferences of *C. septempunctata*. Gut dissections of field collected adults (Triltsch 1999) show that food choice varies during the season and encompasses aphids, pollen and fungal spores. However food can be ranked, with aphids as the highest priority 'essential food', and other items such as pollen, fungal mycelia and organic matter as a lower priority 'less optimal food' (Hodek & Honek 1996). Even a limited addition of 'essential food' (aphids) to a diet of less optimal food increased the reproductive capacity of *C. septempunctata* and *Coccinella transversalis* (Evans et al. 1999; Evans 2000). There is also experimental evidence that the nutritional value of the same aphid species for preimaginal development may vary according to the host plant on which the aphids had been feeding (Giles et al. 2002). In terms of preference, the priority may change depending on food availability and the physiological status of the insect. Thus it has been suggested that during the start of the season, a preference for pollen is related to the insect's need for water (Hodek & Honek 1996).

For adult *C. septempunctata*, the search for food resources and favourable habitats assumes special importance during the seasonal migrations to and from hibernating sites. During the spring migration from hibernating sites, resources are needed to optimise development of the ovarioles and eggs before and during oviposition. In the beginning of this period, food consumption rate is moderate but it reaches a maximum before and during oviposition. The second important period is when the adults are preparing for hibernation, and build a resource of fat body cells that is gradually consumed during the winter (Hodek & Honek 1996).

As *C. septempunctata* is both a carnivore and a herbivore, a link between botanical diversity and preferred habitat can be expected. Thus a favourable habitat should potentially offer both a diversity of prey species and pollen or other organic matter for survival. Consequently, high botanical diversity should be indicative of a favourable environment. The importance of increased botanical diversity has been discussed in connection with mixed cropping and effects on herbivore natural enemies (Vandermeer 1992). A recent review of mixed cropping (Norris and Kogan 2005) states factors such as microclimate and diversity of food have a general importance for the positive effects that have been found in field experiments. Other influential factors may be the host plant species or genotypes that are combined, and soil fertility and water regime. In studies with outdoor microcosms with two levels of soil fertility and a tritrophic system with grasses (Fraser and Grime 1998), aphid and plant biomass responded dramatically to increased fertility as did ladybird feeding. Thus it may be hypothesised that a favourable ladybird habitat should also include fast growing plants. Although volatile cues could play an important role, the knowledge on such mechanisms is still fragmented. In principle, chemical messenger substances could act directly on the insects. For example, Schaller and Nentwig (2000) made olfactometer experiments with ethanol extracts of 22 different plants and found extracts of *Berberis vulgaris* and *Tripleurospermum inodoratum* to be attractive.

However messenger substances could also act indirectly by inducing responses in neighbouring plants that affect insects that are living on and around these plants (Ninkovic et al. in press) Experiments with adult *C. septempunctata*, barley and two common weeds, *Elytrigia repens* L. Bauv. and *Cirsium arvense* (L.) have led to discussion of plant olfactory cues as a factor that contributes to the aggregated distribution and habitat preferences of *C. septempunctata* adults in barley fields (Ninkovic and Pettersson 2003). An inventory of ladybird food was made in a commercial barley field with plants at the two leaf stage. No aphids or flowering weeds or other sources were present in the field. Estimates of the distribution of *C. septempunctata* showed that the number of adult ladybirds was higher in barley plots containing one of the two weeds than in weed-free barley plots with comparable plant biomass.

In laboratory olfactometer experiments (Ninkovic and Pettersson 2003), the plant combinations were tested for ladybird preference. Neither of the weeds was shown to be directly attractive to adult ladybirds. However, when odour blends of volatiles from barley and either of the two weeds was presented, both were preferred compared to odour of barley only. When the weeds themselves were removed from the odour blend, ladybirds still showed a preference for barley plants previously exposed to *C. arvense* compared to unexposed barley plants. However, the same preference was not shown for barley plants exposed to *E. repens*. The results of the experiments can be taken as support for the hypothesis that plant volatiles can contribute to aggregation in weedy field plots by acting as an arresting factor. The effects of *E. repens* may represent ladybird recognition of a 'broader plant diversity', while those to *C. arvense* invite discussion of how plant interaction via volatiles affect insects living on and around them. Field data supporting host plant-defined habitat preference is presented by Leather et al. (1999).

Plant interaction with the environment is mediated by a wide range of stimuli, of which chemical messenger substances represent one category. So far most of the experimental evidence for ecological effects of chemically-mediated plant/plant communication (allelopathy - Rice 1984) is limited to how one plant affects another plant. The most common biotic challenge to a plant individual is sharing available resources with neighbouring plants. One may speculate that plant/plant communication induces a condition similar to general plant stress which can be recognised by adult ladybirds, leading to similarities with the herbivore-induced effects that are used in a more precise search. This would mean that, under certain conditions, undamaged plants can affect the behaviour of herbivores and their natural enemies (allelobiosis - Pettersson et al. 2003; Ninkovic et al. in press). These results support the hypothesis that allelobiosis may contribute to arresting behaviour, and also that mixed plant species odours may do the same under certain conditions. It may also contribute to a mechanistic explanation of results obtained by Honek and Martinkova (1991) in experiments with maize and *Echinochloa crus-galli.*

Traces of food - damaged plants

The food quality of a given source is decided by several factors, and may vary when affected by external cues. Secondary metabolites may affect not only the suitability of plant material but can also be transmitted to aphids feeding on the plants, making them a less favourable food source (Hodek and Honek 1996). This has been shown for *Adalia bipunctata* (L.) (Francis et al 2001) and for *Hippodamia convergens* Bonvoulor fed with aphids from resistant and non-resistant sorghum cultivars (Rice and Wilde 1989). Thus the food value of a certain aphid may not only depend on its species, but also on which host plant it has been found. It could be expected that learning, adaptation and physiological status would be important factors that increase eating efficiency, reduce searching time and increase the relative values of particular food items (Vet and Dicke 1992; Hodek and Honek 1996). However, there are few published experimental studies that conclusively confirm the extent to which *C. septempunctata* has developed these abilities.

One of the first experimental demonstrations that ladybirds use traces of aphids in finding food sources was given by Hagen (1971). He showed that deposition of aphid honeydew components promotes ladybird presence. In later studies, it has been claimed that the amino acid tryptophan occurring in the honeydew played an important role. However, recent investigations have shown that plots treated with sucrose are significantly more attractive to *C. septempunctata* than untreated plots (Evans and Gunther 2005). Attraction of ladybirds to honeydew can be interpreted in different ways. The most obvious is that it contains an arresting/aggregating factor, but there are other possible explanations. One is that honeydew deposition during aphid feeding indirectly contributes to ladybird aggregation as it is an excellent substrate for fungal epiphytes which also offer a food source for adult ladybirds. Although no experimental evidence seems to be available, it may be that the fungi themselves release cues that support ladybird searching. Sooty moulds sometimes cover the leaf surface to the extent that there is a significant reduction of the photosynthesis of the plant (Vereijken 1979). This raises the possibility that the positive effects observed under field conditions are the result of ladybird responses to a stressed plant condition.

Recent investigations lead to the idea that plant stress responses to herbivory may cause changes which makes the plant more attractive to ladybirds. Aphid attack changes the pattern of volatile compounds emitted by the plant. There is also experimental evidence that changes of the volatile profile in an attacked plant may induce changes in neighbouring plants, making them less attractive to aphids (Pettersson et al. 1996). To what extent this interaction operates under natural conditions is unknown. It can be expected that the particular plant and herbivore species combination will be important for the effects on herbivores (Ninkovic et al. in print) and higher next trophic levels. Olfactometer experiments show that ladybirds prefer aphid-attacked plants to non-attacked plants (Ninkovic et al 2001). This is in line with the elegant studies on mites on lima beans (Dicke 1999; Bruin et al. 1995; Bruin and Dicke 2001) where it has been shown that beans attacked by herbivorous mites are attractive to predatory mites. Similar results have also been reported in relation to the searching behaviour parasitoids of *Cotesia spp.,* for which plant responses to herbivore attack have a decisive importance for prey localisation (Turlings et al. 1995). In this example, the stress condition of a maize plant is induced by the armyworm larvae on which the adult parasitoid oviposits. It has been claimed that a substance, volicitin, in the saliva of the caterpillar induces a change in the volatile profile of the attacked the maize, which is then detected by the parasitoid during its search for oviposition sites (Alborn et al. 1997).

Some chemicals related to herbivore damage have been shown to release a positive response in adult *C. septempunctata.* Exposure of plants to volatile *cis* – jasmone, a common plant volatile, induces airborne release of defence compounds that make the plants less acceptable to herbivores such as aphids, and which promotes recruitment of natural enemies such as *C. septempunctata* and aphid parasitoids (Birkett et al. 2000). Pilot studies with methyl salicylate have shown a similar pattern (Ninkovic et al unpublished). Studies indicate that communication between herbivore-attacked plants also influence insect/plant relations in neighbouring plants that are not yet attacked (Bruin et al. 1995; Dicke, 1999; Bruin and Dicke, 2001; Pettersson et al. 1996). Conclusive field data demonstrating the importance of communication between attacked and non attacked plants is still lacking but, based on available results, our hypothesis is that plant responses to herbivore attack provides a lead for third trophic level organisms to find prey/food sources. Induction of responses in neighbouring plants may also contribution to the creation of a favourable habitat cue, supporting the foraging behaviour of *C. septempunctata.*

The aphid alarm pheromone substance E-beta-farnesene (EBF) is a semiochemical with a potentially important role for immediate aphid prey localisation. However, EBF is also a common substance in nature and it has been shown that beta-caryophyllene, another common plant chemical, modifies the ladybird response to EBF (Al abassi et al. 2000). Only when there is an excess of EBF in relation to beta-caryophyllene does the former act as a positive stimulus. Below a threshold ratio it releases no behavioural response. It is still an open question whether there is a variation in content of these substances in certain plant stages/species, and to what extent this may affect the foraging behaviour of *C. septempunctata*.

Aphid population dynamics has a key influence on the ecological success of *C. septempunctata*. The overall regulator of aphid density in a colony is development of winged forms (alatae) as a response to colony density and intermittent feeding (Dixon 1998). However, it has also been shown that chemical cues are involved in regulation of mobility at an earlier stage in the colony development, affecting wingless aphids (apterae). These substances act as an aphid spacing pheromone and are behaviourally active when the colony size exceeds a certain threshold value (Pettersson et al. 1995; Quiroz et al. 1996). Obviously cues indicating high population densities would be valuable to ladybirds in their search for aphid colonies. Olfactometer experiments with the key components in density related substances reported by Quiroz et al (1997, 1998) indicate that these substances have an arresting effect on walking of ladybird adults (Ninkovic et al. unpublished).

Discussion and concluding remarks

The foraging behaviour of ladybirds can be considered at different spatial scales, as discussed by Dixon (2000) and illustrated by examples of active mechanisms given above. One obvious set of stimuli and mechanisms is directly related to available food sources such as aphids and pollen. The aphid alarm pheromone represents such a stimulus that leads the ladybird to a prey over short distances.

The next spatial level – the high quality habitat - is represented by cues that may be related to food sources, but active stimuli can be expected to fill the main purpose of primers for receiving the close range information for different food sources. A typical informative source of this kind would be volatile blends from herbivore (aphid) attacked plants. This represents a plant individual in a specific condition, caused by aphids or possibly other organisms that may serve as food sources. It can be questioned whether this is a general plant stress condition. If so, similarities can be expected with the allelobiotic condition reported in the *Hordeum/ Cirsium* interaction (Ninkovic and Pettersson 2003). Thus certain plant species communities would be more attractive for *C. septempunctata* than others, and the operating mechanism would not always be beneficial for the ladybird as it is based on ecological traits for plant competitiveness.

From a behavioural viewpoint, a semiochemical or a set of preferred cues such as microclimate, host plant odour etc. form a barrier around a preferred habitat which acts as an invisible mechanical barrier. This edge effect is independent of whether the wall is a physical wall or if it is a set of physical or chemical stimuli that creates a division between a preferred and less preferred environment. The relative strength of the behavioural response decides how well expressed the barrier is. This ‘barrier of preference’ is the basis for aggregated distributions, and how strongly it is expressed may vary during different phases of the insect’s population ecology.

An arrestment response is the final result of several behaviour components. Two important parameters are the relative value (RV) of staying in the preferred environment and the temporal dynamics (TD), the time between perception of the stimulus and a behavioural outcome. TD has a relative value i.e. the rank of stimuli preferences/responses to active cues related to different resources such as food. These two elements constitute the basis for a simple theoretical model that predicts the influence of behavioural cues in relation to aggregation, assuming that the food resource is equally available:

- low RV and short TD would result in small, well defined aggregates
- high RV and short TD in distinct, well delimited aggregates
- low RV and long TD in very discrete aggregates, if any at all
- high RV and long TD would give high frequencies but discrete edges

The two parameters of this simplified model can be applied to the population biology of *C. septempunctata* in relation to the presence of aphids in a cereal crop field. Aphid prey is a profoundly preferred food and represents high RV in the model (Hodek and Honek 1996; Majerus 1994). Responses to stimuli representing aphid presence are active over short distances and promote a short TD. Pollen is a survival food, but may be seen as representing a long TD source.

The initial output of the model is very straightforward, and states that where there are aphids available, distinct and pronounced aggregates of foraging *C. septempunctata* can be expected, and where there are few or no aphids, *C. septempunctata* aggregates are not likely to be found. For the individual ladybird this means that further investments in migration/foraging are required. So far the model is a perfect support for the ‘tramp hypothesis’ of foraging behaviour of the sevenspotted lady bird as suggested by Evans (2003).

The model also encourages discussion of the importance of less well known ladybird habitat preferences for aggregation. Pollen is regarded as a less preferred survival food with low RV (Hodek and Honek 1996) and, with no insect learning/habituation capabilities, it can be classified as a long TD which would result in very discrete aggregates if any at all. However, with a learning/habituation ability, TD would be shorter and the aggregates well developed. This would be in line with observations in Ninkovic et al. (2003), and support suggestions by Vet and Dicke (1992). This discussion also lends support to the hypothesis that plant community composition has a positive effect on a aggregation/foraging of *C. septempunctata*.

With regards to plant communities, the general prediction from the model is that both learning and quality of pollen as a food source have an immediate importance for the 'visibility' of the aggregation behaviour of *C. septempunctata*, adding a dynamic element to the 'tramp hypothesis' (Evans 2003). *C. septempunctata* preference for a plant community can be a response to botanical diversity or to plant status as affected by allelobiosis. So far, knowledge on allelobiosis exists mainly as examples from barley cultivars and some weeds. However, if results from these experiments (Pettersson et al. 2003; Ninkovic et al. in press) can be shown to represent a generally occurring mechanism, it is an aspect that should be considered in future studies of *C. septempunctata* foraging behaviour.

In principle, the time taken for searching/foraging means time lost for feeding and digestion. Thus foraging mechanisms and strategies can be considered as decisive ecological traits with high evolutionary status for a species. Migration plays an important role in the ecology of *C. septempunctata*, and the patchy distribution of food resources favours habitat search compared to mechanisms for individual prey foraging. Recent studies on the effects of plant/plant communication on the behaviour of the seven spotted ladybird indicate that allelobiosis is a mechanism that should be considered in future studies of foraging behaviour of *C. septempunctata.*

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