



Lady beetle oviposition behavior in response to the trophic environment

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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

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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).

Alarm pheromones of prey are another set of proximate cues attractive to some coccinellids. The aphid alarm pheromone (*E*)- β -farnesene (*E* β F) is attractive to *A. bipunctata* (Hemptinne et al., 2000c; Francis et al., 2004), *H. convergens* (Acar et al., 2001), *C. septempunctata* (Nakamuta, 1991; Al Abassi et al., 2000), and *H. axyridis* (Verheggen et al., 2007; but also see Mondor and Roitberg, 2000). The response to *E* β F is inhibited by (–)- β -caryophyllene, a chemical present in plants (as is *E* β F); the detection of caryophyllene along with *E* β F indicates a plant (rather than aphid) source of the latter semiochemical (Dawson et al., 1984; Al Abassi et al., 2000).

Female adult *Diomus* sp. and *Exochomus* sp. spend more time searching cassava leaves that were recently infested with mealybugs. However, it is not clear if these lady beetles use a mealybug-associated cue to guide their immigration into different patches or when searching for oviposition sites (van den Meiracker et al., 1990). *C. septempunctata* is attracted to volatiles from infested or previously infested barley plants, but not to uninfested plants or to undisturbed *Rhopalosiphum padi* (L.) (Ninkovic et al., 2001). Lentz et al. (2004) found that *Stethorus punctillum* Weise flew more readily toward beans and cucumbers infested with *Tetranychus urticae* Koch than toward uninfested plants, and more readily toward infested plants than toward mites and plants which were kept separate.

Mated females of *Cycloneda sanguinea* (L.) use a hierarchy of olfactory cues when choosing foraging patches (Sarmiento et al., 2007). They preferentially move toward volatiles of tomatoes infested with the non-essential prey, *Tetranychus evansi* Baker & Pritchard, versus clean air, and toward volatiles of plants infested with essential prey, *Macrosiphum euphorbiae* (Thomas), versus non-essential prey *T. evansi* (Sarmiento et al., 2007). These beetles also use olfactory cues to avoid predation risk by moving toward volatiles of plants with *M. euphorbiae* or *T. evansi* versus plants with prey and the coccinellid egg predator, *Eriopis connexa* (Germar). Thus, this lady beetle uses volatile olfactory cues to discern between patches based both on prey quality and on risk of predation, and chooses the site with the higher prey quality but not at the cost of selecting an oviposition site associated with a predator (Sarmiento et al., 2007).

4.2. Visual cues

Vision is used by adult coccinellids to locate prey within a patch (Nakamuta, 1984; Obata, 1986; Harmon et al., 1998). Just as with olfaction it seems reasonable to examine whether adult lady beetles use this sense in locating high quality patches as sites for reproduction.

4.2.1. Color

Lorenzetti et al. (1997) found more adult coccinellids on stressed corn plants and suggested that plant color was responsible for this trend. Stressed plants tend to be more yellow than mature, healthy foliage, and thus color could indicate the presence of aphids. Several studies show higher capture of particular coccinellids (e.g., *C. maculata* and *C. septempunctata*) on yellow-colored adhesive traps, but other species show no preference among colors (e.g., *H. convergens* and *Hippodamia parenthesis* [Say]) (Capinera and Walmsley, 1978; Maredia et al., 1992; Udayagiri et al., 1997).

In a cage setting, naïve female *H. axyridis* preferred to visit and spend time on yellow pillars versus green ones (Mondor and Warren, 2000). This response to yellow is not fixed, since *H. axyridis* spent more time on pillars of a particular color when this color was reinforced with food during conditioning (Mondor and Warren, 2000). *A. bipunctata* displayed a preference for ovipositing on surfaces of particular colors in paired choice tests (Ipert and Prudent, 1986). The reported order of preference was: red > green > yellow > blue. These authors suggest that red surfaces may be most preferred, since sometimes aphid-damaged foliage turns this color (e.g., apple foliage infested with *Dysaphis* sp.).

4.2.2. Pattern recognition

H. axyridis adults in I-tube assays move toward vertical or horizontal bars and buckthorn foliage preferentially over blank space (Bahlai et al., 2008). An arboreal species that spends a portion of the year on bamboo, *C. nigritus* (F.), moved toward a horizon with a simulated tree more than toward a flat horizon, vertical over horizontal stripes, vertical stripes over a simulated tree, paintings of citrus leaves over squares, and ovate leaves over compound bipinnate leaves (Hattingh and Samways, 1995). These visual preferences help direct *C. nigritus* to habitats where their preferred prey are found (i.e., in trees with ovate leaves). This study also demonstrated that this beetle habituates to short-range cues (e.g., image of a scale insect) at a faster rate than long-range cues, as they are encountered more frequently. A long duration of response to an infrequently encountered long-range cue is needed since reinforcement is not immediate, whereas short-range cues will frequently be accompanied by reinforcement (e.g., contact with prey item) very soon after perceiving the cue.

5. The role of food in reproduction

Food influences lady beetle reproduction in at least two general ways. Egg production requires nutritional intake beyond a maintenance level, and thus high quality food is important for supporting reproductive capacity. Food is also important for a female's offspring, and food-based cues that indicate the quantity or quality of a food item directly influence a female's decision to oviposit.

5.1. Prey abundance

Some aphidophagous lady beetles assess the prey density within a patch, and require a minimum prey density before they will oviposit in an area. Honěk (1978) reported that post-diapause ovariole maturation in *C. septempunctata* subpopulations varied greatly within a landscape, and he noted that this variation was positively correlated with local aphid densities. *C. septempunctata* requires approximately 10 aphids per m² of land area to settle into a habitat and one aphid per 200–400 cm² of leaf area (depending on the crop) before it will mature eggs in a habitat (Honěk, 1980). This minimum number of aphids is likely related to the minimum number of aphid prey required by 1st instars for development. Johki et al. (1988) reported that the densities of adult coccinellids declined once *Aphis citricola* van der Goot and *Toxoptera odinae* van der Goot on the woody ornamental shrub *Pittosporum tobira* (Thunberg) were reduced below a mean of 50 nymphs per colony. This relationship was strongest among smaller lady beetles such as *Scymnus posticalis* Sicard (but also see Sloggett et al., 2008). The arboreal *Aphidecta obliterated* (L.) increased oviposition in response to increasing aphid densities (Oliver et al., 2006). When a habitat reaches a certain minimum prey density that allows survival and development of first instars an 'oviposition window' opens (Kindlmann and Dixon, 1993). To maximize fitness females should lay eggs in the oviposition window, which closes when larval tracks are detected (see Section 7.2) (Kindlmann and Dixon, 1993). In this scenario, younger prey colonies are preferable for oviposition in that they are unlikely to collapse during larval development, and also present less risk from conspecific and heterospecific predators.

5.2. Prey quality

5.2.1. Intraspecific variability in prey

Prey change in their suitability as they age, and so it is expected that coccinellids can distinguish prey of a preferred age (Hodek and Honěk, 2009). When offered young aphids, *A. pisum*, on young

leaves versus old aphids on old leaves, *C. septempunctata* preferentially oviposits near the young ones (Hemptinne et al., 1993; but also see Hemptinne et al., 2000b). When a mix of aphid instars was offered on either young or old leaves, no difference in oviposition occurred, which suggests that females are discerning the quality of prey and not using a plant-based cue indicative of host plant age. *A. bipunctata* 1st instars require two small (1st–3rd instar) aphids, *Drepanosiphum platanoides* (Schrank), per day for maximum survival (Dixon, 1970). First instars are not capable of preying on late-instar and adult aphids; they have a specific requirement for small prey, another reason for females to oviposit near an aphid colony early in its development. Different aphid morphs can also have a substantial effect on the number of eggs produced by a coccinellid (Wipperfurth et al., 1987).

The same type of oviposition preference is demonstrated by coccidophages. *C. nigritus* laid significantly more eggs when exposed to scale colonies of mixed age than to any one particular stage regardless of the density (Ponsonby and Copland, 2007). *C. nigritus* avoids red scale, *Aonidiella aurantii* Makell, infestations that are so large (>60 scales per cm²) that they cause the rapid decline of the host plant (Erichsen et al., 1991).

A prey species' host plant also can affect its suitability as food, and subsequently affect lady beetle reproduction (Hodek and Honěk, 2009). Francis et al. (2001) demonstrated that *A. bipunctata* fed *Myzus persicae* (Sulzer) from plants with no or low levels of glucosinolates had higher fitness (as measured by fecundity and egg viability) than those fed *M. persicae* from plants with high levels of glucosinolates. There are other examples of lady beetle development and reproduction being adversely affected when fed aphids reared on resistant plants (Rice and Wilde, 1989; Martos et al., 1992). Similar effects have been documented in coccinellids that feed on mealybugs and whiteflies reared on resistant plants or different plant species (Le Rü and Mitsipa, 2000; Al-Zyoud et al., 2005). It is unknown if gravid lady beetles are able to discern between prey colonies of the same species but on different host plants. This may be of interest to determine how sophisticated coccinellids are at maximizing fitness and could be of applied consequence in diverse polyculture plantings.

5.2.2. Interspecific differences in prey

Even among lady beetles that feed mostly on aphids, not all prey are equally suitable for reproduction (Blackman, 1967; Omkar and Mishra, 2005; Cabral et al., 2006). In Belgium, *H. axyridis* is frequently found feeding on *Microlophium carnosum* (Buckton) from nettle compared with other common species in the landscape (Almedi et al., 2007). *M. carnosum* is preferred by *H. axyridis* over *A. pisum* and *Sitobion avenae* (F.), and females preferentially oviposit near this prey species (Almedi et al., 2008). However, in no-choice tests *A. bipunctata* oviposited near marginally suitable, toxic, and high quality aphid species indiscriminately (Fréchette et al., 2006). This result highlights that prey quality should be viewed in the context of the different prey items and their abundance in a landscape. The results of Almedi et al. (2007, 2008) strongly suggest that when preferred prey are present in adequate numbers that females lay eggs accordingly. Gravid females refrain from ovipositing (at least for a few hours) the entire egg clutch if conditions are unfavorable (Evans and Dixon, 1986).

Aggregation and reproduction of coccinellids to a specific prey differs among species. In alfalfa where the densities of aphids and *H. postica* (Gyllenhal) (Col.: Curculionidae) larvae were manipulated, only *C. septempunctata* aggregated to high densities of *H. postica* larvae when aphid densities were low (other species tested were *H. convergens* and *H. quinquesignata* [Kirby]; Evans and Toler, 2007). *C. septempunctata*, *Coccinella transversalis* (F.), *Coccinella transversoguttata* Faldermann, and *H. axyridis* reduce or cease their reproductive output when aphids are removed from their diets

(Evans et al., 1999; Evans, 2000; Evans and Gunther, 2005). However, feeding on alternative prey such as *H. postica* larvae and sugar or nectar generally improves reproduction in coccinellids over single-prey diets (Evans, 2009; Lundgren, 2009).

5.3. Non-prey foods and reproduction

Coccinellids, such as *C. maculata*, *H. axyridis*, and *H. tredecimpunctata tibialis* (Say), respond to corn anthesis by increasing oviposition (Wright and Laing, 1980; Cottrell and Yeargan, 1998b; Lundgren et al., 2004). Despite having similar adult densities, more *C. maculata* eggs occur on plants in plots undergoing pollen shed than on same-age plants that were detasseled prior to anthesis (Cottrell and Yeargan, 1998b). Lundgren et al. (2004) also reported that *C. maculata* egg density increases during anthesis, and although adults and larvae frequently consumed corn pollen, adult densities did not increase significantly from pre-anthesis densities. *H. axyridis* and *H. convergens* oviposit more during anthesis, but the causal factor for this increase in reproduction could be related to prey availability (Wright and Laing, 1980), although *H. axyridis* larvae also rely on corn pollen at this point in the season (Lundgren et al., 2004). Pollen and sugar are key food-resources for lady beetles emerging from diapause in the spring but alone do not allow for egg production (Hemptinne and Desprets, 1986; Lundgren, 2009) with *C. maculata* being an exception (Lundgren and Wiedemann, 2004).

Under some circumstances, honeydew is an arrestant of coccinellid foraging as it often indicates prey presence (Carter and Dixon, 1984; Ide et al., 2007). But some coccinellids avoid ovipositing near sticky substances, possibly because a large amount of honeydew is often associated with declining colonies (Iperti and Prudent, 1986; Johki et al., 1988). However, small amounts of honeydew along with aphid odors can elicit oviposition of gravid females even when aphids are absent (Evans and Dixon, 1986).

6. Non-food cues and preferences

Food is not the only consideration for reproductive females, and sometimes coccinellids will lay eggs entirely in the absence of food for their offspring (described in Banks, 1956; Evans and Dixon, 1986). Iperti (1965) noted that in similar laboratory conditions, coccinellids oviposited on different sites within the rearing cages. He hypothesized that this was due to coccinellids expressing differing degrees of geotropism, phototropism, hygrotropism and thigmotaxis. *A. bipunctata* prefers to oviposit on curved surfaces over flat ones and smooth surfaces rather than those covered by filter paper (Iperti and Prudent, 1986). Several reports indicate that negative geotaxis leads to eggs being placed toward the top of plants and cages (Ewert and Chiang, 1966; Iperti and Quilici, 1986). *Propylea quatuordecimpunctata* (L.) displays negative phototaxis and oviposits in shaded areas of an enclosure (Iperti and Quilici, 1986). It may be that studies such as these reveal more about where coccinellids reside and consequently oviposit than their preferences for oviposition sites. Still they are useful indicators of how adults distribute themselves and narrow down where oviposition is likely to occur within a habitat.

6.1. Plant-based cues

Many mass-produced lady beetles will not oviposit in empty enclosures, but will oviposit in larger cages containing a small twig (Smirnoff, 1958). *C. septempunctata* prefers to oviposit on corrugated cardboard with congealed 33% strawberry gelatin (Jello®) (Shands et al., 1970). *A. bipunctata*, *C. transversoguttata*, *Cycloneda munda* (Say), and *C. maculata* oviposit more often on surfaces

treated with alcohol extracts of *Juniperus virginiana* (L.) wood (Boldyrev et al., 1969). When further examined, the extracts that stimulate oviposition in *C. maculata* are high-molecular weight polyphenols such as O-coumaric, salicylic and protocatechuic acids, fluorescein, tannin, and widdrol (Smith et al., 1973). Ethanol extracts from teak, cinnamon, clove, guaiacol, and resorcinol also stimulate oviposition by *C. maculata* (Smith and Williams, 1976). These extracts not only increased incidence of oviposition at a particular location but also the total number of eggs per female. Ipert and Prudent (1986) reported that *A. bipunctata* oviposited more on surfaces treated with extracts of cypress and fennel than on untreated surfaces. *A. bipunctata* and *C. septempunctata* prefer to oviposit on barberry (*Berberis vulgaris* (L.) twigs more than on those of apple or other shrubs with similar physical characteristics to barberry (Shah, 1983). Additionally, *Prunus cerasus* (L.) twigs sprayed with water extracts of barberry leaves or twigs had more eggs laid on them than did untreated branches. In line with this oviposition behavior, *C. septempunctata* moves toward the smell of chopped barberry leaves and flower heads of *Tripleurospermum inodorum* (L.) (Asteraceae) that are devoid of prey (Schaller and Nentwig, 2000).

It is hard to determine if these oviposition responses to plant-based chemicals have any role in egg laying decisions outside of laboratory conditions. These studies do hint at a role of chemosensation in oviposition decisions and these chemicals could have utility in predator rearing or manipulating populations in a field setting.

6.2. Avoidance of cannibalism and intraguild predation

Egg cannibalism and predation by other lady beetle species are common sources of mortality for coccinellid eggs (Mills, 1982; Wright and Laing, 1982; Agarwala and Dixon, 1992; Hodek and Honěk, 1996; Hironori and Katsuhiko, 1997; Lucas, 2005; Snyder, 2009; Weber and Lundgren, 2009). Thus selection should favor oviposition strategies that reduce the impact of these trophic factors.

6.2.1. *C. maculata* as a case study

The oviposition behavior of *C. maculata* has been well studied, and it illustrates several reproductive strategies employed by coccinellids to minimize egg predation. On plants with high numbers of aphids and predators, placing eggs away from prey colonies can increase egg survival in comparison to eggs laid near the prey (Coderre et al., 1987; Schellhorn and Andow, 1999). *C. maculata* egg clutches are most often found on the bottom half of corn plants (Coderre et al., 1987; Schellhorn and Andow, 1999). This differs from other coccinellids commonly found in corn that oviposit higher on the plant where prey is more abundant (Hodek and Honěk, 1996; Schellhorn and Andow, 1999). This oviposition behavior may not have evolved strictly as a strategy to avoid egg predation but clearly this is benefit derived from it.

Host plants can have a dramatic effect on the survival of coccinellid eggs, and *C. maculata* and other species preferentially lay eggs on plants that offer protection from predation. Obrycki and Tauber (1985) reported that *C. maculata* and possibly *H. convergens* oviposit most often on potato hybrids (*Solanum tuberosum* × *S. berthaultii*) with patches of dense glandular trichomes, even though adult and immature coccinellids were found most often on the hybrids with fewer leaf hairs (Obrycki and Tauber, 1985). Cottrell and Yeargan (1998a) reported that more *C. maculata* eggs were found on the weed *Acalypha ostryifolia* Ridell than on the crop in cornfields. Subsequent screenings revealed that many cultivated and weedy species (notably velvetleaf, *Abutilon theophrasti* Medicus, and tomato, *Lycopersicon esculentum* [Mill.]) with glandular trichomes are preferred oviposition plants for *C. maculata* (Griffin and Yeargan, 2002a; Seagraves and Yeargan, 2006), even though adults prefer

to spend their time on glabrous plants (Staley and Yeargan, 2005). Prey numbers do not affect oviposition by *C. maculata* on these plant surfaces (Griffin and Yeargan, 2002b). Gravid females do not use long-distance cues to find these plants, but evaluate their suitability based on proximate cues (Griffin and Yeargan, 2002a).

It appears that a driving force behind *C. maculata*'s preference for ovipositing on pubescent plants is that eggs on these plants experience reduced predation. A great deal of predation on *C. maculata* eggs comes from older larvae and adult conspecifics (Cottrell and Yeargan, 1998a,b). Pubescent plant surfaces are difficult for larvae and adults to walk on due to the physical texture of the leaves (Elsey, 1974; Belcher and Thurston, 1982; Shah, 1982; Obrycki, 1986). *C. maculata* eggs laid on pubescent *A. ostryifolia* and *A. theophrasti* experience a 55% reduction in egg cannibalism compared to those eggs laid on corn (over 24 h) (Cottrell and Yeargan, 1998a; Griffin and Yeargan, 2002b). Neonate larvae from pubescent plants disperse by falling to the ground and walking to neighboring crop plants (Cottrell and Yeargan, 1999; Seagraves and Yeargan, 2006).

6.2.2. Ants

Ants that tend aphids frequently have adverse effects on natural enemies, including lady beetles (Majerus et al., 2007). Lady beetles are attacked by ants at ant-tended colonies and preferentially forage on non-tended aphids (Way, 1963; Styrsky and Eubanks, 2007). Although it has not been tested it is likely that a female's fitness would suffer if eggs were laid near ant-tended aphids if other options were available. Banks (1962) reported that within 48 h of their attachment, ants had removed the eggs of *A. bipunctata* from bean plants where *Aphis fabae* Scolpoli resided. The myrmecophilous coccinellid, *Coccinella magnifica* Redtenbacher, as an adult is found in close association with ant-tended aphid colonies. However, *C. magnifica* larvae are frequently attacked at ant-tended aphid colonies (albeit less frequently than *C. septempunctata* larvae) and ovipositing females seem to discern between tended and untended aphid colonies, and preferentially oviposit near ant-free aphids (Sloggett and Majerus, 2003).

6.2.3. Oviposition behaviors that indirectly reduce predation

Sakuratani and Nakamura (1997) documented that in the colder season *C. septempunctata* oviposits on the underside of non-plant materials with high thermal conductivity even when aphids are present on plants. Ferran et al. (1989) found most eggs of *C. septempunctata* on soil lumps, stones, and wild plants instead of on wheat plants, where most other life stages were found. Similarly, Lövei and Radwan (1988) reported that the location of coccinellid eggs in an orchard shifted as the season became warmer. In this case, twigs and branches were preferred sites early in the season, and the undersides of leaves were preferred later in the season. These oviposition behaviors are advantageous in that they shorten development time and thereby reduce the chance of egg predation.

7. Deterrent cues from conspecific and intraguild predators

Coccinellids avoid oviposition when they come in contact with predators or evidence of their presence (Hemptinne et al., 1992; Merlin et al., 1996). This phenomenon is interpreted as a strategy to avoid threats to the survival of their offspring, including competition and predation (e.g., intraguild predation and cannibalism). The signals used by coccinellids to identify predators may originate from actual contact, or through indicators of a predator's presence (e.g., larval tracks). Each coccinellid species produces specific (or a mixture of) alkanes that constitute a chemical signature that is used for defense and mate recognition (Hemptinne and Dixon,

2000; Magro et al., 2007). These chemicals emanate from all stages and affect conspecifics, heterospecific coccinellids, other predators, and even parasitoids (Nakashima et al., 2004; Magro et al., 2007; Chauhan and Weber, 2008; Rutledge et al., 2008). Many of the responses to these hydrocarbon tracks have been interpreted as behaviors to avoid food competition and predation. This avoidance is practiced by the potential victim (Nakashima et al., 2004; Rutledge et al., 2008) but also by the ovipositing mother of a potential victim. This latter type is reviewed below (Section 7.2).

7.1. Deterrence by presence of adult predators

Gravid lady beetles in laboratory experiments oviposit less when in the presence of other lady beetles. *A. bipunctata* females lay fewer eggs when in the presence of female *H. axyridis* or *C. septempunctata* (Kajita et al., 2006). Aspects of the study design (i.e., daily dish changes) suggest that direct contact among individuals caused the observed effect, but olfactory cues can not be ruled out. However, Doumbia et al. (1998) reported that *A. bipunctata* oviposition was undeterred when they were reared in Petri dishes that formerly contained conspecific adults (that would have left chemical cues). Thus, oviposition deterrence by conspecific adults in *A. bipunctata* does not seem to be mediated by chemical cues, although there is evidence that adults use olfactory cues to detect conspecifics (Al Abassi et al., 1998; Schaller and Nentwig, 2000). *H. axyridis* females laid fewer eggs when grouped with conspecifics than when alone or grouped with *Sasajiscymnus tsugae* (Sasaji and McClure) or *Laricobius nigrinus* Fender (Coleoptera: Derodontidae) (Flowers et al., 2005). Females of *Menochilus sexmaculatus* laid fewer eggs in the presence of an immobilized conspecific adult female or larva (Agarwala et al., 2003b). Immobilized *C. transversalis* females or larvae also reduced oviposition, but immobilized adult or larval *Scymnus pyrocheilus* Mulsant or an *Ischiodon scutellaris* (F.) (Diptera: Syrphidae) maggot did not affect oviposition (Agarwala et al., 2003b). *Coccinella undecimpunctata* (L.) fed *ad libitum* does not oviposit in the presence of adult *H. axyridis*, but the presence of conspecifics does not inhibit oviposition (Soares and Serpa, 2006). *C. septempunctata* does not oviposit in the presence of a conspecific adult female, but will oviposit near eggs and 2nd instars (Hemptinne et al., 1993).

The work reported on oviposition deterrence by the presence of con- and heterospecific adults has been conducted in artificial conditions. It remains to be determined how important this behavior would be in agricultural or natural systems. However these do have important bearing on the design of appropriate mass rearing methods and possibly the use of lady beetles in augmentation biological control.

7.2. Oviposition deterrent chemicals in tracks and frass

Numerous coccinellids can detect oviposition-deterrent semiochemicals (ODS) in the tracks of conspecific larvae, and adjust their behavior accordingly (Růžička, 1997, 2001a,b, 2003, 2006; Doumbia et al., 1998; Oliver et al., 2006; Magro et al., 2007; Michaud and Jyoti, 2007) (Table 1). Oviposition behavior may change in response to ODS of heterospecific larvae as well, but this is less common (Table 1). These documented effects very compelling but it must be recognized that they have all been generated in the laboratory where conditions (i.e., substrate, rate of degradation) are much different than those that would occur in the field. Our ability to gain insight into chemical oviposition deterrents will be enhanced as active components and the organisms and specific stages that emit them are identified. This information will allow for elegant manipulations in the laboratory and attempts to document these effects in more naturalistic settings.

The greater number of records of conspecific (compared to heterospecific) ODS may be partially explained by the greater relative importance of cannibalism to the reproductive success of the female compared to non-cannibalism IGP. Coccinellid eggs are chemically defended against predation by other coccinellids, but not from cannibalism (Agarwala and Dixon, 1992; Hemptinne et al., 2000a,d; Pervez and Gupta, 2004). Another reason that oviposition deterrence is more common in conspecific than heterospecific larval tracks is that in some laboratory tests the assayed female and heterospecific larvae are allopatric; thus the species have no common evolutionary history of coexistence. However, laboratory tests using allopatric species may provide insight into which behaviors are novel versus coevolved.

When sympatric species are examined there still tends to be stronger deterrence from conspecifics, but significant effects from the tracks of heterospecific larvae have been documented. For example, *C. maculata* prefers to consume conspecific eggs over *H. convergens* eggs in choice tests (Michaud and Jyoti, 2007). Even though *C. maculata* prefers to consume conspecific eggs, it still poses a predation risk to *H. convergens* eggs, and females of the latter species respond by reducing oviposition in the presence of larvae of the former species (Michaud and Jyoti, 2007).

The ability of adult tracks to deter oviposition is reported less frequently than the deterrent properties of larval tracks, but evidence suggests that tracks from adults may influence oviposition. *Propylea dissecta* (Mulsant) was deterred by conspecific adult tracks and this effect lasted at least 10 d (Mishra and Omkar, 2006). This deterrence was due to adult tracks (likely produced by the tarsi) as the study controlled for feces. At this date only Mishra and Omkar (2006) have reported an effect of adult tracks, while Doumbia et al. (1998) reported a lack of effect with *A. bipunctata*. Larval tracks may be more deterrent than those of adults as larvae are more frequent consumers of coccinellid eggs than adults (Cottrell and Yeargan 1998a,b). However this difference in the frequency of effect may simply reflect that larvae leave more of a chemical signal than adults, as they use their anal disc to adhere to surfaces. This latter explanation has merit as adult lady beetles readily consume eggs of both conspecific and heterospecific coccinellids (Cottrell, 2005). It has been shown that many eggs are chemically defended from predation by heterospecific coccinellids (Agarwala and Dixon, 1992; Hemptinne et al., 2000a). Interestingly adults, particularly *H. axyridis*, are not deterred from consuming heterospecific coccinellid eggs.

7.2.1. Physiology of ODS

The ODS of *A. bipunctata* larvae originate from the anal disc on the tenth abdominal segment (Laubertie et al., 2006). The chemical or combination of chemicals responsible for deterrence are chloroform-soluble and made up of at least 40 different hydrocarbons, mainly alkanes (Hemptinne et al., 2001). The chemical properties of ODS affect their ability to spread, adhere to plant surfaces, and their persistence (up to 30 d, see below). Chloroform extracts of *Cheilomenes sexmaculata* (F.) deter oviposition by conspecifics (Klewer et al., 2007). Klewer et al. (2007) elucidated that (*Z*)-pentacos-12-ene is the key, but not sole, chemical responsible for deterring oviposition. Receptors on the maxillary palpi of *Cycloneda limbifer* Casey and *Ceratomegilla undecimnotata* Schneider perceive ODS; individuals whose palpi are ablated are not deterred from ODS-marked surfaces (Růžička, 2003).

The longevity of ovipositional deterrence by ODS in larval tracks varies among lady beetles. Conspecific larval tracks of *C. septempunctata* deterred oviposition for less than 24 h, whereas those of *Semidalia undecimnotata* (Schneider), *A. bipunctata*, and *C. limbifer* were active on conspecific females for at least 5, 10, and 30 d, respectively (Hemptinne et al., 2001; Růžička, 2002). It is interesting to note that the parasitoid *Apidius ervi* Haliday is deterred from foraging for only 24 h by tracks of adult and larval *C. septempunctata* (Nakashima et al.,

Table 1
Deterrence of oviposition in lady beetles by the larval tracks of con- or heterospecific larvae.

Species assayed	Conspecific track deterrence	Heterospecific track ^a	Deterrent effect
<i>Adalia bipunctata</i> (L.)	Yes (Doubbia et al., 1998)	<i>Adalia decimpunctata</i> <i>Coccinella septempunctata</i>	No (Doubbia et al., 1998) Yes (Magro et al., 2007) No (Doubbia et al., 1998) Yes (Magro et al., 2007)
<i>Adalia decempunctata</i> (L.)	Yes (Magro et al., 2007)	<i>Adalia bipunctata</i> <i>Coccinella septempunctata</i>	Yes (Magro et al., 2007) Yes (Magro et al., 2007)
<i>Aphidecta obliterated</i> (L.)	Yes (Oliver et al., 2006)	<i>Adalia bipunctata</i> <i>Chrysopa carnea</i> (Stephens)	Yes ^b (Oliver et al., 2006) Yes ^b (Oliver et al., 2006)
<i>Ceratomegilla undecimnotata</i> Schneider	Yes (Růžička, 2003)	<i>Leis dimidiata</i> <i>Ceratomegilla undecimnotata</i>	No (Růžička, 2003) Yes (Růžička, 2006)
<i>Cheilomenes sexmaculata</i> (F.)	Yes (Růžička, 2006)	<i>Cycloneda limbifer</i> <i>Hippodamia dimidiata</i> (F.)	Yes (Růžička, 2006) No (Růžička, 2006)
<i>Coccinella septempunctata</i> (L.)	Yes (Růžička, 1997, 2001a; Magro et al., 2007)	<i>Adalia bipunctata</i> <i>Adalia decempunctata</i> <i>Chrysopa oculata</i> <i>Chrysopa perla</i> <i>Cycloneda limbifer</i> <i>Leis dimidiata</i> <i>Semiadalia undecimnotata</i> <i>Leis dimidiata</i> <i>Semiadalia undecimnotata</i> <i>Ceratomegilla undecimnotata</i> <i>Chrysopa oculata</i> Say <i>Chrysopa perla</i> (L.) <i>Coccinella septempunctata</i>	No (Doubbia et al., 1998) No (Magro et al., 2007) No (Magro et al., 2007) Yes (Růžička, 1997, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) Yes (Růžička, 2001a) Yes (Růžička, 2001a) No (Růžička, 2003) No (Růžička, 2001a, 2003) No (Růžička, 2001a, 2003) No (Růžička, 2001a, 2003) No (Yasuda et al., 2000)
<i>Cycloneda limbifer</i> Casey	Yes (Růžička, 2001a)	<i>Coleomegilla maculata</i> (DeGeer) <i>Chrysopa oculata</i> <i>Chrysopa perla</i> <i>Coccinella septempunctata</i> <i>Cycloneda limbifer</i> <i>Semiadalia undecimnotata</i> <i>Leis dimidiata</i> <i>Chrysopa oculata</i> <i>Chrysopa perla</i> <i>Coccinella septempunctata</i> <i>Cycloneda limbifer</i>	Yes (Michaud and Jyoti, 2007) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) Yes (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a) No (Růžička, 2001a)
<i>Harmonia axyridis</i> (Pallas)	Yes (Yasuda et al., 2000)		No (Yasuda et al., 2000)
<i>Hippodamia convergens</i> Guérin	Yes (Michaud and Jyoti, 2007)		Yes (Michaud and Jyoti, 2007)
<i>Leis dimidiata</i> (F.)	No (Růžička, 2001a)		No (Růžička, 2001a)
<i>Semiadalia undecimnotata</i> (Schneider)	Yes (Růžička, 2001a)		No (Růžička, 2001a)

^a All species are Coleoptera: Coccinellidae, except for *Chrysopa* spp. (Neuroptera: Chrysopidae).

^b Marginal effect (see discussion in Oliver et al., 2006).

2004). The interspecific variation in the reported duration of deterrence by ODS is likely an artifact that the reported experiments used different amounts of larvae, duration of exposure, and age of tracks at start of assay. If this amount of variation in the longevity holds up after standardized experiments this would suggest that there is a difference in the persistence of the active components among different species' tracks, or that species detect different compounds that vary in their rate of breakdown.

7.2.2. Density dependence and ODS

Naturally, the level of deterrence produced by ODS of coccinellids is density dependent (Doubbia et al., 1998; Oliver et al., 2006). For example, in *Cryptolaemus montrouzieri* Mulsant, which only oviposits in close association with mealybug ovisacs, the level of oviposition deterrence was positively correlated with the density of conspecific larvae (Hemptinne et al., 1993). The strength of density dependent deterrence can decrease as a female beetle ages: *A. bipunctata* females that had oviposited for at least 30 d were less deterred by conspecific larval tracks than females that had laid eggs for fewer than 10 d (Fréchette et al., 2004). During long assays, fewer naïve *A. bipunctata* females oviposited than females that were exposed to conspecific tracks continuously from eclosion (Fréchette et al., 2004).

7.2.3. Frass

An indication of the presence of competitors is their frass. *Propylea japonica* (Thunberg) oviposition is deterred by the water

extracts of both conspecific and *H. axyridis* larval frass (Agarwala et al., 2003a). However, *H. axyridis* oviposition was deterred by the water extract of conspecific larval frass, but not the extract of *P. japonica* frass (Agarwala et al., 2003a). *P. japonica* displays greater discretion in its oviposition, perhaps because it is less competitive in intraguild interactions with other lady beetles. For both species the strength of deterrence decreased as the frass aged. Coccinellid frass in the form of dry cylindrical pellets is likely to fall off of plants. Therefore it remains questionable how often reproductive females encounter larval frass. It is likely that the long-chain hydrocarbon larval tracks are a more frequently encountered signal of potential competitors and predators (Section 7.2).

8. Interaction of positive and negative cues

Few studies concurrently examine multiple factors on oviposition to determine how lady beetles respond to the myriad factors that influence their oviposition under realistic conditions. An exception is work by Michaud and Jyoti (2007), which examines the effect of con- and hetero-specific larval tracks in combination with the presence or absence of prey. *H. convergens* oviposition was deterred on plants that had been exposed to conspecific or *C. maculata* larvae. In this system, the negative effect of con- and hetero-specific tracks is stronger than the positive stimulus of prey (Michaud and Jyoti, 2007). In contrast to the work on *H. convergens*, *A. obliterated* females clearly incorporate both the presence of ODS

and prey availability in their oviposition decisions (Oliver et al., 2006).

Just as with intraguild predation (Weber and Lundgren, 2009), as we learn more about the cues that elicit or deter oviposition much work will be needed to determine how adult ladybeetles integrate competing cues in complex realistic situations (Weber and Lundgren, 2009).

9. Conclusions

Coccinellids use sensory cues to select oviposition sites that improve their reproductive success. Both the presence and quality of food has a very strong effect on retention of adults in a habitat and on their reproductive output. However, their response to food cues may be superseded by responses to deterrent cues associated with potential conspecific and heterospecific predators. There is a need to take on the more difficult task of examining the impact of larval track deterrence in crop field situations, particularly the behavior of females that are deterred and the distance traveled to resume oviposition. To advance this area it would be informative to examine the response of females of differing age, previous exposure to ovipositional deterrents, mating status, and egg loads to different visual and olfactory cues. Investigations into what is required for lady beetle oviposition and how to elicit this response may provide better information for using this predator group in biological control.

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