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6 **Lady Beetle Oviposition Behavior in Response to the Trophic Environment**

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

41 **Key words:** Coccinellidae, reproductive strategy, intraguild predation, cannibalism, honeydew,
42 frass, larval tracks

43 **1. Introduction**

44 Maternal reproductive decisions affect the local distribution of larval coccinellid
45 populations within a habitat, and these decisions are driven in large part by trophic interactions
46 with other organisms. Coccinellid larvae are voracious predators but are much less mobile than
47 the adult stage, thus they often remain in patches selected by their mother. Accordingly, the
48 distributions of food resources critical to larval development (Kindlmann and Dixon, 1993) as
49 well as intraguild predation, including cannibalism, at the selected oviposition site strongly
50 influence the reproductive success of a female (Cottrell and Yeargan, 1998a; Schellhorn and
51 Andow, 1999). Understanding the factors that influence oviposition behavior can be used to
52 design cropping systems that augment densities of coccinellid predators (Seagraves and Yeargan,
53 2006).

54 Ferran and Dixon (1993) suggested that to fill our knowledge gaps and improve the
55 effectiveness of lady beetles we should examine adult behaviors and sensory capabilities of these
56 predators that operate during oviposition. Here, I build upon an earlier review on the topic of
57 reproductive decisions (Evans, 2003) by focusing on recent work in the field and by examining
58 the sensory cues that affect the selection of habitat patches, and that elicit or deter oviposition
59 once in habitats. This behavior is not a step-wise hierarchical decision-making process but a
60 suite of responses to overlapping sets of stimuli perceived by a gravid female. An understanding
61 of how predators perceive and respond to positive and negative trophic signals, and how these
62 affect their fitness, can greatly improve their utility in biological pest management.

63

64 **2. General model of lady beetle reproduction**

65 Chandler (1965) suggested that a balance between olfactory and visual cues from prey and
66 infested plants drives the oviposition decisions of predators. However a less structured model
67 (reviewed by Evans, 2003) of how oviposition occurs in lady beetles has emerged with
68 subsequent research. In this scenario, lady beetles fly through a landscape and randomly land on
69 plants. When prey is located, they initiate a local search pattern leading to their aggregation in
70 areas of high prey density. Satiation typically ensues, which reduces their tendency to disperse
71 and leads to a localization of oviposition. Indirect support for this general decision-making
72 framework comes from the numerous observations of aphidophagous coccinellids that oviposit
73 in areas of high prey density (Banks, 1956; Dixon, 1959; Wratten, 1973; Ives, 1981; Mills,
74 1982). Obviously this model relies upon work done with coccinellids whose life-history is based
75 around their sternorrhynchan prey. Although there are certainly caveats to this model, it still
76 provides a framework for discussing the current knowledge of the reproductive decisions of
77 coccinellids and likely applies to species that feed on mites and powdery mildew which also tend
78 to be clumped in distribution.

79

80 **3. Habitat selection by females**

81 Critical to understanding lady beetle reproduction and their use in biological control is how
82 the adults come to be in a particular habitat. Although it is conceivable that a coccinellid may
83 eclose into a habitat with abundant food resources, it is more likely that it must disperse at some
84 point over its adult life when prey becomes depleted (Obata, 1986). Kindlmann and Dixon
85 (1999) show that prey quantity can become scarce during larval development. Individual species
86 likely respond to habitat quality at different scales. For instance, *Adalia bipunctata* (L.),
87 *Hippodamia tredecimpunctata* (L.), and *Hippodamia convergens* Guérin immigrant populations

88 responded to increased aphid density in maize at the level of the plant, whereas *Coleomegilla*
89 *maculata* (De Geer) only responded to increasing aphid densities at the plot (10 × 10 m) level
90 (Schellhorn and Andow, 2005). Although much of the work reviewed here is not specific to
91 gravid females it offers insight into the processes that ultimately determine the distribution of
92 adults and thus to some extent oviposition at a landscape level.

93
94 **3.1. Immigration.** Information on sensory capabilities of foraging lady beetles challenge
95 the traditional view (Hodek, 1993) that immigration of lady beetles is purely a random process
96 which has been often questioned (see Hodek and Honěk, 1996, pg. 102). Cardinale et al. (2006)
97 found immigration by *Coccinella septempunctata* (L.), *Coleomegilla maculata*, and *Harmonia*
98 *axyridis* (Pallas) into alfalfa patches was not correlated with aphid abundance. Krivan (2008)
99 examined data on *Coccinella septempunctata* from Honěk (1982) using models that assumed
100 immigration to be random, influenced by prey presence, or influenced by both prey and the
101 presence of conspecifics. The model that assumed random immigration best fits the data. Note
102 that the studies cited above focus on a narrow range of species, especially *C. septempunctata*,
103 that are widely regarded as highly vagile habitat generalists (Hodek and Michaud, 2008). The
104 coccidophagous lady beetle *Chilocorus nigritus* clearly moves toward sensory stimuli to locate
105 habitat patches with prey as opposed to settling in them after a random search (Hattingh and
106 Samways, 1995). Additionally, there are many studies that report the directional movement of
107 adult lady beetles to particular habitats in response to sensory cues, and it seems likely that these
108 cues are influencing non-random habitat selection by coccinellids to some degree (see section 4
109 below). Whether specific lady beetle species use sensory stimuli specifically to direct
110 immigration remains to be investigated or incorporated into any descriptive models.

111

112 **3.2. Emigration.** The availability of food and habitat characteristics are often coupled to a
113 coccinellid's propensity for emigration. For example, providing non-prey foods, such as sucrose
114 solution, within farmland can increase the residence time of lady beetles within a patch (Ewert
115 and Chiang, 1966; Evans and Richards, 1997; Van Der Werf et al., 2000). Also, female *C.*
116 *septempunctata* and *Hippodamia variegata* (Goeze) remain longer on fireweed stems with
117 greater aphid numbers (Ives et al., 1993). *Coccinella trifasciata* (L.) departs alfalfa fields when
118 aphid numbers drop below 0.3 per stem, and the larger *Coccinella californica* Mannerheim
119 emigrates at an unknown higher threshold (Frazer, 1988). The physical shape of a habitat can
120 also influence the dispersal of a coccinellid. For example, square-shaped cabbage patches
121 retained adult lady beetles longer than "I"-shaped patches of equal area, presumably due to the
122 square shape having a lower perimeter to area ratio. Adults encountered boundaries and edges
123 less frequently in the square plots, thus lowering emigration (Grez and Prado, 2000).

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

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

145

146 **4. Proximate cues involved in coccinellid foraging.**

147 **4.1. Olfactory cues.** Olfactory cues are used by some adult lady beetles to direct their
148 movement toward prey (Colburn and Asquith, 1970; Obata, 1986; Nakamuta, 1991; Schaller and
149 Nentwig, 2000). *Coleomegilla maculata* electroantennogram (EAG) tests showed a positive
150 response to aphid semiochemicals and to corn volatiles (Zhu et al., 1999). Zhu and Park (2005)
151 reported that young aphid-infested soybean plants emit more methyl salicylate than uninfested
152 plants, and traps baited with this compound caught significantly more *Coccinella septempunctata*
153 (but not *Harmonia axyridis*) adults than did control traps. *Harmonia axyridis* adults move
154 toward olfactory cues from buckthorn and apple foliage, particularly aphid-infested foliage
155 (Bahlai et al., 2008) and also toward pea aphid colonies (Mondor and Roitberg, 2000; Verheggen

156 et al., 2007). *Coccinella septempunctata* responds to olfactory cues from *Toxoptera aurantii*
157 (Boyer), *T. aurantii* cuticle, and aphid-damaged tea shoots (Han and Chen, 2002). Honeydew
158 collected from *T. aurantii* evokes a particularly strong EAG response from *C. septempunctata*
159 (Han and Chen, 2002). In contrast, Scaller and Nentwig (2000) found that *C. septempunctata*
160 adults were not attracted to the odor of *Acyrtosiphon pisum* (Harris) honeydew. *Stethorus*
161 *punctum picipes* (Casey) is attracted to the synthetic plant compounds methyl salicylate, (Z)-3-
162 hexenyl acetate, cis-3-hexen-1-ol, and benzaldehyde, which are associated with herbivore
163 damaged plants (James, 2003; James and Price, 2004; James 2005).

164 Alarm pheromones of prey are another set of proximate cues attractive to some
165 coccinellids. The aphid alarm pheromone (E)- β -Farnesene (E β F) is attractive to *A. bipunctata*
166 (Hemptinne et al., 2000c; Francis et al., 2004), *Hippodamia convergens* (Acar et al., 2001), *C.*
167 *septempunctata* (Nakamuta, 1991; Al Abassi et al., 2000), and *Harmonia axyridis* (Verheggen et
168 al., 2007; but also see Mondor and Roitberg, 2000). The response to E β F is inhibited by (-)- β -
169 caryophyllene, a chemical present in plants (as is E β F); the detection of caryophyllene along
170 with E β F indicates a plant (rather than aphid) source of the latter semiochemical (Dawson et al.,
171 1984; Al Abassi et al., 2000).

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

179 *Tetranychus urticae* Koch than toward uninfested plants, and more readily toward infested plants
180 than toward mites and plants which were kept separate.

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

191
192 **4.2. Visual cues.** Vision is used by adult coccinellids to locate prey within a patch
193 (Nakamuta, 1984; Obata, 1986; Harmon et al., 1998). Just as with olfaction it seems reasonable
194 to examine whether adult lady beetles use this sense in locating high quality patches as sites for
195 reproduction.

196 **4.2.1. Color.** Lorenzetti et al. (1997) found more adult coccinellids on stressed corn
197 plants and suggested that plant color was responsible for this trend. Stressed plants tend to be
198 more yellow than mature, healthy foliage, and thus color could indicate the presence of aphids.
199 Several studies show higher capture of particular coccinellids (e.g., *Coleomegilla maculata* and
200 *Coccinella septempunctata*) on yellow-colored adhesive traps, but other species show no

201 preference among colors (e.g., *Hippodamia convergens* and *Hippodamia parenthesis* [Say])
202 (Capinera and Walmsley, 1978; Maredia et al., 1992; Udayagiri et al., 1997).

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

211 4.2.2. *Pattern recognition.* *Harmonia axyridis* adults in I-tube assays move toward
212 vertical or horizontal bars and buckthorn foliage preferentially over blank space (Bahlai et al.,
213 2008). An arboreal species that spends a portion of the year on bamboo, *Chilocorus nigritus* (F.),
214 moved toward a horizon with a simulated tree more than toward a flat horizon, vertical over
215 horizontal stripes, vertical stripes over a simulated tree, paintings of citrus leaves over squares,
216 and ovate leaves over compound bipinnate leaves (Hattingh and Samways, 1995). These visual
217 preferences help direct *C. nigritus* to habitats where their preferred prey are found (i.e., in trees
218 with ovate leaves). This study also demonstrated that this beetle habituates to short-range cues
219 (e.g., image of a scale insect) at a faster rate than long-range cues, as they are encountered more
220 frequently. A long duration of response to an infrequently encountered long-range cue is needed
221 since reinforcement is not immediate, whereas short-range cues will frequently be accompanied
222 by reinforcement (e.g., contact with prey item) very soon after perceiving the cue.

223

224 5. The role of food in reproduction.

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

230

231 **5.1. Prey abundance.** Some aphidophagous lady beetles assess the prey density within a
232 patch, and require a minimum prey density before they will oviposit in an area. Honěk (1978)
233 reported that post-diapause ovariole maturation in *Coccinella septempunctata* subpopulations
234 varied greatly within a landscape, and he noted that this variation was positively correlated with
235 local aphid densities. *Coccinella septempunctata* requires approximately 10 aphids per m² of
236 land area to settle into a habitat and one aphid per 200-400 cm² of leaf area (depending on the
237 crop) before it will mature eggs in a habitat (Honěk, 1980). This minimum number of aphids is
238 likely related to the minimum number of aphid prey required by 1st instars for development.
239 Johki et al. (1988) reported that the densities of adult coccinellids declined once *Aphis citricola*
240 van der Goot and *Toxoptera odinae* van der Goot on the woody ornamental shrub *Pittosporum*
241 *tobira* (Thunberg) were reduced below a mean of 50 nymphs per colony. This relationship was
242 strongest among smaller lady beetles such as *Scymnus posticalis* Sicard (but also see Sloggett et
243 al., 2008). The arboreal *Aphidecta obliterated* (L.) increased oviposition in response to increasing
244 aphid densities (Oliver et al., 2006). When a habitat reaches a certain minimum prey density that
245 allows survival and development of first instars an 'oviposition window' opens (Kindlmann and
246 Dixon, 1993). To maximize fitness females should lay eggs in the oviposition window, which

247 closes when larval tracks are detected (see section 7.2) (Kindlmann and Dixon, 1993). In this
248 scenario, younger prey colonies are preferable for oviposition in that they are unlikely to collapse
249 during larval development, and also present less risk from conspecific and heterospecific
250 predators.

251 **5.2. Prey quality.**

252 *5.2.1. Intraspecific variability in prey.* Prey change in their suitability as they age, and so it
253 is expected that coccinellids can distinguish prey of a preferred age (Hodek and Honěk, 2009;
254 this issue). When offered young aphids, *Acyrtosiphon pisum*, on young leaves versus old aphids
255 on old leaves, *C. septempunctata* preferentially oviposits near the young ones (Hemptinne et al.,
256 1993; but also see Hemptinne et al., 2000b). When a mix of aphid instars was offered on either
257 young or old leaves, no difference in oviposition occurred, which suggests that females are
258 discerning the quality of prey and not using a plant-based cue indicative of host plant age. *Adalia*
259 *bipunctata* 1st instars require two small (1st-3rd instar) aphids, *Drepanosiphum platanoides*
260 (Schrank), per day for maximum survival (Dixon, 1970). First instars are not capable of preying
261 on late-instar and adult aphids; they have a specific requirement for small prey, another reason
262 for females to oviposit near an aphid colony early in its development. Different aphid morphs
263 can also have a substantial effect on the number of eggs produced by a coccinellid (Wipperfürth
264 et al., 1987).

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

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

282
283 5.2.2. *Interspecific differences in prey.* Even among lady beetles that feed mostly on
284 aphids, not all prey are equally suitable for reproduction (Blackman, 1967; Omkar and Mishra,
285 2005; Cabral et al., 2006). In Belgium, *H. axyridis* is frequently found feeding on *Microlophium*
286 *carosum* (Buckton) from nettle compared with other common species in the landscape
287 (Alhmedi et al., 2007). *Microlophium carosum* is preferred by *H. axyridis* over *Acyrtosiphon*
288 *pisum* and *Sitobion avenae* (F.), and females preferentially oviposit near this prey species
289 (Alhmedi et al., 2008). However, in no-choice tests *Adalia bipunctata* oviposited near
290 marginally suitable, toxic, and high quality aphid species indiscriminately (Fréchette et al.,
291 2006). This result highlights that prey quality should be viewed in the context of the different
292 prey items and their abundance in a landscape. The results of Almedi et al. (2007; 2008)

293 strongly suggest that when preferred prey are present in adequate numbers that females lay eggs
294 accordingly. Gravid females refrain from ovipositing (at least for a few hours) the entire egg
295 clutch if conditions are unfavorable (Evans and Dixon, 1986).

296 Aggregation and reproduction of coccinellids to a specific prey differs among species. In
297 alfalfa where the densities of aphids and *Hypera postica* (Gyllenhal) (Col.: Curculionidae) larvae
298 were manipulated, only *Coccinella septempunctata* aggregated to high densities of *H. postica*
299 larvae when aphid densities were low (other species tested were *Hippodamia convergens* and
300 *Hippodamia quinquesignata* [Kirby]; Evans and Toler, 2007). *Coccinella septempunctata*,
301 *Coccinella transversalis* (F.), *Coccinella transversoguttata* Faldermann, and *Harmonia axyridis*
302 reduce or cease their reproductive output when aphids are removed from their diets (Evans et al.,
303 1999; Evans, 2000; Evans and Gunther, 2005). However, feeding on alternative prey such as
304 *Hypera postica* larvae and sugar or nectar generally improves reproduction in coccinellids over
305 single-prey diets (Evans, 2009; Lundgren, 2009; this issue).

306
307 **5.3. Non-prey foods and reproduction.** Coccinellids, such as *Coleomegilla maculata*,
308 *Harmonia axyridis*, and *Hippodamia tredecimpunctata tibialis* (Say), respond to corn anthesis by
309 increasing oviposition (Wright and Laing, 1980; Cottrell and Yeargan, 1998b; Lundgren et al.,
310 2004). Despite having similar adult densities, more *C. maculata* eggs occur on plants in plots
311 undergoing pollen shed than on same-age plants that were detasseled prior to anthesis (Cottrell
312 and Yeargan, 1998b). Lundgren et al. (2004) also reported that *C. maculata* egg density
313 increases during anthesis, and although adults and larvae frequently consumed corn pollen, adult
314 densities did not increase significantly from pre-anthesis densities. *Harmonia axyridis* and
315 *Hippodamia convergens* oviposit more during anthesis, but the causal factor for this increase in

316 reproduction could be related to prey availability (Wright and Laing, 1980), although *Harmonia*
317 *axyridis* larvae also rely on corn pollen at this point in the season (Lundgren et al., 2004). Pollen
318 and sugar are key food-resources for lady beetles emerging from diapause in the spring but alone
319 do not allow for egg production (Hemptinne and Desprets, 1986; Lundgren, 2009, this issue)
320 with *C. maculata* being an exception (Lundgren and Wiedenmann 2004).

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

327

328 **6. Non-food cues and preferences**

329 Food is not the only consideration for reproductive females, and sometimes coccinellids
330 will lay eggs entirely in the absence of food for their offspring (described in Banks, 1956; Evans
331 and Dixon, 1986). Iperti (1965) noted that in similar laboratory conditions, coccinellids
332 oviposited on different sites within the rearing cages. He hypothesized that this was due to
333 coccinellids expressing differing degrees of geotropism, phototropism, hygrotropism and
334 thigmotactism. *Adalia bipunctata* prefers to oviposit on curved surfaces over flat ones and
335 smooth surfaces rather than those covered by filter paper (Iperti and Prudent, 1986). Several
336 reports indicate that negative geotaxis leads to eggs being placed toward the top of plants and
337 cages (Ewert and Chiang, 1966; Iperti and Quilici, 1986). *Propylea quatuordecimpunctata* (L.)
338 displays negative phototaxis and oviposits in shaded areas of an enclosure (Iperti and Quilici,

339 1986). It may be that studies such as these reveal more about where coccinellids reside and
340 consequently oviposit than their preferences for oviposition sites. Still they are useful indicators
341 of how adults distribute themselves and narrow down where oviposition is likely to occur within
342 a habitat.

343 **6.1. Plant-based cues.** Many mass-produced lady beetles will not oviposit in empty
344 enclosures, but will oviposit in larger cages containing a small twig (Smirnoff, 1958). *Coccinella*
345 *septempunctata* prefers to oviposit on corrugated cardboard with congealed 33% strawberry
346 gelatin (Jello®) (Shands et al., 1970). *Adalia bipunctata*, *C. transversoguttata*, *Cycloneda*
347 *munda* (Say), and *Coleomegilla maculata* oviposit more often on surfaces treated with alcohol
348 extracts of *Juniperus virginiana* (L.) wood (Boldyrev et al., 1969). When further examined, the
349 extracts that stimulate oviposition in *C. maculata* are high-molecular weight polyphenols such as
350 O-coumaric, salicylic and protocatechuic acids, fluorescein, tannin, and widdrol (Smith et al.,
351 1973). Ethanol extracts from teak, cinnamon, clove, guaiacol, and resorcinol also stimulate
352 oviposition by *C. maculata* (Smith and Williams, 1976). These extracts not only increased
353 incidence of oviposition at a particular location but also the total number of eggs per female.
354 Iperiti and Prudent (1986) reported that *A. bipunctata* oviposited more on surfaces treated with
355 extracts of cypress and fennel than on untreated surfaces. *A. bipunctata* and *Coccinella*
356 *septempunctata* prefer to oviposit on barberry (*Berberis vulgaris* (L.) twigs more than on those
357 of apple or other shrubs with similar physical characteristics to barberry (Shah, 1983).
358 Additionally, *Prunus cerasus* (L.) twigs sprayed with water extracts of barberry leaves or twigs
359 had more eggs laid on them than did untreated branches. In line with this oviposition behavior,
360 *C. septempunctata* moves toward the smell of chopped barberry leaves and flower heads of

361 *Tripleurospermum inodoratum* (L.) (Asteraceae) that are devoid of prey (Schaller and Nentwig,
362 2000).

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

367
368 **6.2. Avoidance of cannibalism and intraguild predation.** Egg cannibalism and predation
369 by other lady beetle species are common sources of mortality for coccinellid eggs (Mills, 1982;
370 Wright and Laing, 1982; Agarwala and Dixon, 1992; Hodek and Honěk, 1996; Hironori and
371 Katsuhiko, 1997; Lucas, 2005; Snyder, 2009; Weber and Lundgren, 2009, this issue). Thus
372 selection should favor oviposition strategies that reduce the impact of these trophic factors.

373
374 *6.2.1. Coleomegilla maculata as a case study.* The oviposition behavior of *Coleomegilla*
375 *maculata* has been well studied, and it illustrates several reproductive strategies employed by
376 coccinellids to minimize egg predation. On plants with high numbers of aphids and predators,
377 placing eggs away from prey colonies can increase egg survival in comparison to eggs laid near
378 the prey (Coderre et al., 1987; Schellhorn and Andow, 1999). *Coleomegilla maculata* egg
379 clutches are most often found on the bottom half of corn plants (Coderre et al., 1987; Schellhorn
380 and Andow, 1999). This differs from other coccinellids commonly found in corn that oviposit
381 higher on the plant where prey is more abundant (Hodek and Honěk, 1996; Schellhorn and
382 Andow, 1999). This oviposition behavior may not have evolved strictly as a strategy to avoid
383 egg predation but clearly this is benefit derived from it.

384 Host plants can have a dramatic effect on the survival of coccinellid eggs, and *C. maculata*
385 and other species preferentially lay eggs on plants that offer protection from predation. Obrycki
386 and Tauber (1985) reported that *C. maculata* and possibly *Hippodamia convergens* oviposit most
387 often on potato hybrids (*Solanum tuberosum* x *S. berthaultii*) with patches of dense glandular
388 trichomes, even though adult and immature coccinellids were found most often on the hybrids
389 with fewer leaf hairs (Obrycki and Tauber, 1985). Cottrell and Yeargan (1998a) reported that
390 more *C. maculata* eggs were found on the weed *Acalypha ostryifolia* Ridell than on the crop in
391 cornfields. Subsequent screenings revealed that many cultivated and weedy species (notably
392 velvetleaf, *Abutilon theophrasti* Medicus, and tomato, *Lycopersicon esculentum* [Mill.]) with
393 glandular trichomes are preferred oviposition plants for *C. maculata* (Griffin and Yeargan,
394 2002a; Seagraves and Yeargan, 2006), even though adults prefer to spend their time on glabrous
395 plants (Staley and Yeargan, 2005). Prey numbers do not affect oviposition by *C. maculata* on
396 these plant surfaces (Griffin and Yeargan, 2002b). Gravid females do not use long-distance cues
397 to find these plants, but evaluate their suitability based on proximate cues (Griffin and Yeargan,
398 2002a).

399 It appears that a driving force behind *C. maculata*'s preference for ovipositing on
400 pubescent plants is that eggs on these plants experience reduced predation. A great deal of
401 predation on *C. maculata* eggs comes from older larvae and adult conspecifics (Cottrell and
402 Yeargan, 1998a; b). Pubescent plant surfaces are difficult for larvae and adults to walk on due to
403 the physical texture of the leaves (Elsley, 1974; Belcher and Thurston, 1982; Shah, 1982;
404 Obrycki, 1986). *Coleomegilla maculata* eggs laid on pubescent *Acalypha ostryifolia* and
405 *Abutilon theophrasti* experience a 55% reduction in egg cannibalism compared to those eggs laid
406 on corn (over 24 h) (Cottrell and Yeargan, 1998a; Griffin and Yeargan, 2002b). Neonate larvae

407 from pubescent plants disperse by falling to the ground and walking to neighboring crop plants
408 (Cottrell and Yeargan, 1999; Seagraves and Yeargan, 2006).

409
410 6.2.2. *Ants*. Ants that tend aphids frequently have adverse effects on natural enemies,
411 including lady beetles (Majerus et al., 2007). Lady beetles are attacked by ants at ant-tended
412 colonies and preferentially forage on non-tended aphids (Way, 1963; Styrsky and Eubanks,
413 2007). Although it has not been tested it is likely that a female's fitness would suffer if eggs
414 were laid near ant-tended aphids if other options were available. Banks (1962) reported that
415 within 48 h of their attachment, ants had removed the eggs of *Adalia bipunctata* from bean plants
416 where *Aphis fabae* Scopoli resided. The myrmecophilous coccinellid, *Coccinella magnifica*
417 Redtenbacher, as an adult is found in close association with ant-tended aphid colonies.
418 However, *C. magnifica* larvae are frequently attacked at ant-tended aphid colonies (albeit less
419 frequently than *C. septempunctata* larvae) and ovipositing females seem to discern between
420 tended and untended aphid colonies, and preferentially oviposit near ant-free aphids (Sloggett
421 and Majerus, 2003).

422 6.2.3. *Oviposition behaviors that indirectly reduce predation*. Sakuratani & Nakamura
423 (1997) documented that in the colder season *Coccinella septempunctata* oviposits on the
424 underside of non-plant materials with high thermal conductivity even when aphids are present on
425 plants. Ferran et al. (1989) found most eggs of *C. septempunctata* on soil lumps, stones, and
426 wild plants instead of on wheat plants, where most other life stages were found. Similarly, Lövei
427 and Radwan (1988) reported that the location of coccinellid eggs in an orchard shifted as the
428 season became warmer. In this case, twigs and branches were preferred sites early in the season,
429 and the undersides of leaves were preferred later in the season. These oviposition behaviors are

430 advantageous in that they shorten development time and thereby reduce the chance of egg
431 predation.

432

433 **7. Deterrent cues from conspecific and intraguild predators.**

434 Coccinellids avoid oviposition when they come in contact with predators or evidence of
435 their presence (Hemptinne et al., 1992; Merlin et al., 1996). This phenomenon is interpreted as a
436 strategy to avoid threats to the survival of their offspring, including competition and predation
437 (e.g., intraguild predation and cannibalism). The signals used by coccinellids to identify
438 predators may originate from actual contact, or through indicators of a predator's presence (e.g.,
439 larval tracks). Each coccinellid species produces specific (or a mixture of) alkanes that
440 constitute a chemical signature that is used for defense and mate recognition (Hemptinne and
441 Dixon, 2000; Magro et al., 2007). These chemicals emanate from all stages and affect
442 conspecifics, heterospecific coccinellids, other predators, and even parasitoids (Nakashima et al.,
443 2004; Magro et al., 2007; Chauhan and Weber, 2008; Rutledge et al., 2008). Many of the
444 responses to these hydrocarbon tracks have been interpreted as behaviors to avoid food
445 competition and predation. This avoidance is practiced by the potential victim (Nakashima et
446 al., 2004; Rutledge et al., 2008) but also by the ovipositing mother of a potential victim. This
447 latter type is reviewed below (section 7.2).

448

449 **7.1. Deterrence by presence of adult predators.** Gravid lady beetles in laboratory
450 experiments oviposit less when in the presence of other lady beetles. *Adalia bipunctata* females
451 lay fewer eggs when in the presence of female *Harmonia axyridis* or *C. septempunctata* (Kajita
452 et al., 2006). Aspects of the study design (i.e., daily dish changes) suggest that direct contact

453 among individuals caused the observed effect, but olfactory cues can not be ruled out. However,
454 Doumbia et al. (1998) reported that *A. bipunctata* oviposition was undeterred when they were
455 reared in Petri dishes that formerly contained conspecific adults (that would have left chemical
456 cues). Thus, oviposition deterrence by conspecific adults in *A. bipunctata* does not seem to be
457 mediated by chemical cues, although there is evidence that adults use olfactory cues to detect
458 conspecifics (Al Abassi et al., 1998; Schaller and Nentwig, 2000). *Harmonia axyridis* females
459 laid fewer eggs when grouped with conspecifics than when alone or grouped with *Sasajiscymnus*
460 *tsugae* (Sasaji and McClure) or *Laricobius nigrinus* Fender (Coleoptera: Derodontidae) (Flowers
461 et al., 2005). Females of *Menochilus sexmaculatus* laid fewer eggs in the presence of an
462 immobilized conspecific adult female or larva (Agarwala et al., 2003b). Immobilized *Coccinella*
463 *transversalis* females or larvae also reduced oviposition, but immobilized adult or larval
464 *Scymnus pyrocheilus* Mulsant or an *Ischiodon scutellaris* (F.) (Diptera: Syrphidae) maggot didn't
465 affect oviposition (Agarwala et al., 2003b). *Coccinella undecimpunctata* (L.) fed *ad libitum* does
466 not oviposit in the presence of adult *H. axyridis*, but the presence of conspecifics does not inhibit
467 oviposition (Soares and Serpa, 2006). *Coccinella septempunctata* doesn't oviposit in the
468 presence of a conspecific adult female, but will oviposit near eggs and 2nd instars (Hemptinne et
469 al., 1993).

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

475

476 **7.2. Oviposition deterrent chemicals in tracks and frass.** Numerous coccinellids can
477 detect oviposition-detering semiochemicals (ODS) in the tracks of conspecific larvae, and adjust
478 their behavior accordingly (Růžička, 1997; Doumbia et al., 1998; Růžička, 2001a; 2001b; 2003;
479 2006; Oliver et al., 2006; Magro et al., 2007; Michaud and Jyoti, 2007) (Table 1). Oviposition
480 behavior may change in response to ODS of heterospecific larvae as well, but this is less
481 common (Table 1). These documented effects very compelling but it must be recognized that
482 they have all been generated in the laboratory where conditions (i.e., substrate, rate of
483 degradation) are much different than those that would occur in the field. Our ability to gain
484 insight into chemical oviposition deterrents will be enhanced as active components and the
485 organisms and specific stages that emit them are identified. This information will allow for
486 elegant manipulations in the laboratory and attempts to document these effects in more
487 naturalistic settings.

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

497 When sympatric species are examined there still tends to be stronger deterrence from
498 conspecifics, but significant effects from the tracks of heterospecific larvae have been

499 documented. For example, *Coleomegilla maculata* prefers to consume conspecific eggs over
500 *Hippodamia convergens* eggs in choice tests (Michaud and Jyoti, 2007). Even though *C.*
501 *maculata* prefers to consume conspecific eggs, it still poses a predation risk to *H. convergens*
502 eggs, and females of the latter species respond by reducing oviposition in the presence of larvae
503 of the former species (Michaud and Jyoti, 2007).

504 The ability of adult tracks to deter oviposition is reported less frequently than the deterrent
505 properties of larval tracks, but evidence suggests that tracks from adults may influence
506 oviposition. *Propylea dissecta* (Mulsant) was deterred by conspecific adult tracks and this effect
507 lasted at least 10 d (Mishra and Omkar, 2006). This deterrence was due to adult tracks (likely
508 produced by the tarsi) as the study controlled for feces. At this date only Mishra and Omkar
509 (2006) have reported an effect of adult tracks, while Doumbia et al. (1998) reported a lack of
510 effect with *A. bipunctata*. Larval tracks may be more deterrent than those of adults as larvae are
511 more frequent consumers of coccinellid eggs than adults (Cottrell and Yeargan 1998a, b).
512 However this difference in the frequency of effect may simply reflect that larvae leave more of a
513 chemical signal than adults, as they use their anal disc to adhere to surfaces. This latter
514 explanation has merit as adult lady beetles readily consume eggs of both conspecific and
515 heterospecific coccinellids (Cottrell 2005). It has been shown that many eggs are chemically
516 defended from predation by heterospecific coccinellids (Agarwala and Dixon, 1992; Hemptinne
517 et al., 2000a). Interestingly adults, particularly *H. axyridis*, are not deterred from consuming
518 heterospecific coccinellid eggs.

519 *7.2.1. Physiology of ODS.* The ODS of *A. bipunctata* larvae originate from the anal disc on
520 the tenth abdominal segment (Laubertie et al., 2006). The chemical or combination of chemicals
521 responsible for deterrence are chloroform-soluble and made up of at least 40 different

522 hydrocarbons, mainly alkanes (Hemptinne et al., 2001). The chemical properties of ODS affect
523 their ability to spread, adhere to plant surfaces, and their persistence (up to 30 d, see below).
524 Chloroform extracts of *Cheilomenes sexmaculata* (F.) deter oviposition by conspecifics (Klewer
525 et al., 2007). Klewer et al. (2007) elucidated that (Z)-pentacos-12-ene is the key, but not sole,
526 chemical responsible for deterring oviposition. Receptors on the maxillary palpi of *Cycloneda*
527 *limbifer* Casey and *Ceratomegilla undecimnotata* Schneider perceive ODS; individuals whose
528 palpi are ablated are not deterred from ODS-marked surfaces (Růžička, 2003).

529 The longevity of ovipositional deterrence by ODS in larval tracks varies among lady
530 beetles. Conspecific larval tracks of *Coccinella septempunctata* deterred oviposition for less than
531 24 h, whereas those of *Semiadalia undecimnotata* (Schneider), *A. bipunctata*, and *Cycloneda*
532 *limbifer* were active on conspecific females for at least 5, 10, and 30 d, respectively (Hemptinne
533 et al., 2001; Růžička, 2002). It is interesting to note that the parasitoid *Apidius ervi* Haliday is
534 deterred from foraging for only 24 h by tracks of adult and larval *C. septempunctata* (Nakashima
535 et al., 2004). The interspecific variation in the reported duration of deterrence by ODS is likely
536 an artifact that the reported experiments used different amounts of larvae, duration of exposure,
537 and age of tracks at start of assay. If this amount of variation in the longevity holds up after
538 standardized experiments this would suggest that there is a difference in the persistence of the
539 active components among different species' tracks, or that species detect different compounds
540 that vary in their rate of breakdown.

541 7.2.2. *Density dependence and ODS*. Naturally, the level of deterrence produced by ODS
542 of coccinellids is density dependent (Doubria et al., 1998; Oliver et al., 2006). For example, in
543 *Cryptolaemus montrouzieri* Mulsant, which only oviposits in close association with mealybug
544 ovisacs, the level of oviposition deterrence was positively correlated with the density of

545 conspecific larvae (Hemptinne et al., 1993). The strength of density dependent deterrence can
546 decrease as a female beetle ages: *A. bipunctata* females that had oviposited for at least 30 d were
547 less deterred by conspecific larval tracks than females that had laid eggs for fewer than 10 d
548 (Fréchette et al., 2004). During long assays, fewer naïve *A. bipunctata* females oviposited than
549 females that were exposed to conspecific tracks continuously from eclosion (Fréchette et al.,
550 2004).

551 7.2.3. *Frass*. An indication of the presence of competitors is their frass. *Propylea japonica*
552 (Thunberg) oviposition is deterred by the water extracts of both conspecific and *H. axyridis*
553 larval frass (Agarwala et al., 2003a). However, *H. axyridis* oviposition was deterred by the water
554 extract of conspecific larval frass, but not the extract of *P. japonica* frass (Agarwala et al.,
555 2003a). *Propylea japonica* displays greater discretion in its oviposition, perhaps because it is less
556 competitive in intraguild interactions with other lady beetles. For both species the strength of
557 deterrence decreased as the frass aged. Coccinellid frass in the form of dry cylindrical pellets is
558 likely to fall off of plants. Therefore it remains questionable how often reproductive females
559 encounter larval frass. It is likely that the long-chain hydrocarbon larval tracks are a more
560 frequently encountered signal of potential competitors and predators (section 7.2).

561

562

563 **8. Interaction of positive and negative cues**

564 Few studies concurrently examine multiple factors on oviposition to determine how lady beetles
565 respond to the myriad factors that influence their oviposition under realistic conditions. An
566 exception is work by Michaud and Jyoti (2007), which examines the effect of con- and hetero-
567 specific larval tracks in combination with the presence or absence of prey. *Hippodamia*

568 *convergens* oviposition was deterred on plants that had been exposed to conspecific or
569 *Coleomegilla maculata* larvae. In this system, the negative effect of con- and hetero-specific
570 tracks is stronger than the positive stimulus of prey (Michaud and Jyoti 2007). In contrast to the
571 work on *H. convergens*, *Aphidecta obliterated* females clearly incorporate both the presence of
572 ODS and prey availability in their oviposition decisions (Oliver et al., 2006).

573 Just as with intraguild predation (Weber and Lundgren, 2009, this issue), as we learn
574 more about the cues that elicit or deter oviposition much work will be needed to determine how
575 adult ladybeetles integrate competing cues in complex realistic situations (Weber and Lundgren,
576 2009, this issue).

577

578 **9. Conclusions.**

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

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ACCEPTED MANUSCRIPT

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1011 **Table 1. Deterrence of oviposition in lady beetles by the larval tracks of con- or**
 1012 **heterospecific larvae.**

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

1013 ^a All species are Coleoptera: Coccinellidae, except for *Chrysopa* ssp. (Neuroptera: Chrysopidae)

1014 ^b Marginal effect (see discussion in Oliver et al., 2006)