



Lady beetle oviposition behavior in response to the trophic environment

Michael P. Seagraves *

USDA-ARS, North Central Agricultural Research Laboratory, 2923 Medary Avenue, Brookings, SD 57006, USA

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ABSTRACT

The food available to coccinellid larvae and their exposure to predation is influenced by where they are placed as eggs. This review examines adult distribution and female oviposition strategies which in turn determine the distribution of coccinellid larvae in habitats. Immigration into a habitat can be influenced by visual and olfactory cues related to habitat quality. Adults are retained in a habitat if sufficient food resources are present. The abundance and quality of food in a habitat affects the reproductive output of a female and survival of larvae. Consequently, there is higher retention and oviposition preference for sites with abundant essential prey. Coccinellids also increase reproduction in response to non-prey foods (i.e., pollen), but avoid ovipositing in areas with copious amounts of honeydew. In laboratory studies, many plant-derived chemicals have been demonstrated to be attractants and oviposition stimulants. The need to place eggs in proximity to food for offspring must be weighed against the risk of cannibalism and intraguild predation. Lady beetles avoid egg predation by reducing oviposition where other adults are present, ovipositing on plants associated with less exposure or incidence of intraguild predation, and avoiding areas with tracks and frass of con- and heterospecific larvae. Indeed, deterrent cues for avoiding predation seem stronger than the positive ones associated with food. An understanding of the resources needed for successful reproduction and larval development in a habitat and the sensory cues that signal these resources, and thus elicit oviposition, may enhance our understanding of the underlying mechanisms affecting coccinellid distribution in habitats.

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1. Introduction

Maternal reproductive decisions affect the local distribution of larval coccinellid populations within a habitat, and these decisions are driven in large part by trophic interactions with other organisms. Coccinellid larvae are voracious predators but are much less mobile than the adult stage, thus they often remain in patches selected by their mother. Accordingly, the distributions of food resources critical to larval development (Kindlmann and Dixon, 1993) as well as intraguild predation, including cannibalism, at the selected oviposition site strongly influence the reproductive success of a female (Cottrell and Yeorgan, 1998a; Schellhorn and Andow, 1999). Understanding the factors that influence oviposition behavior can be used to design cropping systems that augment densities of coccinellid predators (Seagraves and Yeorgan, 2006).

Ferran and Dixon (1993) suggested that to fill our knowledge gaps and improve the effectiveness of lady beetles we should examine adult behaviors and sensory capabilities of these predators that operate during oviposition. Here, I build upon an earlier review on the topic of reproductive decisions (Evans, 2003) by

focusing on recent work in the field and by examining the sensory cues that affect the selection of habitat patches, and that elicit or deter oviposition once in habitats. This behavior is not a step-wise hierarchical decision-making process but a suite of responses to overlapping sets of stimuli perceived by a gravid female. An understanding of how predators perceive and respond to positive and negative trophic signals, and how these affect their fitness, can greatly improve their utility in biological pest management.

2. General model of lady beetle reproduction

Chandler (1965) suggested that a balance between olfactory and visual cues from prey and infested plants drives the oviposition decisions of predators. However a less structured model (reviewed by Evans, 2003) of how oviposition occurs in lady beetles has emerged with subsequent research. In this scenario, lady beetles fly through a landscape and randomly land on plants. When prey is located, they initiate a local search pattern leading to their aggregation in areas of high prey density. Satiation typically ensues, which reduces their tendency to disperse and leads to a localization of oviposition. Indirect support for this general decision-making framework comes from the numerous observations of aphidophagous coccinellids that oviposit in areas of high prey density (Banks, 1956; Dixon, 1959; Wratten, 1973; Ives, 1981; Mills, 1982). Obviously this model relies

* Fax: +1 605 693 5240.

E-mail address: michael.seagraves@ars.usda.gov

upon work done with coccinellids whose life-history is based around their sternorrhynchan prey. Although there are caveats to this model, it still provides a framework for discussing the current knowledge of the reproductive decisions of coccinellids and likely applies to species that feed on mites and powdery mildew which also tend to be clumped in distribution.

3. Habitat selection by females

Critical to understanding lady beetle reproduction and their use in biological control is how the adults come to be in a particular habitat. Although it is conceivable that a coccinellid may enclose into a habitat with abundant food resources, it is more likely that it must disperse at some point over its adult life when prey becomes depleted (Obata, 1986). Kindlmann and Dixon (1999) show that prey quantity can become scarce during larval development. Individual species likely respond to habitat quality at different scales. For instance, *Adalia bipunctata* (L.), *Hippodamia tredecimpunctata* (L.), and *Hippodamia convergens* Guérin immigrant populations responded to increased aphid density in maize at the level of the plant, whereas *Coleomegilla maculata* (De Geer) only responded to increasing aphid densities at the plot (10 × 10 m) level (Schellhorn and Andow, 2005). Although much of the work reviewed here is not specific to gravid females it offers insight into the processes that ultimately determine the distribution of adults and thus to some extent oviposition at a landscape level.

3.1. Immigration

Information on sensory capabilities of foraging lady beetles challenge the traditional view (Hodek, 1993) that immigration of lady beetles is purely a random process which has been often questioned (see Hodek and Honěk, 1996, p. 102). Cardinale et al. (2006) found immigration by *Coccinella septempunctata* (L.), *C. maculata*, and *Harmonia axyridis* (Pallas) into alfalfa patches was not correlated with aphid abundance. Křivan (2008) examined data on *C. septempunctata* from Honěk (1982) using models that assumed immigration to be random, influenced by prey presence, or influenced by both prey and the presence of conspecifics. The model that assumed random immigration best fits the data. Note that the studies cited above focus on a narrow range of species, especially *C. septempunctata*, that are widely regarded as highly vagile habitat generalists (Hodek and Michaud, 2008). The coccidiphagous lady beetle *Chilocorus nigrinus* clearly moves toward sensory stimuli to locate habitat patches with prey as opposed to settling in them after a random search (Hattingsh and Samways, 1995). Additionally, there are many studies that report the directional movement of adult lady beetles to particular habitats in response to sensory cues, and it seems likely that these cues are influencing non-random habitat selection by coccinellids to some degree (see Section 4). Whether specific lady beetle species use sensory stimuli to direct immigration remains to be investigated or incorporated into any descriptive models.

3.2. Emigration

The availability of food and habitat characteristics are often coupled to a coccinellid's propensity for emigration. For example, providing non-prey foods, such as sucrose solution, within farmland can increase the residence time of lady beetles within a patch (Ewert and Chiang, 1966; Evans and Richards, 1997; Van Der Werf et al., 2000). Also, female *C. septempunctata* and *Hippodamia variegata* (Goeze) remain longer on fireweed stems with greater aphid numbers (Ives et al., 1993). *Coccinella trifasciata* (L.) departs alfalfa fields when aphid numbers drop below 0.3 per stem, and the larger

Coccinella californica Mannerheim emigrates at an unknown higher threshold (Frazer, 1988). The physical shape of a habitat can also influence the dispersal of a coccinellid. For example, square-shaped cabbage patches retained adult lady beetles longer than "I"-shaped patches of equal area, presumably due to the square shape having a lower perimeter to area ratio. Adults encountered boundaries and edges less frequently in the square plots, thus lowering emigration (Grez and Prado, 2000).

Coccinellid individuals sometimes disperse even from high quality habitats (Ives, 1981; Frazer, 1988), which illustrates the innate predisposition of some species toward dispersal. Even in patches of high prey density, some individuals are not retained. This leads to females spreading eggs out over several habitat patches, which may constitute a bet-hedging strategy (Frazer and Raworth, 1985; Evans, 2003). Factors affecting emigration have not been investigated specifically for gravid females. It remains unclear if females oviposit in locations where they are fed enough to produce eggs or if they actively gauge the amount and quality of 'nursery' prey (*sensu* Dixon, 2000). At times coccinellids will settle into a habitat and remain even if sufficient food is not present for oviposition (Honěk, 1978, 1980).

Among coccinellid species the degree of habitat specialization affects how individuals disperse from declining prey abundance. As a case in point, *H. axyridis* emigrated much more quickly than *Mulsantina picta* (Randall) from pines infested with low densities of *Eulachnus rileyi* (Williams) (Sloggett et al., 2008). *M. picta*, which is specialized to live within pine habitats, may persist in patches with lower prey density, whereas *H. axyridis* may be more prone to dispersal from a habitat with dwindling resources. Resources that will retain adults in a habitat differ even among species with similar life histories. Evans and Toler (2007) reported that *H. convergens* and *Hippodamia quinquesignata* (Kirby) aggregate in alfalfa only in response to increasing aphid density, whereas *C. septempunctata* responded to increased densities of an alternative prey (*Hypera postica* larvae) in addition to aphid density. These examples illustrate the challenges inherent in characterizing the mechanisms that drive habitat selection in this heterogeneous group of predators.

4. Proximate cues involved in coccinellid foraging

4.1. Olfactory cues

Olfactory cues are used by some adult lady beetles to direct their movement toward prey (Colburn and Asquith, 1970; Obata, 1986; Nakamura, 1991; Schaller and Nentwig, 2000). *C. maculata* electroantennogram (EAG) tests showed a positive response to aphid semiochemicals and to corn volatiles (Zhu et al., 1999). Zhu and Park (2005) reported that young aphid-infested soybean plants emit more methyl salicylate than uninfested plants, and traps baited with this compound caught significantly more *C. septempunctata* (but not *H. axyridis*) adults than did control traps. *H. axyridis* adults move toward olfactory cues from buckthorn and apple foliage, particularly aphid-infested foliage (Bahlai et al., 2008) and also toward pea aphid colonies (Mondor and Roitberg, 2000; Verheggen et al., 2007). *C. septempunctata* responds to olfactory cues from *Toxoptera aurantii* (Boyer), *T. aurantii* cuticle, and aphid-damaged tea shoots (Han and Chen, 2002). Honeydew collected from *T. aurantii* evokes a particularly strong EAG response from *C. septempunctata* (Han and Chen, 2002). In contrast, Schaller and Nentwig (2000) found that *C. septempunctata* adults were not attracted to the odor of *Acyrtosiphon pisum* (Harris) honeydew. *Stethorus punctum picipes* (Casey) is attracted to the synthetic plant compounds methyl salicylate, (*Z*)-3-hexenyl acetate, cis-3-hexen-1-ol, and benzaldehyde, which are associated with herbivore damaged plants (James, 2003, 2005; James and Price, 2004).

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