

# FORAGING BEHAVIOUR OF PREDACEOUS LADYBIRD BEETLES: A REVIEW

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## ABSTRACT

We review the foraging behaviour of predaceous ladybirds in the light of current knowledge. Ladybirds should forage optimally to maximise their resources; however, they are limited – among other things – by their poor visual acuity. Ladybird foraging behaviour includes location of the habitat of its prey, location of prey and prey-selection. Chemical cues are important in locating the habitats of their prey. This is further driven by volatiles or semiochemicals emitted by injured plants, particularly in response to attack by herbivores. Various chemicals induce positive electroantennographic responses in ladybirds that guide them to prey sites. Honeydew secreted by aphids along with alarm pheromones or kairomones act as secondary chemical cues that narrow the search from extensive to intensive and help in prey location. Visual cues further aid prey-location and enable foraging adults to locate areas with patchy or abundant prey. Thereafter, ladybirds select their prey, which starts with random attacks that result in prey selection in terms of size and palatability. Prey selection seems to be host plant driven, i.e. aphids sequester host plant chemicals, which are imbibed by ladybirds. This is evident from the fact that nutritious prey cultured on toxic host plants are usually less preferred or rejected. Foraging ladybirds, especially larvae, can perceive ladybird footprints or odours that deter them from foraging. The above information could be useful in biocontrol programmes in which foraging ladybirds are manipulated by using chemicals as attractants or rearing aphids on nutritious host plants.

**Keywords:** aphids; Coccinellidae; cues; searching behaviour; semiochemicals

## Introduction

Ladybird beetles (Coleoptera: Coccinellidae) are economically important predaceous insects having a wide prey range (Dixon 2000; Omkar and Pervez 2004a; Pervez and Omkar 2004; Hodek et al. 2012; Omkar and Pervez 2016). Their foraging behaviour is well studied because of their biocontrol potential. Riddick (2017) attempted to identify the conditions suitable for the biocontrol of aphids using ladybirds, in terms of their foraging potential in greenhouses. Hodek and Evans (2012) consider the foraging behaviour of ladybirds to be an important aspect of their relationships with food and reproduction. To become successful foragers, these ladybirds might experience a trade-off between the time available for foraging and the availability of prey (Heit et al. 2007). However, ladybirds are reported walking aimlessly in dense aphid colonies, even walking over aphids and leaving them unharmed (Murdie 1971). Hence, ladybirds are also referred to as ‘blundering idiots’, as pointed out by Hodek and Evans (2012).

Initially, the researches focussed on behavioural aspects of ladybirds related to foraging. This was followed by theories and formulating hypotheses that need empirical testing in terms of the dynamics of foraging patterns in ladybirds. The area concentrated search foraging model (Wiens 1976) states that predators, for example, ladybirds, initially forage extensively for patches of prey and once found switch to searching intensively and consuming prey. However, if prey is absent or rare predators forage more extensively by quickly moving in straight lines and rarely halting (Ferran and Dixon 1993), thereby minimizing the wastage of time and energy. Hodek and

Evans (2012) while reviewing food relationships in ladybirds, commented that progress in the field of chemoeology helped in better understanding the intricacies of coccinellid foraging behaviour. Hence, there is a need to present updated information on foraging behaviour, especially in the light of advances in chemoeology. We review the literature, with an emphasis on current knowledge, to better understand the foraging patterns of coccinellids. We concentrated on the cues used by ladybirds to locate their habitats and in searching and selecting their prey. Issues regarding how their foraging ability can be manipulated are also addressed.

## Optimal Foraging and the Prospects of Using Ladybirds in Biocontrol

Foraging ladybirds in search of food and oviposition sites visit many patches of prey (Dixon 2000). Optimal foraging theory assumes that predators decide and select optimal food resources to maximize their rate of food intake and hence improve their fitness and reproduction (Stephen and Krebs 1986). According to the optimal foraging theory, ladybirds should select the most profitable prey and reject unprofitable prey (Crawley and Krebs 1992). However, a few of the assumptions of this model, for instance, predators should estimate the profitability of a patch of prey even before entering it, are unrealistic due to the poor visual acuity of ladybirds (Roger 1999). Predators, particularly female ladybirds, search for patches of prey in which to lay eggs that will provide their offspring with food (Kindlmann and Dixon 1993). Hence, various costs and benefits are associated with optimal foraging.

Costs are usually expressed in terms of time and energy consumed in selecting prey or the habitat of their prey and the associated risks. Prey selection is largely dependent on factors, like success in capturing prey, handling time and energy content of the prey. For instance, ladybirds attack small and intermediate sized prey as they are easy to capture. Similarly, handling time of small prey is less than that of large prey (Pervez and Omkar 2003). However, the energetic value of large prey is greater. Age and size of the ladybirds affect their foraging efficiency, for instance, old and big ladybirds are better at searching and capturing prey.

According to the assumptions of the optimal foraging theory, ladybirds should maximize their rate of successful encounters with prey per unit time. The foraging time includes time spent travelling between prey patches as well as that spent intensively searching a patch (Ferran and Dixon 1993). Hungry ladybirds resort to more intensive searching and are simultaneously less selective in their choice of prey. Ladybirds spend most time in patches where prey is abundant and/or prey is palatable (Roger 1999). Kindlmann and Dixon (2010) present a metapopulation model describing this theory by further adding components, like egg-window dynamics and within- and between-season dynamics. They conclude that the effect of predators on aphid populations is likely to be less late in the season than very early in the season, as aphid colonies are then small. Kindlmann and Dixon (1999a,b) question the effectiveness of aphidophagous ladybirds in controlling aphids as their generation time ratio (GTR) relative to that of aphids is greater than one as ladybirds develop more slowly. It is predicted that in aphid-ladybird systems, owing to the large GTR, reproduction of ladybirds should be correlated with the age of aphid colony rather than the number of aphids, and top-down regulation is weaker (Kindlmann and Dixon 2001). Results of field experiments support the GTR hypothesis, as the aphidophagous ladybirds do not have a significant negative effect on the peak numbers of the aphids (Kindlmann et al. 2015). Hence, because of their high GTR aphidophagous ladybirds are unable to regulate aphid populations in the field.

## Dynamics of the Foraging Behaviour of Ladybirds

Foraging in ladybirds can be categorized broadly into three phases, *viz.* (1) location of the habitat of their prey, (2) location of their prey and (3) prey selection (Hodek 1993). These phases are driven by several factors like chemical cues, visual cues, host plant architecture, foraging deterrent pheromones, *etc.* These factors are discussed in detail below:

### Chemical Cues

Hinkelman (2012) reports that foraging based on sensory cues outperforms that based on the chance encoun-

tering of resources and suggests that natural selection might favour foragers that switch to depending on sensory cues rather than encountering resources. Amongst the sensory cues, chemicals play a pivotal role in locating the habitat of their prey. Hatano et al. (2008) review this aspect and emphasize the importance of semiochemicals in prey selection by natural enemies. Similarly, Pettersson et al. (2008) give an account of the chemical stimuli important in the foraging behaviour of the seven-spot ladybird, *Coccinella septempunctata* Linnaeus. Tapia et al. (2010) also report that semiochemicals are key factors in predator-facilitation, *i.e.* presence of predators on an aphid-infested plant trigger the release of alarm pheromones by the aphids. These pheromones bring other ladybirds to the prey site that may synergistically or antagonistically affect a decrease in the aphid population. It is widely held that volatiles emitted by plants injured by herbivores are used by foraging ladybirds to locate their prey. Increasing laboratory evidence indicates that ladybirds are more attracted to damaged than undamaged host plants (Ninkovic et al. 2001; Han and Chen 2002a; Francis et al. 2004). Pare and Tumlinson (1999) are of the opinion that plants change their volatile profiles after being attacked by herbivores, particularly aphids, and thereby emit compounds synthesized *de novo*, which attract and guide natural enemies towards their prey.

Olfactometer experiments indicate that adults of *C. septempunctata* are attracted in greater numbers to twigs and leaves of different host plants infested with aphids than to aphids alone (Khan et al. 2017). Similarly, adults of the ladybird, *Cycloneda sanguinea* Linnaeus take less time to locate olfactometer chambers containing the aphid, *Myzus persicae* Sulzer infesting leaves of tomato, *Lycopersicon esculentum* Mill than chambers containing only *M. persicae* or leaves of tomato (Heit et al. 2008). This further indicates that foraging is largely driven by volatiles released by aphid-infested plants. The mycophagous ladybird, *Psyllobora vigintimaculata* (Say) is attracted to squash plants, *Cucurbita moschata* Duchesne, infested with powdery mildew, *Podosphaera* sp. (Tabata et al. 2011). However, aphidophagous ladybirds tend to visit undamaged plants to feed on pollen and nectar in the absence of prey (Michaud and Qureshi 2005). Similarly, certain plant volatiles are attractive for ladybirds, regardless of the plants being infested or not, and these volatiles can be used to attract ladybirds (Ninkovic and Pettersson 2003). On the contrary, adults of the ladybird *Eriopis connexa* (Germar) are not attracted to aphid infested plants in an artificial environment (Tapia et al. 2010). This probably indicates that integration of other cues might trigger or support its foraging behaviour.

Hatano et al. (2008), in their review, list chemicals from several aphid-plant complexes along with their effects on ladybirds. The soybean plant, *Glycine max* L., emits methyl salicylate when attacked by the aphid *Aphis glycines* Matsumura (Zhu and Park 2005). Applying this compound to the antennae of *C. septempunctata* results in

a positive electro antennographic (EAG) response. Similarly, benzaldehyde is emitted when the aphid, *Toxoptera aurantii* (Boyer de Fonscolombe), attacks shoots of *Camellia sinensis* L., in response to which *C. septempunctata* exhibits a positive EAG response and is attracted to the plant (Han and Chen 2002a, b). Similarly, methyl salicylate is an herbivore-induced plant volatile, which triggers ladybirds to aggregate on aphid infested plants for feeding and oviposition (Salamanca et al. 2017). These chemicals are perceived over very long distances by sensillae present on the antennae of adult ladybirds (Omkar and Pervez 2008). A few chemicals are listed below that could be used as attractants for these ladybirds and thus may be helpful in aphid biocontrol (Table 1).

Further, honeydew secreted by aphids, acts as a secondary olfactory cue in attracting predators, particularly ladybirds, to aphid prey. Artificial spraying of honeydew attracts ladybirds, e.g. *Hippodamia* sp. to aphid habitats, thereby making it useful in integrated pest management (IPM) programmes (Hagen et al. 1971; Evans and Richards 1997). Larvae of the ladybird, *H. convergens* stay longer in patches contaminated with honeydew compared to clean patches (Purandare and Tenhumberg 2012). In addition, these larvae are unable to distinguish between high and low-quality aphid honeydew. However, it also acts as an arrestant for certain predators and prolongs their searching time (Ide et al. 2007).

Foraging ladybirds also perceive kairomones released by aphids (e.g. alarm pheromones) and use them as secondary cues for prey location and thereby switch from extensive to intensive search (Francis et al. 2004, 2005). Aphids on being attacked by a ladybird larva also release *E-β-farnesene*, which attracts other conspecific larvae to attack the prey (Hemptinne et al. 2000). Cornicle secretions and cuticular chemicals of aphids are also secondary cues for foraging ladybirds (Seagraves 2009).

### Visual Cues

It is an established fact that chemical cues help in locating the habitat of the prey. Further, other cues and signals are also perceived by foraging ladybirds. Amongst these cues, visual cues are considered to be the major ones. However, they are rarely mentioned in the literature

where more importance is given to chemical cues. Bahlai et al. (2008) suggest that adult *H. axyridis* depend upon long-range visual cues to locate host habitats. Adult ladybirds tend to be attracted by silhouetted shapes and foliage of host plants regardless of olfactory cues. Adults of *Chilocorus nigritus* (Fabricius) prefer to forage near horizons that simulate treelines over flat horizons (Hattingh and Samways 1995). Most ladybirds prefer to forage during daytime, as they can use visual cues for finding prey. This is evident from the increased aphid consumption in daytime compared to that at night (Harmon et al. 1998). In addition, ladybirds, for instance, *C. septempunctata* consume a greater number of *A. pisum* that contrast in colour with the background. Certain ladybirds, viz. *H. convergens*, *Coleomegilla maculata* (deGeer), *H. axyridis* and *C. septempunctata*, consume more red individuals of *A. pisum* than green ones (Harmon et al. 1998). Similarly, naive adults of *H. axyridis* are more attracted to yellow than green pillars (Mondor and Warren 2000), as yellow pillars resemble stressed or young plants that are more likely to be infested with aphids (Lorenzetti et al. 1997). Most of the foraging activity of the ladybird *Propylea dissecta* (Mulsant) occurs in daytime (Mishra and Omkar 2004). However, the major life events such as mating, oviposition, hatching and moulting occur at night, which indicate the importance of visual cues that are needed for the ladybird to forage. Heit et al. (2007) did not find any difference in the foraging behaviour of adult male and female *C. sanguinea* during the morning and afternoon. However, as the day progressed, they noticed a decline in foraging probably due the fact that other activities, such as mating, are more likely to occur later in the day.

Ferran and Dixon (1993) suggest that conditioning in ladybirds affects their foraging ability. Learning from previous experience helps them to switch from extensive to intensive search. For instance, laboratory-reared *H. axyridis* have a strong affinity for pea aphids (*A. pisum*) and any sign or smell of this prey enables the predator to switch to intensive search (Ettifouri and Ferran 1993).

### Locomotor Activity

The locomotor activity of predators plays a crucial role in their foraging behaviour (Bell 1990). Heit et al.

**Table 1** List of the allelochemicals released by plants attacked by aphids that attract ladybirds.

Ladybird	Prey	Host Plant	Allelochemical	Reference
<i>Coccinella septempunctata</i>	<i>Aphis glycines</i>	<i>Glycine max</i> L.	Methyl salicylate	Zhu and Park (2005)
<i>C. septempunctata</i>	<i>Toxoptera aurantii</i>	<i>C. sinensis</i>	Benzaldehyde	Han and Chen (2002a)
<i>C. septempunctata</i>	–	–	(Z)-jasmone	Birkett et al. (2000)
<i>C. septempunctata</i>	–	–	(E)-β-farnesene	Al Abassi et al. (2000)
<i>Hippodamia convergens</i>	Eggs of <i>Ostrinia nubilalis</i> Hübner	<i>Vaccinium macrocarpon</i> Ait	Methyl salicylate	Salamanca et al. (2017)
<i>H. convergens</i>	<i>M. persicae</i>	–	(E)-β-farnesene	Acar et al. (2001)
<i>A. bipunctata</i>	<i>M. persicae</i> <i>A. pisum</i>	–	(E)-β-farnesene	Francis et al. (2004)

(2007) in their series of experiments found that locomotory activity decreases significantly when the adults encounter plant leaves infested with high or low numbers of aphids compared to when they search uninfested leaves. Ladybirds forage differently in the field compared to in the laboratory. The ladybird, *Harmonia axyridis* (Pallas) forages, attacks, kills and consumes prey at a faster rate in the field than in the laboratory (Latham and Mills 2009). Longer legs are likely to enable it to move faster (Teuscher et al. 2009). However, adults of the ladybird, *C. maculata*, attacking whitefly in greenhouses are impeded by trichomes (small hair-like outgrowths from the epidermis of a plant) whereas the smaller ladybird, *Delphastus catalinae* (Horn) is not affected by trichomes (Lucas et al. 2004). In addition, their locomotor activity is significantly greater in the afternoon than in the morning.

Certain aphids, for example the pea aphid, *A. pisum*, may detect ladybirds and respond by dropping from the plant (Losey and Denno 1998). Thus, significantly reducing the foraging efficiency of the ladybirds, which in the case of *H. axyridis* can be as much as 40% (Francke et al. 2008).

### Plant Architecture

Plant architecture is important in the food choice of insect predators, particularly ladybirds, as their larvae crawl over and capture prey on the surfaces of plants (Reynolds 2011). Plant structures, particularly, their morphological features like texture, shape and size have a great effect on the foraging success of ladybirds. Plant architecture has a direct effect on the walking speed and attack rate. This also affects the host preference of ovipositing ladybirds. However, increase in the heterogeneity of plant structures decreases the foraging capacity of ladybirds. For example, larvae of the ladybird *C. septempunctata* forage less successfully for pea aphids, *A. pisum*, on highly branched varieties than on normal varieties of peas (Legrand and Barbosa 2003). Even the surface texture of plants, *i.e.* hairiness or slipperiness, affect the foraging ability of ladybird larvae. Trichomes reduce the foraging and walking speed of predators (Stavrinos and Skirvin 2003; Riddick and Simmons 2014). Similarly, waxy plants reduce the foraging success of ladybirds, for instance, larvae of *H. convergens* are more successful foraging for aphids on non-waxy cabbage than on a waxy variety (Chang et al. 2006). The effect of leaf waxes is however largely ignored in the literature. In addition, larvae of *C. septempunctata* are less effective in foraging and killing prey on foliage, which has more junctions (Legrand and Barbosa 2000).

Presence of wax on the surface of plants, especially leaves, plays a significant role in the foraging ability of ladybird larvae. Increase in surface wax reduces the walking speed and searching efficiency of coccinellid larvae, and also tends to result in the larvae losing adhesion and falling from leaves (Rutledge and Eigenbrode 2003; Rutledge et al. 2008). The adhesion of foraging larvae

depends on the texture and surface wax on leaves, for instance, the presence of crystalline epicuticular wax on the pea plant, *P. sativum* (Eigenbrode et al. 2008). A morphological study of the way *Cryptolaemus montrouzieri* Mulsant adheres to plants surfaces combined with measurements of the forces that keeps beetles attached to plant surfaces is reported by Gorb et al. (2008).

### Effect of Footprints / Foraging Deterrent Pheromones

Adults and larvae of ladybirds leave trails or footprints (Mishra et al. 2012; Kumar et al. 2014a) in the form of non-volatile hydrocarbons (Magro et al. 2007), which deter other foraging ladybirds. These chemicals may be referred to as deterrent pheromones as they inhibit foraging activity (Ruzicka and Zemek 2008; Moser et al. 2010). The first instar larva of an aphidophagous ladybird, *Cycloneda limbifer* Say respond to conspecific larval tracks by avoiding or leaving such microhabitats (Ruzicka and Zemek 2008). This probably indicates that foraging larvae balance the spatial variation in the concentration of larval tracks by shifting from microhabitats with high to lower concentrations of larval tracks. Thus, in field condition, it is likely that the regulation of prey-location might be driven by the ratio between attractant and deterrent pheromone-cues. Active foraging of early instars in uninvaded or less contaminated aphid colonies reduces the risk of cannibalism or intraguild predation. In contrast, older instars search more effectively for better aphid colonies because they are less at risk. It seems that ladybird larvae optimize their distribution between aphid colonies according to the densities of both prey and larval tracks (Dixon et al. 1997; Kindlmann and Dixon 1999b).

In predatory guilds, small ladybirds are more easily deterred from foraging possibly because they are more vulnerable to intraguild predation (Kumar et al. 2014b). The fitness parameters, particularly growth-rate and conversion-efficiency, of small ladybirds even declines due to reduced foraging in habitats previously visited by other predators (Kumar et al. 2014a). In addition to deterring foraging, ladybirds' footprints also reduce the settling of herbivores, like aphids (Ninkovic et al. 2013) and psyllids (Seo et al. 2018), thereby resulting in declines in pest populations.

### Issues Pertaining to the Manipulation of Ladybirds' Foraging Efficiencies

Prey density dependent searching efficiency and prey consumption by ladybirds can be best described by a functional response (Pervez and Omkar 2003, 2005; Omkar and Pervez 2004b). It is widely held that most ladybirds exhibit a Type II functional response, *i.e.* they show a negative prey density dependence response in

which their rate of prey consumption decreases with increase in prey density. It is noticeable in the field and laboratory (Pervez and Omkar 2010) that ladybirds distribute themselves spatially and temporally on plants. Thus, their effectiveness as biocontrol agents can be manipulated and certain ladybirds with different spatio-temporal distribution tendencies can be manipulated for synergistically effecting the mortality of prey populations (Omkar and Pervez 2011). This can be beneficial as there is little interference between heterospecific ladybirds attacking the same prey. However, certain risks are associated with the tandem release of large and small ladybirds in aphid infested microhabitats (Omkar et al. 2014).

Prey-preference studies indicate that ladybirds have an affinity and preference for certain prey over others (Guroo et al. 2017; Pervez and Kumar 2017). In addition, this prey-preference depends largely on the host plant, as aphids sequester host plant allelochemicals and use them as a defence against ladybirds. For instance, *Acyrtosiphon nipponicus* (Aphididae), feeds on *Paederia scandens* (Lour.) Merr. (Rubiaceae) and secretes paederoside, an iridoid glycoside and lipids from its cornicles that helps it to defend itself from *H. axyridis*, as this chemical forces the ladybird to release the aphid and flee from the aphid colony (Nishida 2014). Thus, aphids sequestering such allelochemicals become toxic and unpalatable for ladybirds, which then avoid further attacking and consuming these aphids. Hence, despite this aphid being highly preferred when raised on suitable host plants, it is avoided when raised on a toxic host. Thus, we can manage the prey preference capabilities of ladybirds by providing aphids raised on suitable and nutritious hosts rather than toxic host plants.

## Conclusions

It is evident from this review that the foraging behaviour of ladybirds has been extensively investigated and modelled. However, the dynamics of searching behaviour are not well understood. Undoubtedly, mainly chemical cues guide foragers towards prey habitats. Such chemicals should be used in biocontrol programmes in order to attract foraging ladybirds to sites where prey are abundant. Visual cues are also important in facilitating the finding and selecting prey. However, this tendency greatly varies between ladybird species. Foraging deterrent pheromones are seemingly more responsible for changes in the foraging patterns of ladybirds after the prey has been located. Early instars avoid foraging in patches previously visited by predators. Furthermore, it would be risky if older instars pupate in colonies inhabited by numerous early instars, as later in their development these larvae are likely to attack the immobile defenceless pupae. Ladybirds that feed on toxic and unfamiliar prey and ignore nutritious prey during their search for prey are still

hard to explain. Advances in chemoecology have helped in our understanding of the intricacies of foraging patterns in ladybirds. However, more information regarding nature, structure and function of chemicals is needed to understand the details of foraging patterns of larvae and adult ladybirds and to implement them in biocontrol programmes.

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