

BioControl
DOI 10.1007/s10526-007-9125-x

2

3 **Intraguild predation involving *Harmonia axyridis*:** 4 **a review of current knowledge and future perspectives**

5 **Judith K. Pell · Jason Baverstock · Helen E. Roy · Remy L. Ware ·**
6 **Michael E. N. Majerus**

7 Received: 10 August 2007 / Accepted: 8 October 2007
8 © International Organization for Biological Control (IOBC) 2007

9 **Abstract** As an effective generalist predator of aphids and other hemipteran pests
10 *H. axyridis* has been a successful biological control agent. However, the very functional
11 traits that have contributed to its success in this regard also implicate it as an intraguild
12 predator that poses a significant risk not only to the diversity of other natural enemies of
13 Hemiptera (and their associated ecosystem services), but to biodiversity more widely. In
14 this paper we will specifically review the existing data on intraguild predation involving
15 *H. axyridis*, and consider the strength and symmetry of such interactions both within its
16 native guild and within exotic guilds where it has established as an invasive alien. We will
17 use these studies to interpret the observed population declines in predator diversity in the
18 field, predict species at risk in regions not yet invaded and consider implications for
19 resulting ecosystem services. We will also indicate gaps in our knowledge that require
20 further study in order to identify opportunities for mitigation.

21 **Keywords** Coccinellidae · *Harmonia axyridis* · Aphidophagous guild ·
22 Intraguild predation · Predators · Parasitoids · Pathogens · Ecosystem services

23 **Introduction**

24 Terrestrial ecosystems support a diversity of species that are directly and indirectly linked
25 to each other within food webs that span multiple trophic levels. Natural enemy species (in
26 the context of this paper we will collectively call these ‘predators’ as they all have a trophic
27 relationship with their hosts/prey) contribute to the population regulation of species in both

A1 J. K. Pell (✉) · J. Baverstock
A2 Department of Plant and Invertebrate Ecology, Rothamsted Research, Harpenden, Hertfordshire
A3 AL5 2JQ, UK
A4 e-mail: judith.pell@bbsrc.ac.uk

A5 H. E. Roy
A6 Biological Records Centre, CEH Monks Wood, Abbots Ripton, Huntingdon PE28 2LS, UK

A7 R. L. Ware · M. E. N. Majerus
A8 Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH, UK



Editor Proof

28 the same and lower trophic levels (top down pressure) and in this way influence the
29 structure of the community as a whole. In the case of aphids these natural enemies
30 (aphidophages) include specialist and generalist predators, parasitoids and pathogens
31 (Völkl et al. 2007). Together they represent a 'guild', i.e., a community of species that
32 share the same host/prey resource (Polis et al. 1989; Rosenheim et al. 1995). As aphids are
33 often pests in managed ecosystems these natural enemies provide a valuable pest man-
34 agement ecosystem service that can be manipulated within biological control strategies
35 (e.g., Barbosa 1998; Gurr et al. 2004; Losey and Vaughan 2006; Powell and Pell 2007; Pell
36 2008).

37 Different 'predator' taxa play different ecological roles within the guild (Rosenheim
38 et al. 2004a). 'Intermediate predators' function from the third trophic level suppressing
39 herbivores, whereas 'top predators' mainly operate from the fourth trophic level sup-
40 pressing 'intermediate predators' and, consequently, releasing herbivore populations from
41 control (Polis 1994; Rosenheim 1998). Intraguild predation occurs when one of two spe-
42 cies competing for the same host/prey also consumes its competitor, and can be a strong
43 force structuring communities. Omnivorous intraguild predation can be asymmetric when
44 one of the two species (the intraguild predator) always preys on the other (the intraguild
45 prey), or symmetric when both species prey on each other to a greater or lesser extent
46 (Polis et al. 1989; Polis and Holt 1992; Rosenheim et al. 1995). The intraguild predator
47 benefits not only from the nutritive value of the meal, but also from the removal of a
48 competitor. Coincidental intraguild predation occurs when a parasitoid or pathogen is
49 consumed while still developing within its herbivore host and, in this case, the herbivore
50 and the intraguild prey are directly linked (Polis et al. 1989). Intraguild predators function
51 as both 'intermediate' and 'top predators' by feeding on both herbivores and 'intermediate
52 predators'.

53 The impact of intraguild predation on community structure and diversity can be
54 extremely variable, complex and difficult to predict (Rosenheim et al. 2004a; Snyder and
55 Evans 2006; Straub et al. 2008). Many studies have assessed the prevalence of intraguild
56 predation in aphidophagous guilds (Polis et al. 1989; Rosenheim et al. 1995; Holt and
57 Polis 1997; Müller and Brodeur 2002; Lucas 2005; Pell 2008) and reported it to be a
58 widespread phenomenon with implications for both predator diversity within the guild and
59 the pest management ecosystem services that the guild delivers.

60 As an effective generalist predator of aphids and other hemipteran pests *Harmonia*
61 *axyridis* (Pallas) (Coleoptera: Coccinellidae) has been widely and repeatedly augmented or
62 introduced for biological control. As such, it has contributed significantly to pest sup-
63 pression in a wide variety of managed ecosystems including pecan, apple, sweet corn,
64 alfalfa, cotton, tobacco, wheat and soybean (Teddars and Schaefer 1994; Buntin and
65 Bouton 1997; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Wells and
66 McPherson 1999; Wells et al. 2001; Musser and Shelton 2003; Koch 2003; Majerus et al.
67 2006; Roy et al. 2006). However, the very functional traits that have made *H. axyridis* an
68 effective biological control agent, also implicate it as an intraguild predator that poses
69 significant risk to the diversity of other natural enemies of Hemiptera and their ecosystem
70 services. Although natural enemy diversity in its native range remains relatively stable in
71 the presence of *H. axyridis* (Kuznetsov 1988, 1997), wherever it has established after
72 introduction as an exotic species, it has been associated with declines in native natural
73 enemies, particularly native coccinellids (Majerus et al. 2006; Roy et al. 2006; Snyder and
74 Evans 2006). These declines have been attributed to direct interspecific competition for
75 resources with less competitive/fecund natural enemies (Michaud 2002) but are also likely
76 to be strongly influenced by its role as an intraguild predator.



77 There are a number of functional traits that determine the nature, symmetry and
78 outcome of intraguild predation including: relative size (incidence of mortality is often
79 inversely correlated with size) (Majerus 1994; Evans 2000), aggressive strategies and
80 mandibular structure (Yasuda et al. 2001), degree of feeding and habitat specificity,
81 mobility (sessile stages are particularly vulnerable), defence strategies and abundance of
82 extraguild prey (Polis et al. 1989; Lucas et al. 1998; Roy et al. 2006; Straub et al. 2008).
83 In this paper we will specifically review the existing, largely experimental, data on these
84 traits for *H. axyridis*, and discuss their strength and symmetry both within its native guild
85 and within exotic guilds where it has established as an invasive alien. We will use these
86 studies to interpret the observed population declines in natural enemy diversity in the field,
87 predict species at risk in regions not yet invaded and consider implications for resulting
88 ecosystem services. We will also identify gaps in our knowledge that require further study
89 in order to identify opportunities for mitigation.

90 Current knowledge

91 Intraguild predation between *H. axyridis* and coccinellids of other species

92 Eggs

93 The relative size and mobility of the intraguild predator and prey are known to influence
94 the outcome of intraguild predation, both showing an inverse correlation with the incidence
95 of mortality (Huey and Pianka 1981; Sengonca and Frings 1985; Rosenheim et al. 1995;
96 Lucas et al. 1998). In coccinellids this equates to the immature stages being more
97 vulnerable than adults, and eggs being particularly threatened (Sato and Dixon 2004;
98 Cottrell 2007).

99 *Harmonia axyridis* adults and larvae find eggs of many insect species acceptable as
100 prey; laboratory stocks are often maintained on eggs of the Mediterranean flour moth,
101 *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) (Berkvens et al. 2008). Cottrell (2004)
102 reports that *H. axyridis* adults attacked eggs of *Coleomegilla maculata* (De Geer)
103 (Coleoptera: Coccinellidae) and *Olla v-nigrum* (Mulsant) (Coleoptera: Coccinellidae) more
104 frequently than adults of these species attacked *H. axyridis* eggs, and attest that intraguild
105 predation of eggs is a serious threat for these species. However, cannibalism and predation
106 of coccinellid eggs are most often associated with larval stages (Dixon 2000; Cottrell 2007)
107 and, for some species, may be affected by the relative abundance of extraguild prey (Sato
108 et al. 2003); at low aphid or coccid densities, coccinellid larvae are more likely to engage
109 in cannibalism or intraguild predation. In addition, the tendency for intraguild predation by
110 larvae varies between species both as intraguild predators and intraguild prey. Cannibalism
111 and intraguild predation by *H. axyridis* are commonly observed, both in the laboratory and
112 the field, even when aphids or coccids are abundant (M.E.N. Majerus and R.L. Ware
113 personal observation). A recent study concluded that *H. axyridis* larvae were more likely to
114 engage in intraguild predation of the eggs of *C. maculata*, *Cycloneda munda* (Say)
115 (Coleoptera: Coccinellidae), *Hippodamia convergens* Guérin-Méneville (Coleoptera:
116 Coccinellidae) and *O. v-nigrum* than for *H. axyridis* eggs to be the intraguild prey of the
117 larvae of these species (Cottrell 2007). This is in agreement with previous work of Cottrell
118 (2004) demonstrating that neither *C. maculata* nor *O. v-nigrum* larvae can complete
119 development on *H. axyridis* eggs whereas *H. axyridis* can complete development on a diet
120 of either *C. maculata* or *O. v-nigrum* eggs.



121 Defensive adaptations (chemical or physical) are often effective in reducing the
122 susceptibility of sessile life stages, such as eggs, prepupae and pupae to intraguild pre-
123 dation and cannibalism. The chemical defences of coccinellid eggs have been well studied
124 (Agarwala and Dixon 1992; Hemptinne and Dixon 2000). Indeed, while intrinsic toxicity
125 or unpalatability is governed by de novo synthesis of species-specific alkaloids (Pasteels
126 et al. 1973; King and Meinwald 1996), Hemptinne and Dixon (2000) demonstrated the
127 existence of extrinsic chemicals on the surface of some species' eggs that act as deterrents
128 against intraguild predation. Ware et al. (2008b) have recently discussed the role of
129 surface deterrents on eggs of the European species *Calvia 14-guttata* (L.) (Coleoptera:
130 Coccinellidae) as a defence against intraguild predation by *H. axyridis*. A similar
131 phenomenon has been speculated for the eggs of the Japanese species *Eocaria muii*
132 Timberlake (Coleoptera: Coccinellidae) (Ware et al. 2008a). The defensive chemistry of
133 *H. axyridis* eggs themselves has been implicated as pivotal to the observed resistance of
134 *H. axyridis* eggs to predation by other aphidophages that appear to find them unpalatable
135 (Alam et al. 2002; Sato and Dixon 2004). Interestingly, similar alkanes to those found on
136 the surface of *H. axyridis* eggs are also present in larval tracks and act as oviposition
137 deterring semiochemicals for other ladybirds, thus reducing egg cannibalism and intraguild
138 predation (Magro et al. 2007).

139 *Larvae and pupae*

140 Ware and Majerus (2008) have comprehensively examined intraguild predation of
141 immature stages of British and Japanese coccinellids by *H. axyridis*. A total of 12 species
142 of coccinellid (Coleoptera: Coccinellidae) were included in this laboratory study: eight
143 derived from British populations (*Coccinella 7-punctata* L., *Adalia 2-punctata* (L.), *Adalia*
144 *10-punctata* (L.), *Propylea 14-punctata* (L.), *C. 14-guttata*, *Anatis ocellata* (L.), *Harmonia*
145 *4-punctata* (Pontoppidan), *Coccinella 5-punctata* L.) and four from Japanese populations
146 (*Coccinella 7-punctata brucki* Mulsant, *Cheilomenes 6-maculatus* (Fabricius), *Propylea*
147 *japonica* Thunberg and *E. muii*). In general, *H. axyridis* was an intraguild predator of all
148 species, with the exception of *A. ocellata*. The important conclusions of this study were
149 that there was no obvious difference between the susceptibilities of Japanese and British
150 coccinellids to intraguild predation by *H. axyridis*, and intraguild predation by *H. axyridis*
151 represents a serious threat for many species in Britain (Ware and Majerus 2008).

152 The relatively large size of *H. axyridis* throughout its life cycle undoubtedly contributes
153 to its success as an intraguild predator following the 'size matters' hypothesis. In predatory
154 interactions between coccinellid larvae it is generally the larger that eats the smaller,
155 assuming both are mobile (Majerus 1994). Notably, in comparative tests between fourth
156 instar larvae of *H. 4-punctata*, *H. axyridis* and *A. ocellata*, which have similar behavioural
157 and physical defences, the level of intraguild predation was directly correlated to size. Larvae
158 of the largest species, *A. ocellata*, won the majority of encounters with *H. axyridis*, while the
159 smallest species, *H. 4-punctata*, lost most such encounters (Ware and Majerus 2008).

160 There are few reports of other larval coccinellids successfully attacking *H. axyridis*, and
161 most evidence suggests that the immature stages of *H. axyridis* are resistant to reciprocal
162 attacks. In a laboratory study assessing the interactions between *H. axyridis* and
163 *C. 7-punctata*, Yasuda et al. (2001) attributed the greater success of the former to its higher
164 attack rates and greater escape ability. Recent research is beginning to confirm the importance
165 of chemical defence of *H. axyridis* larvae as a means of preventing counter-attacks (Ware and
166 Majerus 2008), and larvae are known to produce similar defensive alkaloids to those present



167 within eggs and released by adults (Pasteels et al. 1973; King and Meinwald 1996). Further
168 studies have also implicated the role of superior physical defences (spines rather than hairs) in
169 larval stages of *H. axyridis* compared to other species (Ware and Majerus 2008).

170 In the field, coccinellid larvae tend to disperse from a plant when prey abundance is low
171 (Sato 2001) and this reduces the incidence of cannibalism and intraguild predation by
172 larger larvae and adults (Sato et al. 2003). However, emigration is a precarious strategy for
173 an immature coccinellid, so there is a trade-off between emigrating or remaining on a plant
174 with a low prey density and risking cannibalism or intraguild predation. *Harmonia axyridis*
175 commonly co-occurs with *C. 7-punctata brucki* and *P. japonica* in their native Japanese
176 range (Yasuda and Shinya 1997; Sato 2001). In a Japanese field study of these three
177 coccinellid species co-occurring on shrubs both *C. 7-punctata brucki* and *H. axyridis*
178 larvae emigrated in response to low prey density whereas *P. japonica* larvae did not (Sato
179 2001). The prevalence of intraguild predation and cannibalism of *C. 7-punctata brucki* and
180 *H. axyridis* larvae was low whereas no *P. japonica* larvae completed their development on
181 the shrubs and this was assumed to be as a consequence of intraguild predation. In further
182 studies it was confirmed that the early emigration of *C. 7-punctata brucki* larvae enabled
183 them to escape from intraguild predation by *H. axyridis* larvae (Sato et al. 2003) and that
184 the late emigration of *P. japonica* larvae accounted for the high incidence of intraguild
185 predation by *H. axyridis* larvae (Sato et al. 2003).

186 *Propylea japonica* is also a smaller species than either *H. axyridis* or *C. 7-punctata*
187 *brucki* and so this further supports the hypothesis that 'size matters' in intraguild predation.
188 Ware and Majerus (2008) also report *P. japonica* larvae as highly palatable intraguild prey
189 with little physical defence from attack by *H. axyridis*. It is interesting to note from field
190 studies in Japan that *C. 7-punctata brucki* are active earlier in the spring than *H. axyridis*
191 (Takahashi and Naito 1984; Sato 2001). Therefore, *H. axyridis* are more likely to expe-
192 rience a scarcity of aphids, which are abundant in spring and early summer, than
193 *C. 7-punctata brucki*. Consequently, *H. axyridis* is likely to be more reliant on intraguild
194 prey to complete their development than is *C. 7-punctata brucki* (Sato et al. 2003).

195 Adults

196 Adult coccinellids are generally less susceptible to predation than immature stages due to
197 their protective elytra and aposematic colour patterns (Majerus 1994). However, they are
198 exposed to a particularly vulnerable period just after eclosion, when their elytra are still
199 soft. Ware and Majerus (2008) report observations of attacks made on eclosing or newly
200 eclosed adults by larvae, when no other food was available. Fourth instar *H. axyridis* larvae
201 were observed to attack and consume new adults of *A. 10-punctata*, *A. ocellata*,
202 *C. 14-guttata*, *C. 7-punctata brucki* and *E. muiri*, after not having attacked them as pupae
203 (Ware and Majerus 2008). However, the consumption of newly eclosed *H. axyridis* adults
204 was rare, and only performed by conspecific larvae and larvae of the congeneric species
205 *H. 4-punctata*. This supports the speculation that the defensive chemistry of *H. axyridis*
206 adults may make them unpalatable to other coccinellids (Hough-Goldstein et al. 1996).

207 Intraguild predation between *H. axyridis* and non-coccinellid predators

208 Coccinellids are common within aphidophagous guilds and most studies considering the
209 role of *H. axyridis* as an intraguild predator have focussed on interactions within the



Editor Proof

210 Coccinellidae. However, *H. axyridis* interacts with many other predatory insects at the
211 community level. Lacewings (Neuroptera) are both abundant as aphid predators in natural
212 systems, and as components of biological control strategies. In a laboratory study,
213 Phoofolo and Obrycki (1998) demonstrated that there was no difference in the develop-
214 ment time or survival of *H. axyridis* (and also *C. maculata*) fed on a diet of pea aphids,
215 *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae), or eggs of the lacewing,
216 *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). In contrast, *C. carnea* was
217 unable to develop successfully when fed on *H. axyridis* eggs.

218 A further study examined the interactions between adult *H. axyridis*, *C. carnea* and the
219 gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) in the presence of
220 the soybean aphid, *Aphis glycines* Matsumara (Hemiptera: Aphididae), in microcosms and
221 field cages (Gardiner and Landis 2007). *Harmonia axyridis* engaged in intraguild predation
222 with both *C. carnea* and *A. aphidimyza* and was predicted to contribute to declines in both
223 species in the field. Phoofolo and Obrycki (1998) and Gardiner and Landis (2007) both
224 suggested the potential for *H. axyridis* to be an asymmetrical intraguild predator of
225 *C. carnea*. However, *C. carnea* will consume *H. axyridis* eggs (Phoofolo and Obrycki
226 1998) and recent observations by Fremlin (2007) indicate that *C. carnea* will also attack
227 *H. axyridis* pupae. Therefore, the interaction can be considered to be (weakly) symmet-
228 rical. Further research is required to expand our knowledge on interactions between
229 neuropterans and *H. axyridis*.

230 The spined soldier bug, *Podisus maculiventris* Say (Heteroptera: Pentatomidae) is
231 native to North America and has a broad prey range including over 100 species of insect,
232 primarily soft-bodied, slow-moving larvae of Coleoptera and Lepidoptera, but also aphids
233 (McPherson 1980; Herrick and Reitz 2004). Half of the species on which it preys
234 are important crop pests (Herrick and Reitz 2004). *Podisus maculiventris* is therefore
235 loosely linked with many trophic guilds, including that of aphids (McPherson 1980;
236 Hough-Goldstein et al. 1996), and four species of predaceous coccinellid are listed as prey
237 to this predatory bug (McPherson 1980). In laboratory studies, Hough-Goldstein et al.
238 (1996) demonstrated that although *P. maculiventris* did not consume adult *H. axyridis* they
239 did consume *H. axyridis* larvae in 'no choice' treatments. In this study, *H. axyridis* larvae
240 were described as 'aggressive' and often noted to escape predation, whereas adult
241 *H. axyridis* were rejected, presumably as unpalatable, by *P. maculiventris*. Indeed,
242 *P. maculiventris* took four times longer to capture *H. axyridis* larvae compared to *Spodoptera*
243 *frugiperda* Smith (Lepidoptera: Noctuidae) larvae (Hough-Goldstein et al. 1996).

244 A further study demonstrated that interactions between *P. maculiventris* and *H. axyridis*
245 in the presence or absence of extraguild prey (*Spodoptera littoralis* Boisduval (Lepidop-
246 tera: Noctuidae) or *Myzus persicae* (Sulzer) (Hemiptera: Aphididae)) were asymmetric in
247 favour of the bug (De Clercq et al. 2003). *Podisus maculiventris* fed on *H. axyridis* eggs
248 and larvae but rarely on adults. As with interactions amongst coccinellids, this interaction
249 was dependent on the life stage of the bug; fourth instar nymphs and adults were more
250 aggressive in their interactions than second instars nymphs. In contrast, *H. axyridis* rarely
251 attacked *P. maculiventris*. Intraguild predation by *P. maculiventris* on *H. axyridis* was
252 reduced in the presence of *S. littoralis* but not *M. persicae*. De Clercq et al. (2003)
253 interpreted this to infer that *H. axyridis* was a less preferred prey in comparison to
254 *S. littoralis* and this was supported by the longer development time of the bug when fed on
255 *H. axyridis* larvae compared to *S. littoralis*. There was a slight difference in the survival to
256 adulthood of pentatomid nymphs fed on *H. axyridis* compared to *S. littoralis* (70% vs.
257 80–90% respectively) and no nymphs reached adulthood when fed on just aphids
258 (De Clercq et al. 2003).



259 Intraguild predation between *H. axyridis* and parasitoids

260 Intraguild predation between predators and parasitoids is asymmetrical and can be
261 described as both coincidental and omnivorous (Polis et al. 1989). In contrast to the
262 literature on intraguild predation between *H. axyridis* and other predators, particularly
263 coccinellids, there is very little information on such interactions between *H. axyridis*
264 and parasitoids. Previous studies have reported the consumption of parasitized aphids by
265 coccinellids (Wheeler et al. 1968; Ferguson and Stiling, 1996) and that the presence, or
266 recent activity, of predatory coccinellids within an aphid colony can reduce the oviposition
267 rate of aphid parasitoids (Taylor et al. 1998).

268 Takizawa et al. (2000) assessed whether the aphid *Aphis craccivora* Koch (Hemiptera:
269 Aphididae), parasitized by *Aphidius colemani* Viereck (Hymenoptera: Braconidae), were
270 suitable prey for three coccinellid species: *C. 7-punctata*, *P. japonica* and *H. axyridis*. The
271 parasitoid was used at two life stages: 3-day-old larvae within living aphids (coincidental
272 intraguild predation) and sessile aphid 'mummies' containing pupae (asymmetrical
273 omnivorous intraguild predation). Consumption of parasitized aphids containing 3-day-old
274 larvae did not reduce survival or increase development time of any of the coccinellids. In
275 contrast, consumption of aphid 'mummies' increased the development time of all three
276 species and reduced survival to adulthood of *C. 7-punctata* by 70% but did not affect the
277 survival of *H. axyridis* and *P. japonica*. *Coccinella 7-punctata* is considered to be a more
278 aphid-specific predator than *H. axyridis* (Hodek and Honek 1988). It is likely that para-
279 sitized 'mummies' are unsuitable prey and, hence, the low survival rates of *C. 7-punctata*
280 fed on parasitized aphids could be attributed to their aphid-specific dietary requirements
281 (Takizawa et al. 2000). In contrast, *H. axyridis* selectively preyed on pea aphids, *A. pisum*,
282 rather than pea aphid 'mummies' parasitized by *Aphidius ervi* Haliday (Hymenoptera:
283 Braconidae) (Snyder and Ives 2003). Although this would not change the impact of
284 coincidental intraguild predation of larval parasitoids by *H. axyridis*, it does demonstrate
285 that interactions are variable depending on the prey concerned. Similarly, in a study at
286 larger spatial scales Snyder et al. (2004a) found that although *H. axyridis* did prey on
287 'mummies' of the aphid parasitoid *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae)
288 (adult *H. axyridis* showed no discrimination between 'mummies' and aphids although
289 larvae preferred aphids in feeding trials), the overall parasitism level was not affected.

290 Intraguild predation between *H. axyridis* and pathogens

291 Entomopathogenic fungi are common pathogens of aphids and can be involved in both
292 coincidental and omnivorous, asymmetrical or symmetrical, intraguild interactions (Roy
293 and Pell 2000; Völkl et al. 2007). The most common fungal pathogens are host-specific
294 species from the Zygomycetes, order Entomophthorales, although other species from the
295 Ascomycetes, order Hypocreales, some with wide host ranges, are used as biopesticides
296 and could, therefore, be involved in intraguild interactions (Powell and Pell 2007; Pell
297 2008).

298 During the final stages of infection by entomopathogenic fungi the host dies and the
299 fungus sporulates to produce more infective propagules (conidia) for transmission (Inglis
300 et al. 2001; Pell et al. 2001). As the sporulating aphid cadaver is sessile, it is an easy prey
301 item for generalist predators. In a laboratory study, Roy et al. (2008a) assessed the pre-
302 dation of aphid cadavers sporulating with *Pandora neoaphidis* (Remaudière and
303 Hennebert) Humber (Zygomycetes: Entomophthorales) by UK and Japanese-derived



Editor Proof

304 *H. axyridis* relative to that of the UK native species *C. 7-punctata*. Unlike *C. 7-punctata*,
305 which showed a strong preference for aphids over sporulating fungal cadavers, *H. axyridis*
306 showed little discrimination between the prey types and would consume whole, sporulating
307 cadavers. The consumption of whole sporulating cadavers could remove a significant
308 quantity of inoculum from the aphid population, which may result in a reduction in further
309 transmission. As *P. neophidius* only infects aphids, this represents asymmetrical intraguild
310 predation. The strength of intraguild predation by *H. axyridis* collected in the UK differed
311 from those collected in Japan, with *H. axyridis* (UK) showing less discrimination between
312 prey types compared to *H. axyridis* (Japan) (Roy et al. 2008a). Whether feeding on
313 infected cadavers has fitness consequences for *H. axyridis* is unknown.

314 Other entomopathogenic fungi have wider host ranges and may be infective
315 towards both coccinellids and aphids, making the intraguild interaction potentially
316 symmetrical. For example, isolates of the entomopathogenic fungi *Metarhizium*
317 *anisopliae* (Metschnikoff) Sorokin (Ascomycete: Hypocreales), *Paecilomyces fumos-*
318 *oroseus* (Wise) Brown and Smith (Ascomycetes: Hypocreales) and *Beauveria bassiana*
319 (Balsamo) Vuillemin (Ascomycetes: Hypocreales) have been recorded infecting both
320 aphids and coccinellids (e.g., Magalhaes et al. 1988; Keller and Zimmerman 1989; Butt
321 et al. 1994; James and Lighthart 1994; Yeo 2000; Pell and Vandenberg 2002; Ormond
322 et al. 2006). In particular, *B. bassiana* is a major overwintering mortality agent of
323 *C. 7-punctata* (Majerus 1994; Ormond et al. 2006). Roy et al. (2008b) assessed the
324 susceptibility of *H. axyridis* derived from the UK and Japan to *B. bassiana* relative to
325 that of the UK native species *C. 7-punctata* and *A. 2-punctata*. Only doses of 10^9 conidia
326 ml^{-1} resulted in mortality of *H. axyridis*, in contrast, 80% of *C. 7-punctata* and 70% of
327 *A. 2-punctata* exposed to 10^7 conidia ml^{-1} of *B. bassiana* succumbed to infection. In
328 addition, the results suggested that the UK derived strain may be more resistant to
329 infection than the Japanese derived strain. Interestingly, inoculation with *B. bassiana* at a
330 concentration as low as 10^5 conidia ml^{-1} reduced the fecundity of *H. axyridis* (Roy et al.
331 2008b). Whether any of these coccinellids feed on *B. bassiana*-infected cadavers and the
332 implications of this on the symmetry of intraguild predation is unknown. However, in the
333 study of Pell and Vandenberg (2002) the coccinellid *H. convergens* did consume living
334 *Diuraphis noxia* Kurdjumov (Hemiptera: Aphididae) aphids infected by *P. fumosoroseus*
335 but did not consume sporulating aphid cadavers.

336 In both studies by Roy et al. (2008a, b), the interactions involving *H. axyridis* collected
337 from the UK differed from those collected in Japan, with *H. axyridis* from the UK being a
338 stronger intraguild predator of *P. neophidius* and more resistant to *B. bassiana* than the
339 strain from Japan. These are the first studies to indicate fundamental differences between
340 *H. axyridis* subpopulations and demonstrate the importance of assessing genetic and
341 ecological variability amongst such subpopulations.

342 Intraguild predation involving *H. axyridis*: Conclusions to date

343 There is broad agreement, from the studies described above, that *H. axyridis* is a top
344 predator as it is predominantly a strong asymmetrical intraguild predator of other guild
345 members (Hironori and Katsuhiko 1997; Cottrell and Yeargan 1998; Phoofole and Obrycki
346 1998; Yasuda and Ohnuma 1999; Michaud 2002; Sato et al. 2003, 2005; Felix and Soares
347 2004; Snyder et al. 2004b; Kajita et al., 2006; Perez and Omkar 2006; Roy et al. 2006,
348 2008a, b; Cottrell 2007; Ware and Majerus 2008) and as such can dominate in aggressive
349 intraguild interactions and lead to a decline in guild diversity.



350 The key functional traits that make *H. axyridis* such an exceptional intraguild predator
351 are its relatively large size, aggressive behaviour, extreme polyphagy and the possession of
352 effective physical and chemical defence strategies. Together these traits provide the
353 mechanism by which *H. axyridis* impacts on guilds and food webs in general (Teddars and
354 Schaefer 1994; Hodek 1996; Yasuda and Shinya 1997; Yasuda and Ohnuma 1999; Kajita
355 et al. 2000; Koch 2003). It therefore seems likely that *H. axyridis* could disrupt
356 aphidophagous/coccidophagous community structure leading to declines in other species in
357 the guild where it establishes as a non-native species. *Harmonia axyridis* has certainly
358 become abundant and widely distributed as a non-native species throughout North America
359 and Europe (Koch 2003; Brown et al. 2008) and field data from the USA has reported
360 associated negative impacts on native coccinellid species in these regions (Elliott et al.
361 1996; LaMana and Miller 1996; Brown and Miller 1998; Colunga-Garcia and Gage 1998;
362 Lucas et al. 2002; Michaud 2002; Nault and Kennedy 2003). Interestingly, *C. 7-punctata*
363 was also introduced and became established widely in North America prior to the estab-
364 lishment of *H. axyridis* (Gordon 1985). It too displaced native coccinellids and became the
365 dominant predator. However, *H. axyridis* is a more aggressive predator than *C. 7-punctata*;
366 larvae of *H. axyridis* consume those of *C. 7-punctata* but the reverse occurs considerably
367 less frequently (Hironori and Katsuhiko 1997; Yasuda et al. 2004; Ware and Majerus
368 2008). Since the arrival of *H. axyridis* in the USA, it has displaced *C. 7-punctata* as the
369 'top predator' demonstrating the considerable dominance of *H. axyridis* as an intraguild
370 predator of native and exotic coccinellids alike (Snyder et al. 2004b).

371 Similar evidence of declines in native coccinellid species after establishment of
372 *H. axyridis* is accumulating in Europe. For example, evidence suggests that in London
373 numbers of some, but not all, native coccinellids (particularly *A. 2-punctata*) have declined
374 significantly since the arrival of *H. axyridis* in 2004 (Majerus, unpublished data). This is
375 almost certainly due to its superior competitive ability and status as an intraguild predator.
376 From the experimental studies of Ware and Majerus (2008), with consideration of the
377 wider ecologies of *H. axyridis* and British ladybirds, and in the absence of control or
378 mitigation, we anticipate that aphidophagous habitat generalists such as *C. 7-punctata*,
379 *A. 2-punctata* and *P. 14-punctata* will be most at risk from the establishment of
380 *H. axyridis* in the UK, followed by aphidophagous habitat specialists such as *Myzia*
381 *oblongoguttata* (L.) (Coleoptera: Coccinellidae), *Myrrha 18-guttata* (L.) (Coleoptera:
382 Coccinellidae) and *Anisosticta 19-punctata* (L.) (Coleoptera: Coccinellidae). The only
383 species that may be relatively unaffected by invasive *H. axyridis* is *A. ocellata*, and indeed
384 *H. axyridis* could actually be at risk from detrimental interactions with this species where
385 they co-inhabit coniferous woodland. It is thought that the aphidophagous specialist
386 *C. 5-punctata* would be particularly threatened if *H. axyridis* invades unstable river
387 shingle, as it is already considered of conservation concern (Ware et al. 2005). Coccido-
388 phagous species such as *Exochomus 4-pustulatus* (L.) (Coleoptera: Coccinellidae) and
389 *Chilocorus renipustulatus* (Scriba) (Coleoptera: Coccinellidae) and the *Erica/Calluna*
390 heathland specialists *Chilocorus 2-pustulatus* (L.) (Coleoptera: Coccinellidae) and
391 *Coccinella hieroglyphica* L. (Coleoptera: Coccinellidae) are thought to be less at risk, the
392 latter because *H. axyridis* has yet to be recorded from such heathland. Mycophagous,
393 phytophagous and myrmecophilous coccinellids, such as *Thea 22-punctata* (L.) (Coleop-
394 tera: Coccinellidae), *Subcoccinella 24-punctata* (L.) (Coleoptera: Coccinellidae) and
395 *Coccinella magnifica* Redtenbacher (Coleoptera: Coccinellidae) respectively, are likely to
396 be the least threatened by the establishment of *H. axyridis* in Britain.

397 There is clear evidence of declines in diversity of coccinellids in the USA and
398 increasingly in Europe. However, there have been no studies to evaluate impacts on the



399 diversity of other guild members or on biodiversity more widely; these are urgently
400 required, particularly in areas undergoing invasion by *H. axyridis*, if the full implications
401 of its presence are to be evaluated.

402 Knowledge gaps, future perspectives and implications for biodiversity
403 and ecosystem function

404 *Harmonia axyridis* is also a dominant intraguild predator in its native range, as shown by
405 Ware and Majerus (2008) who paired Japanese *H. axyridis* with Japanese native coccin-
406 ellids in their laboratory interaction studies and found that *H. axyridis* was the successful
407 intraguild predator in the majority of cases. It has also prevented the establishment of the
408 introduced coccinellid *A. 2-punctata* in Japan (Sakuratani et al. 2000; Kajita et al. 2006).
409 However, it appears to co-exist with most other guild members (Kuznetsov 1997) whilst
410 causing declines and competitive exclusion of other coccinellid species in regions where it
411 is an invasive exotic (e.g., Colunga-Garcia and Gage 1998; Michaud 2002). In co-evolved
412 communities that utilise limited resources, species will be under selection to either ensure
413 that they win any competitive interaction or that they avoid competition through resource-
414 use complementarity and niche differentiation (Wilby and Thomas 2002a, b; Pell 2008). It
415 is possible that, although *H. axyridis* is the top predator in its native range, other predator
416 populations can escape intraguild predation through spatial or temporal niche differenti-
417 ation. Studies to understand the mechanisms for co-existence with *H. axyridis* in its native
418 range are essential if we are to mitigate existing effects in its invasive range.

419 *Temporal niche differentiation*

420 The co-existence of *H. axyridis* and sympatric species in Asia may, in part, be due to
421 phenological differences that lead to temporal niche differentiation. For example,
422 *C. 7-punctata brucki* is active earlier in the spring in Japan than *H. axyridis* and its larvae
423 are therefore larger and more able to survive in intraguild combat with *H. axyridis*
424 (Takahashi and Naito 1984; Sato 2001). Phenological studies of *H. axyridis* in its non-
425 native range are essential if we are to predict the extent of intraguild predation and
426 consequent impacts on biodiversity. Such studies are underway and in the UK, for
427 example, early indications are that *H. axyridis* emerges from winter in synchrony with
428 most native aphidophagous coccinellids, which contributes to the latter's inability to
429 escape intraguild predation. *Harmonia axyridis* is also multivoltine and remains active for
430 longer through the season, allowing numbers of individuals to build up rapidly. All life
431 stages of *H. axyridis* have been recorded in November (early winter) in the UK (Majerus
432 et al. 2006; Brown et al. 2008). In one study from the USA biological control literature,
433 Flowers et al. (2006) considered intraguild interactions amongst three exotic predators
434 attacking the hemlock woolly adelgid, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae) in
435 hemlock stands in West Virginia. The species included were: specialists, *Laricobius*
436 *nigrinus* (Fender) (Coleoptera: Derodontidae) and the coccinellid *Sasajiscymnus tsugae*
437 (Sasaji & McClure) (Coleoptera: Coccinellidae), and the generalist *H. axyridis*. The
438 authors concluded that intraguild predation by *H. axyridis* was not common because they
439 were phenologically separated and active during different seasons; *L. nigrinus* was most
440 active in spring and *H. axyridis* in summer. This also has implications for the wider guild
441 beyond other coccinellids, for which there is currently very little information.



442 *Associations with ants*

443 Other coccinellid species in *H. axyridis*' native range may escape intraguild predation
444 through associations with ants. Although there are limited studies on myrmecophilous
445 interactions in the native range of *H. axyridis*, it is well documented for some coccinellid
446 species in Europe. Many aphids and coccids are myrmecophilous and gain benefits from
447 being associated with ants, including protection from natural enemies, in exchange for food
448 in the form of honeydew (e.g., Hölldobler and Wilson 1990; Jiggins et al. 1993; Majerus
449 et al. 2007). There is considerable evidence to demonstrate that ants display ownership
450 behaviour, whereby they behave more aggressively towards predators in the vicinity of
451 tended colonies than elsewhere (Way 1963). In the case of coccinellids, this aggression
452 may be directed toward both adults and larvae, the former being chased away (e.g., Itioka
453 and Inoue 1996; Sloggett 1998), while the latter may be picked up and dropped off the
454 plant, or killed (e.g., Jiggins et al. 1993; Sloggett and Majerus 2003). As a result of ant
455 aggression, most coccinellids only feed on ant-tended prey when untended prey are scarce
456 (Sloggett and Majerus 2000). Many coccinellids have defences against ant aggression,
457 which may be behavioural, chemical or physical and lead to variation in tolerance to ants
458 amongst different coccinellid species (Majerus et al. 2007). For example, Sloggett and
459 Majerus (2000) showed a hierarchy in six species of coccinellid living in pine woodland in
460 the UK to aggression from *Formica rufa* (L.) (Hymenoptera: Formicidae) from no toler-
461 ance (*M. 18-guttata* and *A. ocellata*) to high tolerance (*C. magnifica*). Unfortunately, the
462 level of tolerance of *H. axyridis* to ant aggression in either its native or its invasive range is
463 unknown. Should *H. axyridis* be found to be intolerant of ant presence, it is likely that
464 those aphidophages that have a significant degree of ant tolerance, such as *M. oblongo-*
465 *guttata* and *C. 7-punctata*, will find a refuge from some of the effects of intraguild
466 predation and competition imposed by *H. axyridis* in habitats occupied by ant-tended
467 aphids. Experiments to investigate the level of tolerance of *H. axyridis* to common aphid
468 tending ants, such as *F. rufa*, *Lasius niger* (L.) (Hymenoptera: Formicidae) and *Myrmica*
469 *ruginodis* Nylander (Hymenoptera: Formicidae), are urgently needed. The small number of
470 coccinellid species that are true myrmecophiles, i.e., have the closest relationships with
471 ants and associated high tolerance, are likely to have the safest refuge from *H. axyridis*,
472 unless *H. axyridis* is also highly tolerant to ants. These species include *C. magnifica*
473 (Sloggett et al. 2002; Majerus et al. 2007) and *Platynaspis luteorubra* (Goeze) (Völkl
474 1995; Godeau 2000). It is possible that some species that have some tolerance of
475 ants may come under additional selection pressures to improve their tolerance as a result of
476 the presence of *H. axyridis*. In regions now occupied by *H. axyridis*, monitoring the
477 coccinellid presence in the vicinity of nests of *F. rufa* over the next decade would be
478 valuable.

479 *Behavioural interactions*

480 Further work is also required to acquire data on behavioural defence strategies of guild
481 members in the presence of *H. axyridis*, such as dislodgement (dropping behaviour) and
482 escape behaviours which could be extremely important for some species. For example, larvae
483 of the coccinellid *P. 14-punctata* are consumed by *H. axyridis* in laboratory studies con-
484 ducted in Petri dishes, but it is speculated that the highly mobile larvae of this species may
485 have the capability to successfully escape from *H. axyridis* in field situations (Ware and
486 Majerus 2008). We also know that parasitoids and predators can use volatile and chemical



487 cues to avoid competition; both the coccinellid *C. 7-punctata* and the predatory bug
488 *Anthocoris nemorum* (L.) (Heteroptera: Anthocoridae) can detect and avoid surfaces con-
489 taminated by the fungal pathogen *B. bassiana* to which they are susceptible (Meyling and Pell
490 2006; Ormond 2007). In addition, the aphid parasitoid *A. ervi* detects volatiles from the tracks
491 of *C. 7-punctata* and avoids oviposition in nearby aphid populations (Nakashima et al. 2004).
492 Such behavioural responses can ensure co-existence by reducing the risk of intraguild pre-
493 dation. They may contribute to co-existence of *H. axyridis* in its co-evolved native guild
494 populations and are currently being evaluated for *H. axyridis* in the broader UK guild.

495 Other intraguild interactions, such as facilitation, have been recorded for some species
496 and shown to mitigate the effects of intraguild predation on guild diversity and may also
497 apply to *H. axyridis*. For example, although *C. 7-punctata* is an intraguild predator of the
498 aphid-specific pathogenic fungus *P. neoaphidis*, it does not consume whole, fungal
499 cadavers and transmission of the fungus is not reduced. Indeed, *C. 7-punctata* enhances
500 transmission of the fungus and passively vectors it between aphid populations, thereby also
501 aiding pathogen dispersal (Roy et al. 1998, 2001; Roy and Pell 2000). Some of these
502 co-evolved behavioural traits may contribute to the maintenance of guild diversity in the
503 native range of *H. axyridis* and may mitigate its effects on some species in the invasive
504 range. In preliminary studies, *H. axyridis* did enhance transmission and dispersal of
505 *P. neoaphidis* in the laboratory (J. Baverstock personal observation).

506 *Natural enemy release and biotype variation*

507 Differences in functional traits of invasive and non-invasive biotypes of *H. axyridis* may
508 have exacerbated their impact in non-native ecosystems. Although direct comparisons
509 between different biotypes of *H. axyridis* and other natural enemies found in its exotic
510 range have only been made for a limited number of functional traits, they have all dem-
511 onstrated that the UK invasive biotype is a stronger asymmetric intraguild predator than the
512 Japanese biotype. Specifically Roy et al. (2008b) demonstrated that *H. axyridis* from a
513 culture derived from Japan were less likely to consume aphid cadavers supporting the
514 beneficial aphid-specific fungal pathogen *P. neoaphidis* than those derived from the UK.
515 They speculated that *H. axyridis* obtained from non-native populations were derived from
516 biological control cultures and, through microevolution or founder effects, have been,
517 perhaps unintentionally, selected for extreme polyphagy and an increased tendency
518 towards intraguild predation compared to *H. axyridis* in its native range (Roderick and
519 Howarth 1999; Hufbauer and Roderick 2005; Roy et al. 2008a). It would be extremely
520 interesting to compare the strength and symmetry of intraguild interactions between
521 Japanese, UK and US derived *H. axyridis* for a wider range of guild members, from both
522 native and non-native ranges to determine if they function differently in relation to all guild
523 members with which they compete. In addition, UK-derived *H. axyridis* have greater
524 resistance to some natural enemies, such as the fungus *B. bassiana* and the parasitoid wasp,
525 *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae) than do Japanese-derived
526 *H. axyridis*, implying that they have also been released from their own population regu-
527 lators (Koyama and Majerus 2008; Roy et al. 2008b). Evolution of resistance to disease,
528 parasitism and insecticides is not uncommon in insects and may be associated with trade
529 offs in fitness (e.g., Foster et al. 2007; Völkl et al. 2007). For example, although
530 UK-derived *H. axyridis* were less susceptible to infection they were also significantly less
531 fecund when infected than *B. bassiana*-infected *H. axyridis* derived from Japan (Roy et al.



532 2008b). Further research is needed to fully evaluate these interactions and determine
533 whether any associated fitness costs could prove to be *H. axyridis*' weakness.

534 *Going beyond managed ecosystems*

535 The focus of research has largely been on interactions between *H. axyridis* and other
536 coccinellids in managed ecosystems and, until recently, mainly in the USA, which has very
537 different agricultural systems to Europe. However, it is clear from the studies described
538 above that *H. axyridis* can have impacts on many other species and that this has impli-
539 cations beyond managed ecosystems to natural habitats. Such impacts require urgent
540 investigation. *Harmonia axyridis* is dispersive and highly polyphagous and therefore likely
541 to impinge on many foodwebs in many different ecosystems, with the potential to disrupt
542 them all. Although native coccinellids with similar prey and habitat requirements are at
543 greatest risk, other non-coccinellid guild members and non-target species beyond the guild,
544 such as Hemiptera of no economic importance (Majerus et al. 2006), lepidopteran eggs and
545 larvae (Koch 2003; Koch et al. 2006) and all the predators, hyperparasites and pathogens
546 in the higher trophic levels (Roy et al. 2008b) that may also be negatively affected. This
547 represents a significant threat to biodiversity per se, particularly as some of these species
548 are of considerable conservation concern (Koch et al. 2006).

549 *What about scale?*

550 We must also remember that many of the studies to date have been made on a small scale
551 in the laboratory. This does not detract from their value in identifying key protagonists and
552 'worst case scenarios': certainly, a species that is not preyed on by *H. axyridis* in a Petri
553 dish experiment is unlikely to be at risk in the field. However, they do not consider the
554 importance of spatial scale and habitat complexity on niche differentiation and the out-
555 come of contests. Testing hypotheses on these subjects requires experiments to move to
556 larger spatial and temporal scales. The work of Snyder et al. (2004a) demonstrated that,
557 although parasitoid 'mummies' of *A. asychis* were susceptible to intraguild predation by
558 *H. axyridis*, overall parasitism rates were unaffected when experiments were done on a
559 larger spatial scale. It is also important to consider more complex communities, i.e. not just
560 pairs of protagonist species but a more representative guild, if we are to determine whether
561 diversity will decline and what implications this will have for ecosystem services.

562 *Potential implications for ecosystem services*

563 Predators are part of the functional biodiversity in managed ecosystems and, while not the
564 only contributor to herbivore population regulation, they are essential for sustainable pest
565 management through the ecosystem services they provide and that we depend upon. While
566 the abundance of particular species can be enhanced through biological control, the
567 question of 'how many species are required to achieve the required service in the crop?'
568 continues to be a matter of debate (e.g., Denoth et al. 2002; Pell 2008; Straub et al. 2008)
569 and must be considered in the context of the arrival of *H. axyridis* and potential declines in
570 guild diversity. The relationship between predator biodiversity and ecosystem function is
571 poorly understood. From the studies described above, and field observations of declines in



Editor Proof

572 native aphidophages and coccidophages since the arrival of *H. axyridis*, we must consider
573 whether *H. axyridis* as a top predator, will deliver the same ecosystem service when other
574 guild species are excluded or whether this will reduce aphid regulation (prey release) and
575 the reliability of biological control in the long term.

576 Straub et al. (2008) reviewed recent literature on the relative pest suppression function
577 of multiple (more than two) compared to single predator species and found that the rela-
578 tionship between predator diversity and pest suppression was context dependent and could
579 be positive, negative or neutral. Theoretically, if increasing predator diversity encourages
580 intraguild predation, or, as in the case of invasion by *H. axyridis*, an invasive intraguild
581 predator is introduced to the system, then the prediction would be that the equilibrium
582 density of the herbivore would increase and pest control function would be reduced (e.g.,
583 Polis et al. 1989; Finke and Denno 2004). Effectively, trophic cascades would be damp-
584 ened and the herbivore would be released from predation. However, the experimental
585 evidence to support this in a number of communities is mixed. Some studies have docu-
586 mented disruption of pest suppression and others have shown either no change or improved
587 pest suppression in the presence of intraguild predation (Straub et al. 2008). Most recent
588 meta-analysis by Rosenheim and Harmon (2006) and a literature review by Janssen et al.
589 (2006) find no evidence that the presence of intraguild predation disrupts herbivore control.
590 However, there was greater variation than expected between cases, suggesting that pest
591 release depended on system-specific factors, such as the biological traits of the predators
592 and prey, and extrinsic factors, such as the environment: i.e., there was no simple
593 prediction relating intraguild predation to pest release (Straub et al. 2008).

594 However, Straub et al. (2008) have identified particular traits of relevance from the
595 theoretical literature. The first relates to the life history of the intraguild prey. Coincidental
596 intraguild predation of parasitoids and pathogens is likely to be less disruptive to herbivore
597 suppression than omnivorous intraguild predation of other predators because predation of
598 the herbivore and the parasitoid/pathogen are directly linked and intraguild predation will
599 simultaneously result in predation of the herbivore (Rosenheim et al. 1995). However, this
600 may not hold if several generations of the intraguild prey are considered (Snyder and Ives
601 2001). Secondly, the relative mobility and size (foraging mode) of the intraguild predator,
602 intraguild prey and the herbivore can all influence the likelihood of prey release. A 'sit and
603 wait' intraguild predator could disrupt suppression of a sedentary herbivore by a mobile
604 intraguild prey species, although this will depend on the size of the intraguild prey species
605 too. If it is large and highly mobile, it will have a large demand for prey, and if removed
606 from the system by intraguild predation could result in release of the herbivore prey
607 (Rosenheim and Corbett 2003). Furthermore, if the intraguild prey is a similar size to the
608 herbivore then adding a larger intraguild predator will enhance herbivore suppression
609 because predation of the herbivore by the intraguild predator would greatly outweigh the
610 small release from predation achieved by the consumption of the intraguild prey (Diehl
611 1993). The opposite would be the case if the intraguild prey was much larger than the
612 herbivore (Rosenheim and Corbett 2003). There is some experimental support for this
613 second prediction (Rosenheim et al. 2004a, b) but for the most part they remain hypotheses
614 that require experimental evaluation. In addition, they will be influenced by whether the
615 top intraguild predator is co-evolved with the rest of the guild or whether it is an exotic
616 alien species, as is the case with *H. axyridis*. Using the hypotheses above, one could
617 predict from the biological traits of *H. axyridis* that it would release herbivores from
618 control because it consumes intraguild prey that are large and mobile. However, it is itself
619 large, mobile, well defended, multivoltine and highly voracious which could compensate
620 for this, at least in the short term.



Editor Proof

621 Within guilds of predators some species may be functionally redundant if they share
622 traits and their function would be replaced by other species should they be lost (Wilby and
623 Thomas 2002a, b; Ives et al. 2005; Casula et al. 2006). If there are many redundant species
624 within a guild, then a decline in their diversity associated with the arrival of *H. axyridis*
625 may not influence overall function. However, determining whether species are functionally
626 redundant within a guild relies on the ability to divide them into functional groups with
627 similar traits (e.g., prey preference, response to prey density, microhabitat use and phe-
628 nology). Those with similar traits should compete strongly for resources and are, therefore,
629 likely to be functionally redundant.

630 Within the aphidophagous guild there have been studies to demonstrate that increasing
631 the number of species in the guild increases prey suppression, suggesting resource-use
632 complementarity (Powell et al. 2006). However, other workers have shown no such effects
633 and suggest significant redundancy of some guild members (Evans 1991; Chang 1996;
634 Straub and Snyder 2006). The former may be more likely because the latter results could
635 be due to negative and positive interactions between species counteracting each other
636 (Snyder and Ives 2003) or because species that appear functionally redundant under some
637 environmental conditions are functionally diverse when environmental conditions change
638 (Naeem and Li 1997). This effect is encompassed in the 'insurance hypothesis' that
639 maintains that different predators perform better or worse in particular environments and
640 that by maintaining them all provides functional compensation and reliable pest sup-
641 pression despite changing conditions (Loreau et al. 2003). This is essential in managed
642 ecosystems that are fragmented and under constant change (Pell 2008). The multiplicity of
643 responses to change that species from a single functional group are capable of, is critical to
644 landscape scale ecosystem resilience (Elmqvist et al. 2003). There are good examples of
645 this in the aphid/ predator system (Pell 2008). Key aphid mortality factors, which can be
646 parasitoids on some occasions and syrphids, ground predators or entomopathogenic fungi
647 on other occasions, demonstrate the need for diversity as insurance for function (Krauss
648 and Poehling 1996; Hemmati 1999; Östman et al. 2001; Powell et al. 2003, 2004;
649 Tscharrntke et al. 2005; Pell 2008). Declines in guild diversity as a result of introduction of
650 *H. axyridis* could, therefore, reduce the resilience of pest suppression in the long term.

651 A single prey type, or even species, can provide multiple feeding niches that a diversity
652 of predators can use if there is niche complementarity rather than redundancy and this is
653 achieved by resource partitioning and facilitation amongst predators. If there is complete
654 complementarity then predator diversity should increase pest suppression (Wilby and
655 Thomas 2002a, b; Casula et al. 2006). There is significant evidence for resource parti-
656 tioning and facilitation within the aphid/predator system (Pell 2008). For example variation
657 between aphid species, or within a species, provides an opportunity for preference amongst
658 predators. The coccinellid *C. 7-punctata* exploited red morphs of the pea aphid more than
659 green morphs whereas the parasitoid *A. ervi* only attacked green morphs, effectively
660 partitioning the resource between them (Losey et al. 1997). Coccinellid species differ in
661 their response to prey density, some being more effective at low densities and others at
662 high densities, which effectively separates them into complementary niches (Evans 2004;
663 Schellhorn and Andow 2005). A further example of complementarity can be seen for the
664 interactions between *C. 7-punctata*, a foliar aphid predator, and the carabid beetle
665 *Harpalus pennsylvanicus* (DeGeer) (Coleoptera: Carabidae), which is restricted to foraging
666 on the soil surface. As the coccinellid forages, it dislodges aphids that are then consumed
667 by the ground predator, enhancing overall aphid suppression (Losey and Denno 1998).
668 Coccinellid predators and parasitoids also facilitate transmission and dispersal of the
669 beneficial aphid pathogen *P. neoaphidis* (Pell et al. 1997; Fuentes-Contreras et al. 1998;



670 Roy et al. 1998, 2001; Baverstock et al. 2005). Avoidance behaviour of parasitoids and
671 coccinellids in relation to other intraguild predators is common (Nakashima et al. 2004;
672 Meyling and Pell 2006; Ormond 2007). As already described, coccinellid species can also
673 be phenologically separated, thereby partitioning resources temporally and avoiding
674 competition (Takahashi and Naito 1984; Sato 2001; Flowers et al. 2006) or they can have
675 different patch-leaving times (Sato et al. 2003). As there are numerous examples of
676 complementarity amongst aphidophagous species, it follows that the more species there are
677 in the guild, the greater pest suppression will be. This confirms the hypothesis that declines
678 in guild diversity as a result of introduction of *H. axyridis* could reduce effective pest
679 suppression.

680 Summary

681 Overall, the evidence suggests that predator diversity is necessary for resilient pest sup-
682 pression and that includes aphid and coccid control (Stiling and Cornelissen 2005;
683 Cardinale et al. 2006; Pell 2008; Straub et al. 2008). Although intraguild predation does
684 not necessarily interfere with the overall ecosystem service it can interfere with pest
685 suppression in some systems, particularly when the intraguild prey are large compared to
686 the extraguild prey and this is the case for *H. axyridis*. Niche complementarity is almost
687 certainly the mechanism by which *H. axyridis* remains in equilibrium with its co-evolved
688 native guild of predators. In its exotic range, the guild of predators are co-evolved with
689 each other but not with *H. axyridis* and as such come into direct competition with
690 *H. axyridis*. This has significant implications for predator diversity, biodiversity per se and
691 also ecosystem services. Pest management strategies aimed at maintaining predator
692 diversity through habitat manipulation and the diversification of our agricultural land-
693 scapes could help counter declines in predator diversity associated with the arrival of
694 *H. axyridis* (e.g., Barbosa 1998; Landis et al. 2000; Gurr et al. 2004; Pell 2008). Although
695 implications for biodiversity in natural habitats are of grave concern, it is perhaps through
696 the manipulation of managed land, which, for example, represents 70% of land in the UK,
697 that we have the greatest chance of optimising the environment to favour our native
698 diversity in the presence of *H. axyridis*, thereby also protecting diversity in natural
699 habitats. To achieve this we need robust research data to fill the gaps in knowledge
700 identified in this paper and develop mitigation strategies.

701 **Acknowledgements** Judith K. Pell and Jason Baverstock are supported by the Department for Environ-
702 ment, Food and Rural Affairs of the UK (Defra). Rothamsted Research receives grant-aided support from
703 the Biotechnology and Biological Sciences Research Council of the United Kingdom (BBSRC).

704 References

- 707 Agarwala BK, Dixon AFG (1992) Laboratory study of cannibalism and interspecific predation in ladybirds.
708 Ecol Entomol 17:303–309
- 709 Alam N, Choi IS, Song KS, Hong J, Lee CO, Jung JH (2002) A new alkaloid from two coccinellid beetles
710 *Harmonia axyridis* and *Aiolocaria haexapilota*. B Kor Chem Soc 23:497–499
- 711 Barbosa P (ed) (1998) Conservation biological control. Academic Press, San Diego, CA, 396 pp
- 712 Baverstock J, Alderson PG, Pell JK (2005) Influence of the aphid pathogen *Pandora neoaphidis* on the
713 foraging behaviour of the aphid parasitoid *Aphidius ervi*. Ecol Entomol 30:665–672
- 714 Berkvens N, Bonte J, Berkvens D, Deforce K, Tirry L, De Clercq P (2008) Pollen as an alternative food for
715 *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) Biocontrol (this volume)



- 716 Brown MW, Miller SS (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the
717 impact of invasion by *Harmonia axyridis*. Entomol News 109:143–151
- 718 Brown PMJ, Roy HE, Rothery P, Roy DB, Ware RL, Majerus MEN (2008) *Harmonia axyridis* in Great
719 Britain: analysis of the spread and distribution of a non-native coccinellid. Biocontrol (this volume)
- 720 Buntin GD, Bouton JH (1997) Aphid (Homoptera: Aphididae) management in alfalfa by spring grazing
721 cattle. J Entomol Sci 32:332–342
- 722 Butt TM, Ibrahim L, Ball BV, Clark SJ (1994) Pathogenicity of the entomogenous fungi, *Metarhizium*
723 *anisopliae* and *Beauveria bassiana* against crucifer pests and the honey bee. Biocontrol Sci Techn
724 4:207–214
- 725 Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of
726 biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992
- 727 Casula P, Wilby A, Thomas MB (2006) Understanding biodiversity effects on prey in multi-enemy systems.
728 Ecol Lett 9:995–1004
- 729 Chang GC (1996) Comparison of single versus multiple species of generalist predators for biological
730 control. Environ Entomol 25:207–212
- 731 Colunga-Garcia M, Gage SH (1998) Arrival, establishment, and habitat use of the multicolored Asian lady
732 beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environ Entomol 27:1574–1580
- 733 Cottrell TE (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for
734 development of lady beetle larvae. Biol Control 31:362–371
- 735 Cottrell TE (2007) Predation by adult and larval lady beetles (Coleoptera: Coccinellidae) on initial contact
736 with lady beetles eggs. Environ Entomol 36:390–401
- 737 Cottrell TE, Yeargan KV (1998) Intraguild predation between an introduced lady beetle, *Harmonia axyridis*
738 (Coleoptera: Coccinellidae) and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinelli-
739 dae). J Kansas Entomol Soc 71:159–163
- 740 De Clercq P, Peeters I, Vergauwe G, Thas O (2003) Interaction between *Podisus maculiventris* and
741 *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops.
742 Biocontrol 48:39–55
- 743 Denoth M, Frid L, Myers JH (2002) Multiple agents in biological control: improving the odds. Biol Control
744 24:20–30
- 745 Diehl S (1993) Relative consumer sizes and the strength of direct and indirect interactions in omnivorous
746 feeding relationships. Oikos 68:151–157
- 747 Dixon AFG (2000) Insect predator-prey dynamics: ladybird beetles & biological control. Cambridge
748 University Press, Cambridge, UK
- 749 Elliott N, Kieckhefer R, Kauffman W (1996) Effects of an invading coccinellid on native coccinellids in an
750 agricultural landscape. Oecologia 105:537–544
- 751 Elmquist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity,
752 ecosystem change and resilience. Front Ecol Environ 1:488–494
- 753 Evans EW (1991) Intra versus interspecific interactions of ladybeetles (Coleoptera; Coccinellidae) attacking
754 aphids. Oecologia 87:401–408
- 755 Evans EW (2000) Morphology of invasion: body size patterns associated with establishment of *Coccinella*
756 *septempunctata* (Coleoptera: Coccinellidae) in western North America. Eur J Entomol 97:469–474
- 757 Evans EW (2004) Habitat displacement of North American ladybirds by an introduced species. Ecology
758 85:637–647
- 759 Felix S, Soares AO (2004) Intraguild predation between the aphidophagous ladybird beetles *Harmonia*
760 *axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of body weight. Eur J
761 Entomol 101:237–242
- 762 Ferguson KI, Stiling P (1996) Non-additive effects of multiple natural enemies on aphid populations.
763 Oecologia 108:375–379
- 764 Finke DL, Denno RF (2004) Predator diversity dampens trophic cascades. Nature 429:407–410
- 765 Flowers RW, Salom SM, Kok LT (2006) Competitive interactions among two specialist predators and a
766 generalist predator of hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae) in south-western
767 Virginia. Agr Forest Entomol 8:253–262
- 768 Foster SP, Devine G, Devonshire AL (2007) Insecticide resistance. In: Harrington R, van Emden H (eds)
769 Aphids as crop pests. CABI International, pp 261–285, 717
- 770 Fremlin M (2007) Intra-guild predation of harlequin ladybird larvae by lacewing larvae. Bull Amat Entomol
771 Soc 66:110–116
- 772 Fuentes-Contreras E, Pell JK, Niemeyer HM (1998) Influence of plant resistance at the third trophic level:
773 interactions between parasitoids and entomopathogenic fungi of cereal aphids. Oecologia 117:426–432



- 774 Gardiner MM, Landis DA (2007) Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera:
775 Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biol*
776 *Control* 40:386–395
- 777 Godeau J-F (2000) Coccinelles amies des fourmis. 2/2/ Groupe de Travail Coccinula. Feuille de Contact
778 2:10–15
- 779 Gordon RD (1985) The Coccinellidae (Coleoptera) of America North of Mexico. *J New York Entomol Soc*
780 93:1–912
- 781 Gurr GM, Scarratt SL, Wratten SD, Berndt L, Irvin N (2004) Ecological engineering, habitat manipulation
782 and pest management. In: Gurr GM, Wratten SD, Altieri MA (eds) *Ecological engineering for pest*
783 *management: advances in habitat manipulation for arthropods*. CSIRO Publishing, pp 1–12
- 784 Hemmati F (1999) Aerial dispersal of the entomopathogenic fungus *Erynia neoaphidis*. PhD Thesis,
785 University of Reading 186 pp
- 786 Hemptinne JL, Dixon AFG (2000) Defence, oviposition and sex: semiochemical parsimony in two species
787 of ladybird beetles (Coleoptera: Coccinellidae)? A short review. *Eur J Entomol* 97:443–447
- 788 Herrick NJ, Reitz SR (2004) Temporal occurrence of *Podisus maculiventris* (Hemiptera: Heteroptera:
789 Pentatomidae) in North Florida. *Fla Entomol* 87:587–590
- 790 Hironori Y, Katsuihiro S (1997) Cannibalism and interspecific predation in two predatory ladybirds in
791 relation to prey abundance in the field. *Entomophaga* 42:153–163
- 792 Hodek I (1996) Food relationships. In: Hodek I, Honek A (eds) *Ecology of Coccinellidae*. Kluwer Academic
793 Publishers, Dordrecht pp 143–238
- 794 Hodek I, Honek A (1988) Sampling, rearing and handling of aphid predators. In: Minks AK, Harrewijn P
795 (eds) *Aphids, their biology, natural enemies and control*, Vol. 2B. Amsterdam, Elsevier, pp 311–321
- 796 Hölldobler B, Wilson EO (1990) *The ants*. Springer Verlag, Berlin
- 797 Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- 798 Hough-Goldstein J, Cox J, Armstrong A (1996) *Podisus maculiventris* (Hemiptera: Pentatomidae) predation
799 on ladybird beetles (Coleoptera: Coccinellidae). *Fla Entomol* 79:64–68
- 800 Huey RB, Pianka ER (1981) Ecological consequences of foraging mode. *Ecology* 62:991–999
- 801 Huffbauer RA, Roderick GK (2005) Microevolution in biological control: mechanisms, patterns and pro-
802 cesses. *Biol Control* 35:227–239
- 803 Inglis GD, Goettel MS, Butt TM, Strasser H (2001) Use of hyphomycetous fungi for managing insect pests.
804 In: Butt TM, Jackson C, Magan N (eds) *Fungi as biocontrol agents: progress, problems and potential*.
805 CABI, Wallingford, pp 23–69
- 806 Itioka T, Inoue T (1996) The role of predators and attendant ants in the regulation of a population of the
807 citrus mealybug *Pseudococcus citriculus* in a satsuma orange orchard. *Appl Entomol Zool* 31:195–202
- 808 Ives AR, Cardinale BJ, Snyder WE (2005) A synthesis of subdisciplines: predator-prey interactions and
809 biodiversity and ecosystem functioning. *Ecol Lett* 8:102–116
- 810 James RR, Lighthart B (1994) Susceptibility of the convergent lady beetle (Coleoptera, Coccinellidae) to
811 four entomogenous fungi. *Env Entomol* 23:190–192
- 812 Janssen A, Montserrat M, HilleRisLambers R, de Roos AM, Pallini A, Sabelis MW (2006) Intraguild
813 predation usually does not disrupt biological control. In: Brodeur J, Boivin G (eds) *Trophic and guild*
814 *interactions in biological control*. Springer, Dordrecht, The Netherlands, pp 21–44
- 815 Jiggins C, Majerus MEN, Gough U (1993) Ant defence of colonies of *Aphis fabae* Scopoli (Hemiptera:
816 Aphididae), against predation by ladybirds. *Brit J Entomol Nat Hist* 6:129–138
- 817 Kajita Y, Takano F, Yasuda H, Agarwala BK (2000) Effects of indigenous ladybird species (Coleoptera:
818 Coccinellidae) on the survival of an species in relation to prey abundance. *Appl Entomol Zool* 35:473–479
- 819 Kajita Y, Yasuda H, Evans EW (2006) Effects of native ladybirds on oviposition of the exotic species,
820 *Adalia bipunctata* (Coleoptera: Coccinellidae), in Japan. *Appl Entomol Zool* 41:57–61
- 821 Keller S, Zimmerman G (1989) Mycopathogens of soil insects. *Sci Bull* 240–270
- 822 King A, Meinwald J (1996) Review of the defensive chemistry of coccinellids. *Chem Rev* 96:1105–1122
- 823 Koch RL (2003) The multicoloured Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in
824 biological control and non-target impacts. *J Ins Sci* 3:32–47
- 825 Koch R, Venette R, Hutchison W (2006) Predicted impact of an exotic generalist predator on monarch
826 butterfly (Lepidoptera: Nymphalidae) populations: a quantitative risk assessment. *Biol Invasions*
827 8:1179–1193
- 828 Koyama S, Majerus MEN (2008) Differences in attack rates of Japanese and British *Dinocampus*
829 *coccinellae* towards sympatric and allopatric stocks of *Harmonia axyridis* and *Coccinella*
830 *septempunctata*. *Biocontrol* (this volume)
- 831 Krauss U, Poehling HM (1996) Overwintering, oviposition and population dynamics of hoverflies (Diptera:
832 Syrphidae) in northern Germany in relation to small and large-scale landscape structure. *Acta Jutlandica*
833 71:157–169



- 834 Kuznetsov VN, (1988) The Coccinellidae of the far East in Transcaucasia. Zashchita Rastenii. 5(19) (in
835 Russian)
- 836 Kuznetsov VN (1997) Lady beetles of the russian far east, (Memoir Series No. 1). Center for Systematic
837 Entomology, Gainesville, FL
- 838 LaMana ML, Miller JC (1996) Field observation on *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae)
839 in Oregon. Biol Control 6:232–237
- 840 Landis DA, Wratten SD, Gurr GM (2000) Habitat manipulation to conserve natural enemies of arthropod
841 pests in agriculture. Annu Rev Entomol 45:175–201
- 842 Loreau M, Mouquet N, Gonzales A (2003) Biodiversity as spatial insurance in heterogeneous landscapes.
843 PNAS USA 100:12765–12770
- 844 Losey JE, Denno RF (1998) Positive predator-prey interactions: enhanced predation rates and synergistic
845 suppression of aphid populations. Ecology 79:2143–2152
- 846 Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. Bioscience
847 56:311–323
- 848 Losey JE, Ives AR, Harmon J, Ballantyne F, Brown C (1997) A polymorphism maintained by opposite
849 patterns of parasitism and predation. Nature 388:269–272
- 850 Lucas E (2005) Intraguild predation among aphidophagous predators. Eur J Entomol 102:351–364
- 851 Lucas E, Coderre D, Brodeur J (1998) Intraguild predation among aphid predators: characterization and
852 influence of extraguild prey density. Ecology 79:1084–1092
- 853 Lucas E, Gagne I, Coderre D (2002) Impact of the arrival of adults of *Harmonia axyridis* on adults of
854 *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). Eur J Entomol
855 99:457–463
- 856 Magalhaes BP, Lord JC, Wraight SP, Daoust RA, Roberts DW (1988) Pathogenicity of *Beauveria bassiana*
857 and *Zoophthora radicans* to the coccinellid predators *Coleomegilla maculata* and *Eriopis connexa*. J
858 Invertebr Pathol 52:471–473
- 859 Magro A, Tene JN, Bastin N, Dixon AFG, Hemptinne JL (2007) Assessment of patch quality by ladybirds:
860 relative response to conspecific and heterospecific larval tracks a consequence of habitat similarity?
861 Chemoecology 17:37–45
- 862 Majerus MEN (1994) Ladybirds. Harper Collins, London, 320 pp
- 863 Majerus MEN, Strawson V, Roy HE (2006) The potential impacts of the arrival of the harlequin ladybird,
864 *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. Ecol Entomol 31:207–215
- 865 Majerus MEN, Sloggett JJ, Godeau J-F, Hemptinne J-L (2007) Interactions between ants and aphidophagous
866 and coccidophagous ladybirds. Popul Ecol 49:15–27
- 867 McPherson JE (1980) A list of the prey species of *Podisus maculiventris* (Hemiptera: Pentatomidae). Great
868 Lakes Entomol 13:17–24
- 869 Meyling NV, Pell JK (2006) Detection and avoidance of an entomopathogenic fungus by a generalist insect
870 predator. Ecol Entomol 31:162–171
- 871 Michaud JP (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae)
872 and asymmetric competition with a native species, *Cycloneda sanguinea*. Env Entomol
873 31:827–835
- 874 Müller CB, Brodeur J (2002) Intraguild predation in biological control and conservation biology. Biol
875 Control 25:216–223
- 876 Musser FR, Shelton AM (2003) Bt sweet corn and selective insecticides: impacts on pests and predators. J
877 Econ Entomol 96:71–80
- 878 Naeem S, Li S (1997) Biodiversity enhances ecosystem reliability. Nature 390:507–509
- 879 Nakashima Y, Birkett MA, Pye BJ, Pickett JA, Powell W (2004) The role of semiochemicals in the
880 avoidance of the seven-spot ladybird *Coccinella septempunctata* by the aphid parasitoid, *Aphidius ervi*. J
881 Chem Ecol 30:1103–1116
- 882 Nault BA, Kennedy GG (2003) Establishment of multicoloured Asian lady beetle in Eastern North Carolina:
883 seasonal abundance and crop exploitation within an agricultural landscape. Biocontrol 48:363–378
- 884 Ormond E (2007) The overwintering interactions of the seven spot ladybird (*Coccinella septempunctata*)
885 and the entomopathogenic fungus *Beauveria bassiana*. PhD Thesis, Anglia Ruskin University
- 886 Ormond EL, Pell JK, Thomas APM, Roy HE (2006) Overwintering ecology of *Coccinella septempunctata*,
887 *Beauveria bassiana* and *Dinocampus coccinellae*. In: Rossing WAH, Eggenschwiler L, Poehling H-M
888 (eds) Working Group “Landscape management for functional biodiversity” at Zürich-Reckenholz
889 (Switzerland), 16–19 May 2006 IOBC/wprs Bulletin 29, pp 85–88
- 890 Östman O, Ekbom B, Bengtsson J (2001) Farming practice and landscape heterogeneity influence biological
891 control. Basic Appl Ecol 2:365–371
- 892 Pasteels JM, Deroe C, Tursch B, Braekman JC, Daloz D, Hootele C (1973) Distribution et activités des
893 alcaloïdes défensives des Coccinellidae. J Insect Physiol 19:1771–1784



- 894 Pell JK (2008) Ecological approaches to pest management using entomopathogenic fungi; concepts, theory,
895 practice and opportunities. In: Ekesi S, Maniania N (ed) Research Signpost (In press)
- 896 Pell JK, Vandenberg JD (2002) Interactions among *Diuraphis noxia*, the fungal pathogen *Paecilomyces*
897 *fumosoroseus* and the coccinellid *Hippodamia convergens*. *Biocontrol Sci Tech* 12:217–224
- 898 Pell JK, Pluke R, Clark SJ, Kenward MG, Alderson PG (1997) Interactions between two aphid natural
899 enemies, the entomopathogenic fungus, *Erynia neoaphidis* and the predatory beetle, *Coccinella*
900 *septempunctata*. *J Invertebr Pathol* 69:261–268
- 901 Pell JK, Eilenberg J, Hajek AE, Steinkraus DS (2001) Biology, ecology and pest management potential of
902 entomophthorales. In: Butt TM, Jackson C, Magan N (eds) *Fungi as biocontrol agents: progress,*
903 *problems and potential*. CABI International, pp 71–154, 390
- 904 Perez A, Omkar (2006) Ecology and biological control application of multicoloured Asian ladybird,
905 *Harmonia axyridis*. A review. *Biocontrol Sci Tech* 16:111–128
- 906 Phoofofo MW, Obrycki JJ (1998) Potential for intraguild predation and competition among predatory
907 Coccinellidae and Chrysopidae. *Entomol Exp Appl* 89:47–55
- 908 Polis GA (1994) Food web, trophic cascade and community structure. *Aust J Ecol* 19:121–136
- 909 Polis GA, Holt RD (1992) Intraguild predation—the dynamics of complex trophic interactions. *TREE*
910 7:151–154
- 911 Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intra-guild predation: potential
912 competitors that eat each other. *Annu Rev Entomol* 20:297–330
- 913 Powell W, Pell JK (2007) Biological control. In: Harrington R, van Emden H (eds) *Aphids as crop pests.*
914 CABI International, pp 469–513, 717
- 915 Powell W, Walters K, A'Hara S, Ashby J, Stevenson H, Northing P (2003) Using field margin diversifica-
916 tion in agri-environment schemes to enhance aphid natural enemies. In: Rossing WAH, Poehling HM,
917 Burgio G (eds) *Landscape management for functional biodiversity*. IOBC/WPRS Bulletin, 26/4,
918 pp 123–128
- 919 Powell W, A'hara S, Harling R, Holland JM, Northing P, Thomas CFG, Walters KFA (2004) Managing
920 biodiversity in field margins to enhance integrated pest control in arable crops ('3D Farming' Project).
921 Project report No 356. HGCA, 226 pp
- 922 Powell W, Pell JK, Nakashima Y, Baverstock J, Birkett M (2006) Functional biodiversity of aphid natural
923 enemies: positive intra-guild interactions. In: Rossing WAH, Poehling HM, Burgio G (eds) *Landscape*
924 *management for functional biodiversity*. IOBC wprs Bulletin, 29(6), pp 101–104
- 925 Roderick GK, Howarth FG (1999) Invasion genetics: natural colonisations, non-indigenous species and
926 classical biological control. In: Yano E, Matsuo K, Shiyomi M, Andow D (eds) *Biological invasions of*
927 *pests and beneficial organisms*. National Institute of Agro Environmental Sciences, Tsukuba, Japan
- 928 Rosenheim JA (1998) Higher-order predators and the regulation of insect herbivore populations. *Annu Rev*
929 *Entomol* 43:421–447
- 930 Rosenheim JA, Corbett SA (2003) Omnivory and the indeterminacy of predator function: can a knowledge
931 of foraging behaviour help? *Ecology* 84:2438–2448
- 932 Rosenheim JA, Harmon JP (2006) The influence of intraguild predation on the suppression of a shared prey
933 population: an empirical assessment. In: Brodeur J, Boivin G (eds) *Trophic and guild interactions in*
934 *biological control*. Springer, Dordrecht, The Netherlands, pp 1–20
- 935 Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological
936 control agents: theory and evidence. *Biol Control* 5:303–335
- 937 Rosenheim JA, Glik TE, Goeriz RE, Ramert B (2004a) Linking a predator's foraging behaviour with its
938 effects on herbivore population suppression. *Ecology* 85:3362–3372
- 939 Rosenheim JA, Limburg DD, Colfer RG, Fournier V, Hsu CL, Leonardo TE, Nelson EH (2004b) Herbivore
940 population suppression by an intermediate predator, *Phyoseiulus macropilis*, is insensitive to the
941 presence of an intraguild predator: an advantage of small body size? *Oecologia* 140:577–585
- 942 Roy HE, Pell JK (2000) Interactions between entomopathogenic fungi and other natural enemies: impli-
943 cations for biological control. *Biocontrol Sci Tech* 10:737–752
- 944 Roy HE, Pell JK, Clark SJ, Alderson PG (1998) Implications of predator foraging on aphid pathogen
945 dynamics. *J Invertebr Pathol* 71:236–247
- 946 Roy HE, Pell JK, Alderson PG (2001) Targeted dispersal of the aphid pathogenic fungus *Erynia neoaphidis*
947 by the aphid predator *Coccinella septempunctata*. *Biocontrol Sci Tech* 11:99–110
- 948 Roy HE, Brown P, Majerus MEN (2006) *Harmonia axyridis*: a successful biocontrol agent or an invasive
949 threat? In: Eilenberg J, Hokkanen H (eds) *An ecological and societal approach to biological control*.
950 Kluwer Academic Publishers, Netherlands
- 951 Roy HE, Baverstock J, Ware RL, Clark SJ, Majerus MEN, Baverstock KE, Pell JK (2008a). Intraguild
952 predation of the aphid pathogenic fungus *Pandora neoaphidis* by the invasive coccinellid *Harmonia*
953 *axyridis*. *Ecol Entomol* (In press)



- 954 Roy HE, Brown PMJ, Rothery P, Ware RL, Majerus MEN (2008b) Effect of *Beauveria bassiana* on the
955 survival and fecundity of three species of ladybird: *Harmonia axyridis*, *Coccinella septempunctata* and
956 *Adalia bipunctata*. *Biocontrol* (this volume)
- 957 Sakuratani Y, Marsumoto Y, Oka M, Kubo T, Fuji A, Uotani M, Teraguchi T (2000) Life history of *Adalia*
958 *bipunctata* (Coleoptera: Coccinellidae) in Japan. *Eur J Entomol* 97:555–558
- 959 Sato S (2001) Ecology of ladybirds: factors influencing their survival. PhD Thesis, University of East
960 Anglia, UK
- 961 Sato S, Dixon AFG (2004) Effect of intraguild predation on the survival and development of three species of
962 aphidophagous ladybirds: consequences for invasive species. *Agr Forest Entomol* 6:21–24
- 963 Sato S, Dixon AFG, Hironori Y (2003) Effect of emigration on cannibalism and intraguild predation in
964 aphidophagous ladybirds. *Ecol Entomol* 28:628–633
- 965 Sato S, Yasuda H, Evans EW (2005) Dropping behaviour of larvae of aphidophagous ladybirds and its effect
966 on incidence of intraguild predation: interactions between the intraguild prey, *Adalia bipunctata* (L.) and
967 *Coccinella septempunctata* (L.), and the intraguild predator, *Harmonia axyridis* Pallas. *Ecol Entomol*
968 30:220–224
- 969 Schellhorn NA, Andow D (2005) Response of coccinellids to their aphid prey at different spatial scales.
970 *Popul Ecol* 47:281–288
- 971 Sengonca C, Frings B (1985) Interference and competitive behaviour of the aphid predators, *Chrysoperla*
972 *carnea* and *Coccinella septempunctata* in the laboratory. *Entomophaga* 30:245–251
- 973 Sloggett JJ (1998) Interactions between Coccinellids (Coleoptera) and ants (Hymenoptera: Formicidae), and
974 the evolution of Myrmecophily in *Coccinella magnifica* Redtenbacher. PhD thesis, University of
975 Cambridge
- 976 Sloggett JJ, Majerus MEN (2000) Aphid-mediated coexistence of ladybirds (Coleoptera: Coccinellidae) and
977 the wood ant *Formica rufa*: seasonal effects, interspecific variability and the evolution of a coccinellid
978 myrmecophile. *Oikos* 89:345–359
- 979 Sloggett JJ, Majerus MEN (2003) Adaptations of *Coccinella magnifica*, a myrmecophilous coccinellid to
980 aggression by wood ants (*Formica rufa* group). II. Larval behaviour, and ladybird oviposition location.
981 *Eur J Entomol* 100:337–344
- 982 Sloggett JJ, Völkl W, Schulze W, von der Schulenberg JH, Majerus MEN (2002) The ant-associations and
983 diet of the ladybird *Coccinella magnifica* (Coleoptera : Coccinellidae). *Eur J Entomol* 99:565–569
- 984 Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. *Annu Rev Ecol*
985 *Evol S* 37:95–122
- 986 Snyder WE, Ives AR (2001) Generalist predators disrupt biological control by a specialist parasitoid.
987 *Ecology* 82:705–716
- 988 Snyder WE, Ives AR (2003) Interactions between specialist and generalist natural enemies: parasitoids,
989 predators and pea aphid biocontrol. *Ecology* 84:91–107
- 990 Snyder WE, Ballard SN, Yang S, Clevenger GM, Miller TD, Ahn JJ, Hatten TD, Berryman AA (2004a)
991 Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid
992 *Aphelinus asychis* on greenhouse roses. *Biol Control* 30:229–235
- 993 Snyder WE, Clevenger GM, Eigenbrode SD (2004b) Intraguild predation and successful invasion by
994 introduced ladybird beetles. *Oecologia* 140:559–565
- 995 Stiling P, Cornelissen T (2005) What makes a successful biological control agent? A meta-analysis of
996 biological control agent performance. *Biol Control* 34:236–246
- 997 Straub CS, Snyder WE (2006) Experimental approaches to understanding the relationship between predator
998 diversity and conservation biological control. In: Brodeur J, Boivin G (eds) *Trophic and guild inter-*
999 *actions in biological control*. Springer, Dordrecht, The Netherlands, pp 221–239
- 1000 Straub CS, Finke DL, Snyder WE (2008) Are the conservation of natural enemy biodiversity and biological
1001 control compatible goals? *Biol Control* (In press)
- 1002 Takahashi K, Naito A (1984) Seasonal occurrence of aphids and their predators (Col. Coccinellidae) in
1003 alfalfa fields. *Bulletin of the National Grassland Research Institute* 29:62–66 [In Japanese with English
1004 summary]
- 1005 Takizawa T, Yasuda H, Agarwala BK (2000) Effect of three species of predatory ladybirds on oviposition of
1006 aphid parasitoids. *Entomol Sci* 3:465–469
- 1007 Taylor AJ, Müller CB, Godfray HCJ (1998) Effect of aphid predators on oviposition behaviour of aphid
1008 parasitoids. *J Insect Behav* 11:297–302
- 1009 Tedders WL, Schaefer PW (1994) Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the south-eastern United States. *Entomol News* 105:228–243
- 1010 Tscharnkte T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agri-
1011 cultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874



- 1013 Völkl W (1995) Behavioural and morphological adaptations of the coccinellid, *Platynaspis luteorubra* for
1014 exploiting ant-attending resources (Coleoptera: Coccinellidae). *J Insect Behav* 8:653–670
1015 Völkl W, Mackauer M, Pell JK, Brodeur J (2007) Predators, parasitoids and fungal pathogens. In:
1016 Harrington R, van Emden H (eds) *Aphids as crop pests*. CABI International, pp 187–233, 717
1017 Ware RL, Majerus MEN (2008) Intraguild predation of immature stages of British and Japanese coccinellids
1018 by the invasive ladybird *Harmonia axyridis*. *Biocontrol* (this volume)
1019 Ware RL, Majerus MEN, Roy HE, Symington F (2005) The harlequin ladybird arrives in Britain: a threat to
1020 our native species? *Bull Amat Ent Soc* 64:175–186
1021 Ware RL, Evans N, Malpas L, Michie LJ, O'Farrell K, Majerus MEN (2008a) Intraguild predation by the
1022 invasive ladybird *Harmonia axyridis*: 1. British & Japanese coccinellid eggs. *Neobiota* (In press)
1023 Ware RL, Ramon-Portugal F, Magro A, Hemptinne JL, Majerus MEN (2008b) Chemical protection of
1024 *Calvia 14-guttata* eggs against intraguild predation by the invasive ladybird *Harmonia axyridis*.
1025 *Biocontrol* (this volume)
1026 Way MJ (1963) Mutualism between ants and honey-dew producing Homoptera. *Annu Rev Entomol* 8:307–
1027 344
1028 Wells ML, McPherson RM (1999) Population dynamics of three coccinellids in flue-cured tobacco and
1029 functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids
1030 (Homoptera: Aphididae). *Environ Entomol* 28:768–773
1031 Wells ML, McPherson RM, Ruberson JR, Herzog GA (2001) Coccinellids in cotton: population response to
1032 pesticide application and feeding response to cotton aphids (Homoptera: Aphididae). *Environ Entomol*
1033 30:785–793
1034 Wheeler AG, Hayes JT, Stephens JL (1968) Insect predators of mummified aphids. *Can Entomol* 100:221–222
1035 Wilby A, Thomas MB (2002a) Natural enemy diversity and pest control: patterns of pest emergence with
1036 agricultural intensification. *Ecol Lett* 5:353–360
1037 Wilby A, Thomas MB (2002b) Are the ecological concepts of assembly and function of biodiversity useful
1038 frameworks for understanding natural pest control? *Agr Forest Entomol* 4:237–243
1039 Yasuda H, Ohnuma N (1999) Effect of cannibalism and predation on the larval performance of two ladybird
1040 beetles. *Ent Exp Appl* 93:63–67
1041 Yasuda H, Shinya Y (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to
1042 prey abundance in the field. *Entomophaga* 42:153–163
1043 Yasuda H, Kikuchi T, Kindlmann P, Sato S (2001) Relationships between attacks and escape rates,
1044 cannibalism, and intraguild predation in larvae of two predatory ladybirds. *J Ins Behav* 14:373–384
1045 Yasuda H, Evans EW, Kajita Y, Urakawa K, Takizawa T (2004) Asymmetric larval interactions between
1046 introduced and indigenous ladybirds in North America. *Oecologia* 141:722–731
1047 Yeo H (2000) Mycoinsecticides for aphid management: a biorational approach. PhD Thesis, University of
1048 Nottingham 308 pp
1049