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The chemical ecology of *Harmonia axyridis*

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Abstract We review the chemical ecology of the ladybird beetle *Harmonia axyridis* from the perspective of its invasiveness and the deleterious effects it exerts in the regions it has colonised. We outline the nature and quantification of its chemical defence, and discuss the protection this provides against natural enemies, particularly intraguild predators. We consider the role of infochemicals in location of prey, intraspecific communication and intraguild interactions. We also discuss the role of prey allelochemicals in relation to *H. axyridis* extreme dietary generalism. *Harmonia axyridis* poses a number of practical problems for human health and well-being, including "ladybug taint" wine contamination and problems resulting from large aggregations overwintering in buildings. We consider chemical insights into these issues and, in particular, how attractants and repellents might help manage *H. axyridis* populations through a push–pull strategy. We conclude by discussing future perspectives for research.

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Introduction

Chemicals mediate many fundamental ecological functions in insects. There are numerous roles played by chemicals in the ecology of ladybird beetles, including in the finding and consumption of food, detection of mates and competitors, aggregation and defence against natural enemies (Brakefield 1985; Hodek 1996; Hemptinne and Dixon 2000; Pasteels 2007; Durieux et al. 2010). It is therefore unsurprising that an increasing number of studies of the ladybird *Harmonia axyridis* (Pallas) focus on its chemical ecology. The recent worldwide occurrence of this invasive alien species now makes it easily obtainable for any fundamental research project on coccinellids. However, other considerations often render *H. axyridis* a species of choice rather than one of mere convenience (Sloggett 2005). Much research is linked to the causes and consequences of its amazing invasive capacity—it has been called "the most invasive ladybird on Earth" (Roy et al. 2006), and can serve as an important model for studies of invasive alien species (Roy and Wajnberg 2008). Furthermore a sizable proportion of the chemistry-related research carried out on *H. axyridis* is linked to its undesirable non-target effects, including intraguild predation of native ladybirds where it has been introduced (Sloggett et al. 2010), as well as problems resulting from its high numerical abundance, such as overwintering aggregations in buildings (Riddick et al. 2008) and the tainting of wines when it is collected in large numbers along with grapes during harvest (Linder et al. 2009).

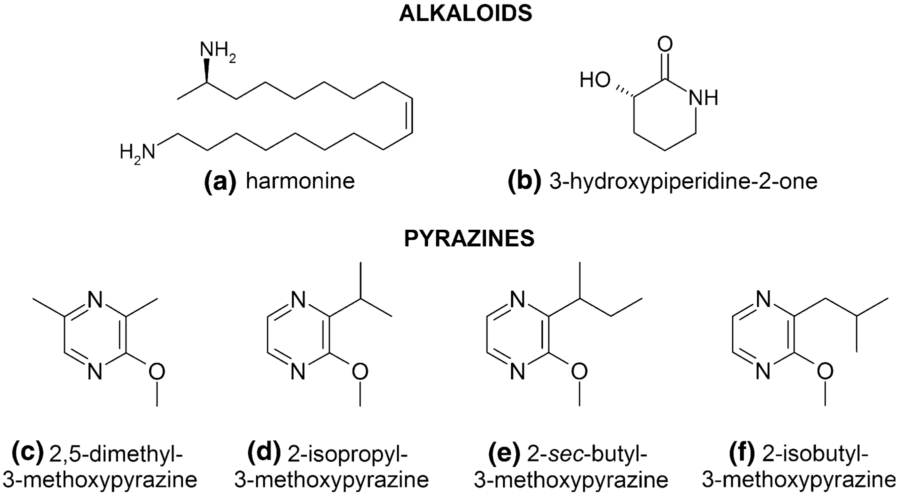
Research on the chemical ecology of *H. axyridis* has in part mirrored previous research on other coccinellid species. However, in some cases it has now advanced beyond other studies, reflecting this species' special status. In this paper we discuss what is currently known about *H. axyridis* chemical ecology, particularly in the context of its invasiveness and undesirable non-target effects. In the initial sections we discuss the fundamentals of *H. axyridis* chemical ecology. The later sections focus on applied aspects and how knowledge of *H. axyridis* chemical ecology can contribute in managing this species and mitigating its deleterious effects. We conclude with a brief consideration of future directions for research.

Chemical defence

Nature and abundance

Harmonia axyridis, like the majority of coccinellids, is protected by alkaloid chemical defences. The alkaloids of *H. axyridis* are the long chain diamine harmonine [(17*R*, 9*Z*)-1,17-diaminooctadec-9-ene] and (*S*)-3-hydroxypiperidin-2-one (Alam et al. 2002; Fig. 1a, b). In addition to the visual signal provided by warning colouration, 2-alkyl-3-methoxypyrazines provide ladybirds with a foul warning smell. Four such compounds have been identified from *H. axyridis*: 2,5-dimethyl-3-methoxypyrazine, 2-isopropyl-3-methoxypyrazine, 2-*sec*-butyl-3-methoxypyrazine, and 2-isobutyl-3-methoxypyrazine (Cudjoe et al. 2005; Cai et al. 2007; Fig. 1c–f). In addition to their warning function, methoxypyrazines may play a role in conspecific attraction in some ladybird species: 2-isopropyl-3-methoxypyrazine is known to fulfil this role in *Coccinella septempunctata* L. (Al Abassi et al. 1998). However, no such investigations have yet been carried out using *H. axyridis*.

Intraspecific variation in harmonine content has been documented in both *H. axyridis* adults (Bezzerides et al. 2007; Fischer et al. 2010a, b) and eggs (Kajita et al. 2010), although no such studies have yet been carried out on 3-hydroxypiperidin-2-one. There appears to be both individual and seasonal variation in adult *H. axyridis* alkaloid content (Bezzerides et al. 2007; Fischer et al. 2010a, b). Bezzerides et al. (2007) have proposed that the colour pattern of adult *H. axyridis* is an "honest" indicator of their alkaloid content. Using North American *H. axyridis*, they found that harmonine concentration correlated strongly with the percentage area of orange in the elytra of non-melanic females and a similar trend, though not significant, was also found in non-melanic males. Bezzerides et al. (2007) hypothesised that a higher proportion of the elytra being covered in orange is an indicator of greater unpalatability. Consequently, melanics (which are largely absent from North America and thus were not studied) might have yet lower levels of chemical defence. Fischer et al. (2010a) reported that pale orange non-melanics do indeed have a greater harmonine content than individuals of other colour forms, including melanics. However, in preliminary work, Sloggett (2010a) found no evidence for greater repellency of European non-melanics compared to melanics as food to other invertebrates, as might be expected with a higher harmonine concentration in non-melanics. Although more extensive testing would be required to confirm his results, he points out that the absence of corresponding work on 3-hydroxypiperidin-2-one makes a definitive interpretation of results based on harmonine alone difficult. Cai et al. (2007) found that the methoxypyrazine concentration was lower in adults with pale orange elytra (termed by them "yellow" individuals). These paler adults were



(a) harmonine **(b)** 3-hydroxypiperidine-2-one

(c) 2,5-dimethyl-3-methoxypyrazine **(d)** 2-isopropyl-3-methoxypyrazine **(e)** 2-*sec*-butyl-3-methoxypyrazine **(f)** 2-isobutyl-3-methoxypyrazine

Fig. 1 Components of *H. axyridis* defensive chemistry

presumably younger, as the elytra darken continuously with the accumulation of carotenoid pigment through a ladybird's life (Majerus 1994). Fischer et al. (2010c) found that dark orange ("red") melanic individuals produced less methoxypyrazine than other colour forms. Interestingly given the role of methoxypyrazines as warning odours for toxicity and repellency, Fischer et al. (2010a, c) concluded that harmonine content and methoxypyrazine emission rate were uncorrelated.

Ecological role

Like the alkaloids of other ladybirds, those of *H. axyridis* probably provide protection against a diversity of invertebrate and vertebrate predators. Indeed, the evidence suggests that even amongst ladybirds, the chemical defences of *H. axyridis* are particularly strong. In a standard toxicity assay, *H. axyridis* chemical defences were more toxic to the cladoceran *Daphnia magna* Straus than those of either *C. septempunctata* or *Adalia bipunctata* (L.) (Nedvěd et al. 2010). Furthermore, in a comparison of the unpalatability of eight ladybird species to the ant *Lasius niger* (L.), only *C. septempunctata* was found to be more unpalatable than *H. axyridis* (Nedvěd et al. 2010). Its strong chemical defences can partially explain the success of *H. axyridis* as an intraguild predator. There are numerous studies that have documented *H. axyridis* unpalatability or toxicity as an intraguild prey both in its native range and where it has been introduced (e.g. Phoofolo and Obrycki 1997; Cottrell 2004; Sato and Dixon 2004; Sato et al. 2009a). It has also been shown that *H. axyridis* eggs with more harmonine are less readily eaten by larval *C. septempunctata* intraguild predators, establishing an unequivocal link between repellency and alkaloid composition in this case (Kajita et al. 2010). This alkaloid-based lack of vulnerability to intraguild predation by other species, makes *H. axyridis* the more likely victor in aggressive intraguild interactions (Sato and Dixon 2004; Sloggett et al. 2009a; Nedvěd et al. 2010).

More generally, its strong chemical defences could potentially make *H. axyridis* less vulnerable to natural enemies in the new areas that it has colonised. However, this is open to question. A number of parasites or parasitoids appear to have been pre-adapted or to be adapting to *H. axyridis* in North America and Europe (e.g. Nalepa and Kidd 2002; Garcés and Williams 2004; Rhule et al. 2010; Roy et al. 2011), suggesting that any chemical defensive benefit against such natural enemies is transitory and, if present at all, obtained through novelty rather than strength. The same is also true for at least some more generalist, predatory natural enemies. Sloggett (2010b) found that the European spider *Araneus diadematus* Clerck readily ate both the native European *C. septempunctata* and the exotic *H. axyridis*. It suffered no ill effects from eating either. He concluded that this generalist predator possessed strong general detoxification mechanisms against diverse prey defensive chemicals, and these remained effective against the novel chemistry of *H. axyridis*.

With this example borne in mind, it may be that *H. axyridis* chemical defences, though strong, provide only a marginally increased benefit against generalist natural enemies in areas that the ladybird is colonising, over either that in *H. axyridis*' natural range or that possessed by at least some of the native ladybird species.

The costs of using chemical defence have been determined in *H. axyridis*. Reflex bleeding by larvae leads to a lower developmental rate and smaller size and weight at adulthood (Grill and Moore 1998; Sato et al. 2009a). The costs related to intraspecific variation in alkaloid content in *H. axyridis* are not known at this time.

Food, feeding and reproduction

Although *H. axyridis* is reputed to be highly polyphagous, it typically feeds on aphids (Hodek 1996; Koch 2003). This prey constitutes a common and abundant food source, exploited by a very rich aphidophagous guild (Lucas 2005). However, aphid populations are structured in colonies and each colony only lasts for a short period of time (Dixon 1998). It is therefore common in the field to find numbers of individuals, either of the same or different aphidophagous species, simultaneously exploiting aphid colonies (Dixon 2000). This situation favours competition, cannibalism and intraguild predation, which act as selective forces on the species (Hodek 1996; Schellhorn and Andow 1999; Dixon 2000; Lucas 2005).

Ladybirds generally are important members of aphidophagous guilds, both in abundance and diversity. Under the above-mentioned constraints, the group has developed several mechanisms to avoid the negative effects of intra- and interspecific interactions. Infochemicals as well as chemical defences are particularly important. They reduce the risk of overcrowding and deter enemies from actually capturing and killing, if contact occurs. All the developmental stages of ladybirds use chemically based strategies to maximise their fitness (Hemptinne and Dixon 2000; Durieux et al. 2010).

Compared to other ladybirds, *H. axyridis* is reputed to be more strongly polyphagous (Hodek 1996; Koch 2003; Berkvens et al. 2008), extremely voracious (Koch et al. 2006; Labrie et al. 2006), strongly competitive (Michaud 2002), highly cannibalistic (e.g. Takahashi 1989; Hironori and Katsuhiro 1997; Osawa 1993; Sato et al. 2003) and an important intraguild predator (see Pell et al. 2008 for review). Some of these factors are clearly linked to its invasiveness and to the deleterious effects it manifests in its new range. Given these particular characteristics, we can ask how the selective pressures related to the clustered distribution of aphids and the consequent aggregation of their natural enemies have shaped the chemical ecology of *H. axyridis*. We address this question in the context of what is already known for ladybirds generally.

Locating prey

Since the 1950s, a general hypothesis of the searching behaviour of aphidophagous ladybirds has been proposed and tested in a number of studies (Banks 1956; van der Werf et al. 2000; Koch 2003). As aphid populations are typically ephemeral and unpredictably distributed, the ladybird foraging strategy consists of flying through a landscape throughout the growing season to locate and colonise favourable habitats in which adults move from aphid colony to aphid colony (Hodek 1973; Evans 2003; see also Brown et al. 2011). When searching for a prey colony in a selected habitat, a so-called extensive searching behaviour occurs, characterised by a relatively high walking speed and low frequency of turning. After physical contact with prey, the extensive foraging behaviour becomes more intensive, with a low walking speed and an increase in the number of directional changes, which favours the likelihood of encountering nearby prey (Banks 1954; Pettersson et al. 2005). If, despite the intensive search pattern, no prey are encountered after a certain period of time, extensive searching behaviour (i.e. increased speed of movement and decreased turning) is resumed (Carter and Dixon 1982). As with other aphidophagous ladybirds, despite being often considered random, the searching behaviour of *H. axyridis* larvae is guided by positive phototaxis and negative geotaxis, resulting in larvae climbing up plants (Kawai 1976).

Although laboratory and field experiments conducted in the decades following the 1950s have confirmed the general model of ladybird search behaviour, only a relatively weak link has been observed between adult foraging activity and prey density (Evans 2003). In the case of *H. axyridis*, Cardinale et al. (2006) found that immigration of adults into alfalfa patches was not correlated with aphid abundance. Other cues have been proposed as contributing to the searching behaviour of ladybird species, to help explain their ability to reduce aphid numbers in natural settings. Accumulated data indicate that additional cues are implicated in enhancing the foraging success of coccinellids: adults and larvae behave according to the perception of visual, gustatory and olfactory cues associated with prey, prey hosts, feeding damage on prey hosts, prey waste products and even conspecifics (Seagraves 2009). However, the different cues involved in the foraging process may vary in importance.

Visual cues have been reported as acting on the migratory and foraging behaviour of ladybird species (Nalepa et al. 2000) but studies are conflicting as to the scale at which they act and as to the visual acuity of ladybirds. *Harmonia axyridis* uses prominently silhouetted objects on a horizon to seek a suitable prey habitat (Obata 1986, 1997; Koch 2003). A recent study by Bahlai et al. (2008) also suggests that adult *H. axyridis* rely on long-range visual cues to locate prey habitats, as they move toward both silhouetted shapes and leaves of prey host plants. Long- and short-range visual perception was demonstrated in both larval and adult *H. axyridis*, with the latter exhibiting the best visual abilities (Lambin et al. 1996). The role of vision in close-proximity foraging behaviour has also been demonstrated in *H. axyridis*, which consumed significantly more aphids in the light than in the dark (Harmon et al. 1998) and which preferentially consumed more red morphs than green morphs of pea aphids, *Acyrthosiphon pisum* (Harris).

In addition to these cues, *H. axyridis* probably receives a number of different foraging-related chemical signals (Obata 1986). In other coccinellid species, the scents of host plants, prey pheromones or the chemicals from competitors are all known to be involved in foraging behaviour (Schaller and Nentwig 2000; Francis et al. 2004; Pettersson et al. 2005). Information on infochemical-mediated foraging behaviour in ladybirds generally remains limited. This is especially the case for *H. axyridis.* Olfactory studies have started only very recently on this species, encouraged by the desire to enhance its effectiveness as a biological control agent and the urgent need to provide alternative solutions to the problems posed by large aggregations, particularly in buildings. As such, much of what we can currently deduce about *H. axyridis* comes from research on other ladybird species.

For the many aphidophagous predators, the plants on which aphids feed play a key role in providing useful cues. Ladybirds, like other aphid predators, would benefit from a mechanism for identifying cues related to herbivore-infested plants, which would increase their chance of encountering a prey. Zhu and Park (2005) showed that methyl salicylate, released in higher amounts from aphid-damaged soybean plants, was attractive to *C. septempunctata*, but not to *H. axyridis*. Other bioassay and field experiments revealed that some monoterpenoids elicit avoidance behaviour in adults, and should be incorporated in strategies aimed at repelling *H. axyridis* (Riddick et al. 2000). Air entrainment extracts of tea shoots damaged by tea aphids (*Toxoptera aurantii* (Boyer de Fonscolombe)) elicited strong electrophysiological responses from *H. axyridis* antennae, as well as strong upwind flight and arrestant behaviour in a wind tunnel (Han and Chen 2002).

Like most aphid natural enemies, aphidophagous ladybird species rely on aphid related infochemicals to locate aphid colonies, or to assess if an aphid colony is too old for their offspring to survive. Previous studies have demonstrated this phenomenon in *H. axyridis* (Verheggen et al. 2007), as well as *A. bipunctata* (Francis et al. 2004). Aphid honeydew probably also plays a role in foraging by the group. Passively released volatile molecules from aphid honeydew may be used by aphid natural enemies, including some ladybird species, in searching for prey (Evans and Dixon 1986; Evans and Richards 1997). Honeydew is known to induce egg laying and attract females towards prey in hoverflies (Leroy et al. 2010). In addition to aphid honeydew, aphid pheromones can be important kairomones in aphid location. In response to predation and other disturbance, many aphid species secrete droplets from their cornicles containing the sesquiterpene (E)-β-farnesene, which acts as an alarm pheromone (Kislow and Edwards 1972; Verheggen et al. 2010). Although (E)-β-farnesene is also a ubiquitous plant volatile, its ephemeral and relatively high emission is perceived by most aphid natural enemy groups including the ladybirds, which exploit this kairomone as an indicator of aphid presence (Zhu et al. 1999; Acar et al.

2001; Francis et al. 2004). Adult *H. axyridis* of both sexes have been found to be strongly attracted to aphid alarm pheromone in bioassays (Mondor and Roitberg 2000; Verheggen et al. 2007). There is ample evidence for the involvement of aphid-related chemical cues in prey location, but they remain poorly understood, especially in *H. axyridis*. The identities of the infochemicals passively or actively emitted by aphids and playing a role in the foraging behaviour of this ladybird, and indeed other ladybird species, are not completely established. Once an aphid is located, natural enemies have to recognise it as potential prey before they consume it. Non-volatile chemical cues can be important to aphid recognition by natural enemies, most notably contact kairomones from the surface of the aphid cuticle as a cue for aphid parasitoids (see Hatano et al. 2008). However, as for all aphidophagous ladybirds, little information is yet available on *H. axyridis* prey acceptance related to aphid cuticular hydrocarbon composition.

Reproductive behavioural response to infochemicals

As for many organisms, adult females of aphidophagous ladybirds, through their foraging and oviposition behaviour, play a major role in the spatial distribution and density of populations. Compared to adult females, the dispersal capacity of the larvae is limited and they often remain in patches selected by their mother. Once a female locates a colony, it oviposits if there are enough aphids for the very small first instar larvae to easily encounter and capture them (Dixon 1959). It will stop if it comes upon larvae (Hemptinne et al. 1992) or chemical cues related to larval presence (Ružička 1997; Doumbia et al. 1998).

Infochemicals that deter ladybird females from oviposition are of different sorts: larval tracks made of non-volatile hydrocarbons that are released by the anal gland as larvae move on plant surfaces (Laubertie et al. 2006), molecules in faeces (Agarwala et al. 2003) and cuticular molecules (Klewer et al. 2007). Deterrence by hydrocarbons is density-dependent (Doumbia et al. 1998; Oliver et al. 2006) and decreases with female age (Fréchette et al. 2004). Conspecific recognition has been shown for many species (Ružička 1997, 2001, 2003; Doumbia et al. 1998; Oliver et al. 2006) but response to heterospecifics is less common (Doumbia et al. 1998; Ružička 2001, 2003; Oliver et al. 2006). Explanations for this difference have been proposed, including heterospecific responses being mediated by habitat overlap or phylogeny (Magro et al. 2007, 2010).

Like the majority of ladybirds, the selection of oviposition sites by *H. axyridis* females is constrained by the presence of conspecifics. They lay fewer eggs when kept in groups than when alone (Flowers et al. 2005), reduce their rates of oviposition when exposed to faeces of larvae of their own species (Agarwala et al. 2003) and are deterred from ovipositing in the presence of conspecific larval tracks (Yasuda et al. 2000; Gil et al. 2004). However, according to the available literature, *H. axyridis* females do not stop laying eggs when they meet heterospecifics or cues related to them. This absence of response was observed for species they co-occur with in their native range and therefore have coevolved with—the Coccinellidae *C. septempunctata*, *Propylea japonica* (Thunberg) and *Sasajiscymnus tsugae* (Sasaji and McClure), and the derodontid coleopteran *Laricobius nigrinus* Fender (Yasuda et al. 2000; Agarwala et al. 2003; Flowers et al. 2005)—but also the non-coevolved syrphid dipteran *Episyrphus balteatus* (DeGeer) (Almohamad et al. 2010, but see also Alhmedi et al. 2010). How can this difference in response to conspecific and heterospecific cues be explained?

In the field, females of *H. axyridis* lay eggs during the increase and peak in aphid abundance and are often the last ladybirds to arrive and attack aphids in a patch (Takahashi 1989; Hironori and Katsuhiro 1997; Osawa 2000; Sato and Dixon 2004; Jansen and Hautier 2008). This is consistent with the fact that the quantity of food required for oviposition is related to body mass and so large species need higher densities of aphids to lay eggs (Dixon 2007). However, as the temporal availability of aphids decreases dramatically once the peak of abundance is attained, the consequence of a late reproductive window is that *H. axyridis* larvae are more likely to face competition for limited food during the later developmental stages than larvae of smaller species. This equates to older larvae suffering more intensively from cannibalism and intraguild predation. Indeed, in *H. axyridis* the fourth instar is a key stage in terms of mortality, but this mortality seems mostly due to a marked incidence of cannibalism (Hironori and Katsuhiro 1997; Kindlmann et al. 2000; Sato et al. 2009b).

From this, it is possible to see why *H. axyridis* responds to conspecific rather than heterospecific cues. An example serves to demonstrate this. In Japan, *H. axyridis* co-occurs mostly with *P. japonica* and *C. septempunctata* (Takahashi 1989; Sato et al. 2003). Females of *P. japonica* avoid egg laying in patches with *H. axyridis* larvae (Agarwala et al. 2003). *C. septempunctata* generally avoids contact with *H. axyridis* (Sato et al. 2003, 2005) and if contact does occur, it is affected adversely (Yasuda and Ohnuma 1999; Yasuda et al. 2001; Sato and Dixon 2004; Rieder et al. 2008). *Harmonia axyridis* is extremely well protected by a number of functional traits, including aggressive strategies and physical and chemical defensive adaptations (Pell et al. 2008; Ware and Majerus 2008 and chemical defence section above). It is therefore more likely to face cannibalism than suffer from intraguild predation. This explains the reluctance of females to oviposit in patches already occupied by conspecifics but not heterospecifics.

Furthermore, existing data on intraguild predation involving *H. axyridis* (see Pell et al. 2008 for review; Sato et al. 2008) suggests that this ladybird is an asymmetrical intraguild predator, being more likely to eat other intraguild species than being preyed upon. As the larvae of *H. axyridis* are more likely to suffer from the limited availability of aphids compared to other species, being an efficient intraguild predator has an adaptive significance by both eliminating competitors and supplying additional food items. If the performance of larvae is not adversely affected and these larvae even benefit from consuming intraguild prey, females of *H. axyridis* should continue to oviposit in aphid colonies occupied by other guild members. This hypothesis needs to be confirmed by further field and laboratory work.

Intraguild prey chemical defences

As stated above, the ephemeral character of aphid colonies together with the fact that aphids are a food source for many species, favours cannibalism and intraguild predation amongst ladybird and other aphid predators. These can affect all developmental stages, but insect eggs, being immobile, are particularly vulnerable (Blum and Hilker 2002). In the ladybirds, much of the information we have is on egg predation and many studies have shown that, in spite of their vulnerability, eggs are far from defenceless. Molecules both on the egg surface and inside the egg play a role in the protection against a wide range of enemies (Pasteels et al. 1973; King and Meinwald 1996; Hemptinne et al. 2000). Chemicals of the egg chorion work to advertise the presence of repellent or sometimes toxic alkaloids inside the egg (Hemptinne et al. 2000). The outcome of predation is affected both by the defensive chemicals present in or on coccinellid eggs and the capacity of predators to deal with them (Weber and Lundgren 2009).

After establishment in different regions as an invasive alien species, *H. axyridis* has been associated with declines in native species at least in part due to its role as an intraguild predator (Pell et al. 2008), and this species has been claimed to be a top-predator in aphidophagous guilds (Dixon 2000). There are only a few studies separately assessing the effect of the external deterrents and inner chemical defences on *H. axyridis* (Sato and Dixon 2004; Cottrell 2007; Ware et al. 2008a, b; Sloggett et al. 2009a). Of all the analysed ladybird species, eggs of *Eocaria muiri* Timberlake and *Calvia quatuordecimguttata* (L.) are almost always avoided and, in the case of this second species, the deterrent effect is due to hexane-soluble molecules coating the eggs (Ware et al. 2008b). In contrast, the eggs of the ladybird *Coleomegilla maculata* (DeGeer) are readily attacked by *H. axyridis,* although they impose a direct cost to the intraguild predator: consumption resulted in high mortality, slowed development and even paralysis of *H. axyridis* larvae (Sloggett et al. 2009a, but see also Cottrell 2007). More palatable ladybird eggs come from a diversity of species including *C. septempunctata*, *Propylea* spp., *Harmonia quadripunctata* (Pontoppidan) and *Hippodamia convergens* Guérin-Méneville (e.g. Ware et al. 2008a; Sloggett et al. 2009a).

In many cases heterospecific eggs are a suitable food source for *H. axyridis*. In the absence or at low levels of extraguild prey, the consumption of heterospecific eggs generally positively affects *H. axyridis* compared with other coccinellid species facing the same rearing conditions (Cottrell 2004, 2005). Suitability is mainly translated into measures of survival, capacity to develop through larval stages and to adulthood, adult weight and reproduction. Unfortunately, the lack of standardised approaches to evaluating the consequences of different intraguild prey consumption makes comparisons difficult. As shown in studies of intraguild predation of *A. bipunctata* (Sato and Dixon 2004; Ware et al. 2009) and by Sloggett et al. (2009a), it is possible for even quite a toxic intraguild prey to be beneficial for *H. axyridis*, depending on the availability of extraguild aphid prey. Comparison of results from different studies should be therefore carried out with care.

Effects of and resistance to prey defensive allelochemicals after consumption

The broad generalist diet of *H. axyridis*, encompassing a wide diversity of aphids, additional insect prey and other types of food (Hodek 1996; Koch 2003; Berkvens et al. 2008), means that this ladybird comes into contact with, and appears to be able to tolerate, a very wide diversity of prey defensive chemistry in its diet. Given that its generalist behaviour is of likely importance to its invasiveness (Majerus et al. 2006; Berkvens et al. 2008), and that its tolerance of intraguild prey defensive chemistry helps make it a successful intraguild predator and threat (Cottrell 2004; Sloggett et al. 2009a), how *H. axyridis* responds to and deals with prey chemistry has been surprisingly poorly studied.

As with other ladybirds (Hodek 1996), the different natural aphid prey of *H. axyridis* vary in their suitability, probably as a consequence of allelochemical content. This is true both in the ladybird's native range (e.g. Hukusima and Kamei 1970; Okamoto 1978) and where it has been introduced (e.g. Ungerová et al. 2010). There have been a number of particularly striking demonstrations of the effects of aphid allelochemicals, shown by feeding *H. axyridis* the same prey aphid from different host plants (Hukusima and Kamei 1970; Okamoto 1978; Fukunaga and Akimoto 2007). For example, Fukunaga and Akimoto (2007) fed *H. axyridis* larvae from the same egg batches either on the aphid *Aulacorthum magnoliae* (Essig and Kuwana) from elder or the same aphid from potato. Larvae fed with aphids from elder exhibited higher mortality and slower growth than those from potato. Interestingly, there was significant genetic variation in performance on both aphids, but it was positively correlated (i.e. lines that performed better on one aphid also performed better on the other) (Fukunaga and Akimoto 2007). These latter findings are mirrored in another study by Ueno (2003), using the prey aphids *Ac. pisum* and *Aphis craccivora* Koch. They indicate that the overall dietary generalism of *H. axyridis* does not arise because the species is composed of subpopulations or individuals that are highly specialised on different individual aphid types, but correspondingly poorly adapted to other aphid prey as a consequence of performance-related trade-offs (see Rana et al. 2002; Ferrer et al. 2008; Sloggett 2008a, b). A single undivided species of individual generalists, as *H. axyridis* appears to be, would, without doubt, make a better invader than a subdivided species of individual specialists.

In addition to naturally arising variation in the suitability of different prey, some novel, native prey might be toxic to *H. axyridis* where it is an invasive alien, because they contain defensive allelochemicals that the ladybird has not encountered in its original range and to which it has consequently not evolved resistance. Testing this hypothesis also gives some insight into the underlying mechanisms of *H. axyridis* prey allelochemical tolerance: it is only likely to be the case if tolerance mechanisms are somewhat chemical-specific. If the ladybird possesses a single, broad, extremely general mechanism for chemical resistance, it is likely to be as effective against novel chemicals as historically encountered chemical types. The issue of prey chemical novelty for invasive *H. axyridis* was investigated by Sloggett et al. (2009a), in a study of intraguild predation of other ladybirds. Larvae from an invasive North American *H. axyridis* population were fed the eggs of four other North American ladybirds with known types of alkaloid defences. Performance on two of these ladybird species, *C. septempunctata* and *H. convergens* was as good as or better than that on pea aphids, while the other two species were either highly distasteful (*Cycloneda munda* (Say)) or toxic (*C. maculata*). The authors argued that *C. munda* and *C. maculata* possessed less common alkaloid defences, which *H. axyridis* would have been unlikely to have encountered in its native range. By contrast, *C. septempunctata* occurs itself in the native range of *H. axyridis* and the alkaloids of *H. convergens* are of such widespread occurrence in aphidophagous ladybirds that it is unlikely that they do not occur there also. Interestingly discrimination against the poorer quality intraguild prey is either weak (Cottrell 2007) or non-existent (Sloggett et al. 2009a), possibly because in its native range the ladybird has evolved resistance to any potential ladybird prey it encounters and rarely needs to discriminate. The "novel alkaloid" argument can be applied to other non-coevolved intraguild prey of *H. axyridis*, most notably *A. bipunctata*, which feeding tests have shown to be of poor quality (Sato and Dixon 2004), even though it appears to be a regular prey of *H. axyridis* where the two now co-occur (e.g., Toda and Sakuratani 2006; Hautier et al. 2011).

Harmonia axyridis intraguild predation of other ladybirds provides a particularly tractable means of studying adaptation to prey allelochemicals by comparison with the use of aphid prey. The large body of work on intraguild predation of ladybirds by *H. axyridis*, both from the laboratory and field, means that there is a clear ecological framework for the interpretation of chemical results. Furthermore, the alkaloids of coccinellids are well-characterised, unlike the chemicals of many aphid prey, making analytical approaches more easily applicable (Sloggett et al. 2010). Use of gas chromatography-mass spectrometry (GC-MS) has facilitated the detection and measurement of many prey ladybird alkaloids within the body of *H. axyridis* after consumption (Fig. 2). It has proven an extremely effective method for detecting *H. axyridis* intraguild predation of other ladybirds after this has occurred (Sloggett et al. 2009b), and, thus far, the majority of published results on such intraguild predation in the field have used this approach more than conventional molecular methods (Hautier et al. 2008, 2011; Aebi et al. 2011; see also Sloggett and Honěk in press). It can also provide information about the mechanisms of toxic alkaloid resistance in the intraguild predator (Sloggett et al. 2010). It was recently used in an ADME (absorption, distribution, metabolism and excretion) study of the fates of two alkaloids from prey ladybird eggs: isopropyleine from the suitable, naturally-co-occurring, "historical" prey, *P. japonica*, with which *H. axyridis* shares a long coevolutionary history, and adaline, from the partially toxic, novel prey, *A. bipunctata*, which *H. axyridis* has only recently encountered where one or other species has been introduced (Sloggett and Davis 2010). The study measured the occurrence of the alkaloids in the whole body, haemolymph and frass of larval *H. axyridis* predators. Isopropyleine declined in the body much more rapidly than adaline. Similarly, although both alkaloids entered the haemolymph of the predator, isopropyleine disappeared within 8 h of prey consumption, while adaline was still detected after 32 h. Only a small proportion of the original alkaloid passed into the frass (Sloggett and Davis 2010). The results indicate that alkaloids to which *H. axyridis* has evolved resistance, such as isopropyleine, are metabolised within the body of the predator to render them harmless. By contrast the more toxic, generally novel alkaloids cannot be metabolised and persist in the body, probably giving rise to their detrimental effects. As with other studies comparing historical prey or alkaloids with novel ones, this work indicates that *H. axyridis* alkaloid resistance is moderately chemical-specific.

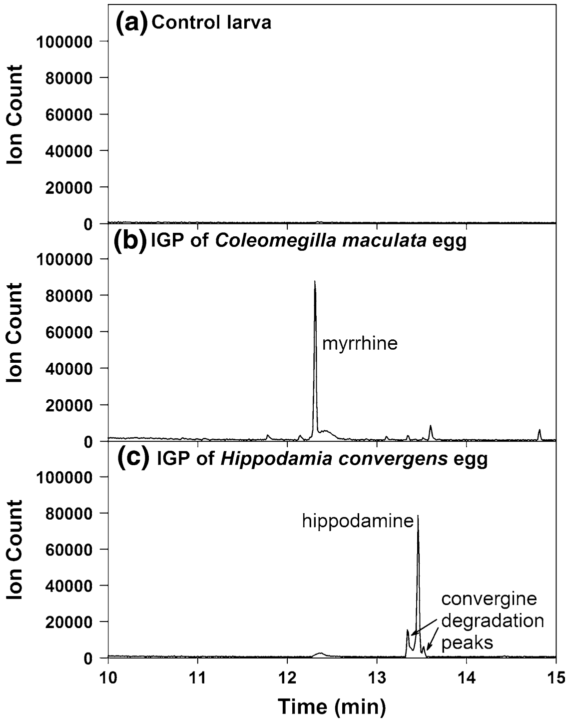


Fig. 2 Gas chromatograms of extracts of whole third instar *H. axyridis* larvae showing the alkaloids of (North American) prey that they have eaten. (**a**) a *H. axyridis* larva that has not eaten any ladybird prey; (**b**) one that has eaten a *Coleomegilla maculata* egg, showing a myrrhine peak; (**c**) one that has eaten a *Hippodamia convergens* egg, showing hippodamine and degraded convergine peaks. From Sloggett et al. (2006, 2010)

There is still a long way to go in understanding the mechanisms of allelochemical resistance, in *H. axyridis* as in other ladybirds or indeed in predators in general (Sloggett et al. 2010). It is therefore of interest whether the findings described here on the allelochemicals of intraguild prey can be extrapolated further to the handling of the allelochemicals of aphid prey by *H. axyridis*. It seems unlikely that a very broad dietary generalist, such as *H. axyridis*, would possess many chemically specialised detoxification mechanisms, each acting in parallel. High metabolic specificity might be expected to lead to strong genetic trade-offs in the tolerance of different prey defensive chemicals, which is clearly not what is observed in relation to aphid prey (Sloggett and Davis 2010; see this section, above). One possibility is that mechanisms for *H. axyridis* resistance to the alkaloids of intraguild ladybird prey are quite specialised, while those for *H. axyridis* resistance to aphid allelochemicals are more general. This remains to be tested. However, as pointed out by Sloggett et al. (2009a), certain species of ladybird intraguild prey, such as *C. septempunctata*, are probably some of the most consistently occurring items in the diet of *H. axyridis*, because they co-occur with the ladybird across a wide variety of habitats containing different aphids. For this reason, highly specific resistance mechanisms might have evolved in *H. axyridis* to cope with ladybird alkaloids. Similar mechanisms might not evolve for the allelochemicals of individual aphid species, as these species will only be encountered for short periods during the adult lifespan or once every few generations in the case of larvae.

Harmonia axyridis **chemistry, humans and human activity**

Autumn migration and aggregations

In addition to problems related to the suppression of native species and intraguild predation, *H. axyridis* poses a number of other more direct issues for human health and well-being in which an understanding of its chemistry provides an insight or even a solution. In particular, mass migrations of *H. axyridis* in search of overwintering sites in the autumn have led to this insect becoming a nuisance pest (Koch and Galvan 2008). The most obvious overwintering sites include houses and other structures within its invasive range (Kidd et al. 1995; Nalepa et al. 1996; Schaefer 2003; Nalepa 2007; Labrie et al. 2008). Adult *H. axyridis* commonly aggregate in houses, in attics, wall voids and other sheltered places. Wang et al. (2011) found that a proclivity for establishing aggregations in houses and other structures is not intrinsic to invasive alien populations of *H. axyridis*. Even in parts of its native range in northern China, adults aggregate on house exteriors. However, in mountainous locales aggregations do not persist: adults leave house interiors within two weeks of initial aggregation formation, migrate to higher elevations and overwinter in shallow caves, crevices, and rocky depressions on montane slopes (Wang et al. 2011). Whether or not chemical cues are involved in establishing and maintaining autumn aggregations is equivocal. However, there is evidence that persistent molecules, deposited on the substrate near the entrance to a preferred aggregation/overwintering site attracts another ladybird species, *A. bipunctata*, to the same sites year after year (Hills 1969; Majerus 1997).

In locales devoid of mountains to draw beetles to higher elevations, *H. axyridis* adults remain in houses in the invasive and native ranges. The aggregating beetles can become active and pose a nuisance in living spaces in houses by their mere presence or by their habit of reflex bleeding when handled roughly or crushed. Reflex blood can stain fabric and similar material. It has an unpleasant odour, in part due to the release of noxious compounds, including methoxypyrazines (see above, section on chemical defence). Methoxypyrazines or alkaloids released from reflex blood may have been responsible for chemical burns on the oral mucosa of a dog that had 16 *H. axyridis* beetles lodged in its mouth (Stocks and Lindsey 2008). Humans can develop allergic reactions to airborne volatiles emanating from dead *H. axyridis* accumulating in wall voids, attics and other inaccessible places in houses (Nakazawa et al. 2007). Mass migrations of *H. axyridis* into commercial vineyards in autumn have caused unintentional harvesting of grapes contaminated with this insect. This happens when, just before harvest, beetles form temporary aggregations within grape clusters, primarily attracted to juices leaking from injured grapes (Galvan et al. 2008a). Wine tainted with *H. axyridis* has a discernible off-taste (Pickering et al. 2004).

Tainting of wines by *H. axyridis*

The phenomenon of so-called "ladybug taint", i.e. *H. axyridis* contamination of grape juice and wine has thus far been primarily limited to the wine industry in the Great Lakes Region in the central and northeastern USA and Ontario in Canada (Pickering et al. 2005, Galvan et al. 2007a). However, recent concerns about potential infestations of *H. axyridis* in European grapes have also been raised, and careful monitoring of the beetle in European vineyards is warranted (e.g., Linder et al. 2009; Hutchison et al. 2010).

Much of the early work on the potential cause of the wine taint has focused on methoxypyrazines (Pickering et al. 2005), as these compounds are also produced by *H. axyridis* (see chemical defence section). The specific methoxypyrazines of interest have included: 2-isopropyl-3-methoxypyrazine (henceforth referred to as IPMP), 2-*sec*-butyl-3-methoxypyrazine (SBMP), and 2-isobutyl-3-methoxypyrazine (IBMP) (Pickering et al. 2007; Galvan et al. 2008b). When *H. axyridis*-infested grape clusters are harvested, the ladybirds are disturbed and respond by reflex bleeding (Galvan et al. 2008b). As they are crushed within the clusters, or directly within the juice, the methoxypyrazines, and probably other beetle compounds, may contaminate the wine throughout vinification (Galvan et al. 2008b).

Pickering et al. (2005) were the first to find a relationship with increasing levels of *H. axyridis* in grape juice and wine, including increased levels of IPMP in white and red commercial juice concentrates from South America. IPMP levels were significantly higher with 10 individuals^{-1} than one individual^{-1} in both the white and red wines made from the juice. However, there were no significant differences observed for IBMP. In a second study, Pickering et al. (2007) assessed the impact of various *H. axyridis* infestation levels on the quality of 'Riesling' wine. Again, they detected higher levels of IPMP with infestations of about three individuals kg^{-1} grapes, when *H. axyridis* were added during the crushing/destemming stage of the process.

In contrast, Galvan et al. (2008b), using headspace sampling with solid-phase microextraction (SPME) and gas chromatography (GC) for quantifying the same methoxypyrazines was inconclusive. These authors found that IPMP concentrations in two red wines were not significantly different across different *H. axyridis* infestation levels. In addition, there were no consistent patterns in IPMP levels among wines made from naturally infested grapes, several years earlier. It is possible that some of the decline in IPMP may have resulted from the longer aging process within the bottle (Galvan et al. 2008b). SBMP was found only in wine artificially infested with *H. axyridis*. Both IPMP and SBMP were also much higher (nearly 20-fold) than IBMP for wines containing *H. axyridis*. Thus, the results were inconclusive with regard to which methoxypyrazines could be most critical in causing the taint, but also suggest that several other compounds, such as 2-5-dimethyl-3-methoxypyrazine, known to occur in *H. axyridis* should be investigated. Many of these same compounds are known to naturally occur in several wines such as Cabernet Sauvignon in California (Galvan et al. 2008b), where tainting by *H. axyridis* is not known to occur.

Regardless of the compounds responsible for tainting wine, the results of Galvan et al. (2008b), and an additional taste-panel study (Galvan et al. 2007a) were used to develop an Integrated Pest Management (IPM) programme that vineyard managers can use now to mitigate the risk of tainted wine. "Action thresholds," or tolerance limits for growers, were developed, based on controlled studies with known *H. axyridis* infestation levels and taste-panel detection. These data were then used to develop the relationship between *H. axyridis* infestations in grape clusters and the subsequent risk of taint in the final wine product. An action threshold of approximately 10% of the grape clusters infested with one or more beetles each was subsequently agreed upon. More conservative growers may use 5% of clusters infested, until more research can be done to further verify the risk to additional grape varieties. These results, coupled with a practical monitoring tool (presence-absence, cluster sampling; Galvan et al. 2007b) formed the basis of an effective IPM plan that has been implemented by many growers in the Minnesota-Wisconsin region in the USA (Hutchison et al. 2010). The programme currently relies on careful monitoring of *H. axyridis* infestations within 2–3 weeks of harvest, and if necessary, the application of insecticide (within 3–4 days of harvest) to effectively remove ladybirds from clusters prior to harvest (Hutchison et al. 2010).

Chemical attractants and repellents as potential management tools

A promising approach to managing *H. axyridis* aggregations generally is the use of chemical repellents and attractants in a push–pull strategy (Riddick and Aldrich 2004), utilising chemical repellents to push beetles away from houses, or away from grape clusters in vineyards, and then using chemical attractants or aggregation pheromone components to pull beetles into collecting vessels or traps. The push–pull strategy is a proven method for managing several important arthropod pests in lieu of conventional control methods (Cook et al. 2007). Chemicals that have demonstrated potential of repelling *H. axyridis* under laboratory conditions include camphor, menthol, DEET (*N*,*N*-diethyl-3-methylbenzamide), and dihydronepetalactone (Riddick et al. 2000, 2004, 2008). The usefulness of laboratory studies to observe the behaviour of *H. axyridis* as they approach treated surfaces is not a trivial pursuit. In one study, beetles tended to avoid contact with treated surfaces by crawling away rather than flying away (Riddick et al. 2008), which might suggest that the same behaviour will occur at surfaces treated with a repellent in the field.

Methoxypyrazines (Al Abassi et al. 1998; Cudjoe et al. 2005; Cai et al. 2007; see section above on chemical defence), β-caryophyllene (Brown et al. 2006) or (*E*)-β-farnesene (Verheggen et al. 2007; see section on locating prey), might all prove useful in pulling ladybirds into traps. Brown et al. (2006) detected β-caryophyllene in the body odour of live *H. axyridis* females, but not males, in the laboratory. Verheggen et al. (2007) showed that *H. axyridis* aggregated toward β-caryophyllene-treated areas inside plastic boxes in the laboratory. A field study showed that traps (attached to the exterior walls of houses) baited with honey or corn pollen captured more *H. axyridis* than those baited with caramel, cocoa, milk, or a blank control (Wang et al. 2011). Apparently, *H. axyridis* utilise plant-based energy sources during migration. Once collected, beetles can be stored at a low temperature over the winter. Exposure of adults to injured grape berries, sugar, and water prior to simulated overwintering (in the laboratory) increased winter survival (Galvan et al. 2008a). More extensive field research will be necessary to test and refine the push–pull strategy at houses and in vineyards in urban and agricultural landscapes, respectively.

Future perspectives for research

Harmonia axyridis seems likely to remain a regularly used model species for research, especially in studies on invasive alien species and their effects where they are introduced. In working with *H. axyridis*, it is important to link studies of its chemical ecology to those of other ladybirds. Only by doing this, will we find out, not only what are general principles across the whole of the (aphidophagous) Coccinellidae, but what it is that makes *H. axyridis* such a uniquely successful species (Sloggett 2005).

Particularly important among studies that might tell us more about the Coccinellidae in general are those on intraspecific chemical communication, including not only the aggregation pheromones considered above, but the role of chemistry in mating behaviour and particularly in the recognition of kin. Studies of coccinellid mating chemistry are largely limited to *A. bipunctata* (Hemptinne et al. 1996, 1998), something extremely surprising given the long history of interest in other aspects of coccinellid mating behaviour (Hodek and Ceryngier 2000 for review). Work on kin-selection in non-eusocial insects remains generally rather sparse (Fellowes 1998; Lihoreau and Rivault 2009). However, several studies of aphidophagous coccinellids, including *H. axyridis*, have suggested that cannibals can distinguish kin from non-kin (Agarwala and Dixon 1993; Joseph et al. 1999; Pervez et al. 2005; Wang et al. 2010). After eliminating a number of potential exogenous cues, Joseph et al. (1999) concluded that the underlying kin-recognition cue in *H. axyridis* was an endogenous one, possibly cuticular in origin, but although it is probably chemical, the exact nature of the cue remains unclear.

Beyond the area of intraspecific chemical communication, intriguing results, discussed in the section on chemical defence, have been obtained connecting quantitative intraspecific variation in chemical defence to colour pattern diversity. Like kin recognition, this is a subject of wider biological interest outside of the Coccinellidae (e.g. Blount et al. 2009). Certainly *H. axyridis* could serve as a model for future work in this area, although if this is to be the case, such work needs to encompass the full complement of *H. axyridis* alkaloids, as is the case for other ladybirds.

Work in the context of *H. axyridis* as an invasive alien aims to identify what it is that makes *H. axyridis* especially well-adapted to this role and to examine the ecological or evolutionary changes that occur to the invader or to other organisms as a consequence of invasion. In this context, the trophic relationships of *H. axyridis*, and their underlying chemistry, are particularly important. Because of its extremely generalist feeding habits, the way in which *H. axyridis* forages and processes its food may, in some ways, differ from that of other more strictly aphidophagous coccinellids, but further comparative work is necessary in order to understand just how different *H. axyridis* is. Similarly, much more work is needed on how *H. axyridis* processes prey allelochemicals, especially those of aphids given its extremely broad aphid prey range. In the future, in the new areas it has colonised will *H. axyridis* better adapt to the allelochemicals of novel prey, notably ladybird intraguild prey alkaloids? Conversely do natural enemies adapt to *H. axyridis* defensive chemistry? Answering the latter question is hindered in part because although we know of the effects of ladybird alkaloids on generalist predators such as ants and birds, we know little about how they mediate relationships between ladybirds, their pathogens, parasites and parasitoids.

Last, but by no means least, is the potential for management of *H. axyridis* using chemicals, particularly during the autumn aggregation period. For example, the use of baits within traps is a new development with great potential for implementation if adults are, in fact, drawn into traps via olfactory responses to honey or pollen (see Wang et al. 2011). A low dose of an insecticide added to the honey or pollen-based baits could kill *H. axyridis* when they consume the bait. It is very important that experiments move out from the lab to the field, as has been done for other ladybirds (e.g. James 2005). More research into developing and testing traps to collect *H. axyridis* as they aggregate on houses or within grape clusters in vineyards is required. This needs to be integrated with studies closely monitoring the autumn migration of *H. axyridis* and ultimately aiming to predict the time that adults will potentially arrive in vineyards (Galvan et al. 2009) and in houses, so that timing of trap use can be optimised.

It is particularly important in the future to further integrate pure and applied strands of research. Studies of sexual and other pheromonal chemistry, of chemical defence and of prey infochemicals provide not only useful self-standing information with which to understand the ecology of *H. axyridis* as a ladybird and an invader, they may also ultimately provide important insights into the chemical management, mitigation and control of invasive alien populations of this species.

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Author Biographies

John J. Sloggett has worked on ladybird chemical ecology for over a decade, as part of wider studies on specialisation in the Coccinellidae.

Alexandra Magro and **Jean-Louis Hemptinne** are carrying out research on the evolution of life history traits and chemical ecology of ladybirds.

François J. Verheggen is interested in the role of semiochemicals in insect–insect and insect–plant interactions, with special emphasis on natural enemies.

William D. Hutchison and students have developed an IPM program for *H. axyridis* as a pest of wine grapes based on an experienced taste panel's ability to detect small concentrations of 'ladybug taint'.

Eric W. Riddick work has examined the use of chemical repellents, attractants, and pheromones to curb *H. axyridis* invasions in autumn.