

Predation of ladybird beetles by the orb-web spider *Araneus diadematus*

John J. Sloggett

Received: 16 November 2009 / Accepted: 6 May 2010
© International Organization for Biological Control (IOBC) 2010

Abstract Ladybirds face a diversity of potential predators from which their main protection is powerful alkaloid-based chemical defence. In the laboratory, adults of the European orb-web spider *Araneus diadematus* Clerck readily consumed the native European ladybird *Coccinella septempunctata* L. and non-melanics and melanics of the exotic *Harmonia axyridis* (Pallas). The spider was little deterred by their defensive chemistry and apparently suffered no ill effects after eating ladybirds. This is particularly notable for *H. axyridis*, which possesses a novel alkaloid not known from European ladybirds and to which European predators are not expected to be adapted. Examination of inhabited *A. diadematus* webs and experimental determination of for how long captured ladybirds remained in webs indicated that $\leq 2\%$ of spiders consume a ladybird each day. Ladybirds and *A. diadematus* are probably complementary rather than antagonistic in controlling crop pests, with ladybirds being at greatest risk from *A. diadematus* predation in autumn, during migration to overwintering sites.

Keywords Araneidae · Aphid biocontrol · Chemical defence · Coccinellidae · Enemy release hypothesis · Predation

Introduction

Ladybird beetles (Coleoptera: Coccinellidae) are attacked and eaten by a diversity of predators including birds, ants, spiders and, in the case of aphidophagous ladybirds, other specialist aphid consumers, including other ladybirds (Majerus 1994; Ceryngier and Hodek 1996; Lucas 2005). Within each predatory group the strength of the interaction with ladybirds depends on both the species of predator and potential ladybird prey involved (e.g. Nentwig 1983; Majerus 1994; Sloggett and Majerus 2000; Yasuda et al. 2004). One mechanistic explanation for this variation lies with the chemical defences of ladybirds, which are comprised of autogenously produced alkaloids along with pyrazines and, rarely, sequestered compounds (Daloze et al. 1995; King and Meinwald 1996); the alkaloids of ladybirds are particularly taxonomically variable (Daloze et al. 1995; Sloggett et al. 2009a). Interspecific variability in individual predator–prey interactions can result from differential toxicity or repellency of alternative chemical defences (e.g. Marples 1993a, b) and because some predators are adapted to resist the defensive chemicals of certain ladybirds (Sloggett et al. 2009b; Sloggett and Davis 2010).

Handling Editor: Patrick De Clercq

J. J. Sloggett (✉)
Tussen Beide Markten 45, 9712 CC Groningen,
The Netherlands
e-mail: johnsloggett@yahoo.co.uk

For some predator groups, we also have at least a partial idea of how the ecological context and interspecific ecological variation can ultimately explain the varying strengths of predator–prey interaction observed (e.g. Majerus and Majerus 1997; Sloggett et al. 1999; Lucas 2005). However, for other types of predator we lack this interpretive framework, in many cases because observations and/or experiments on predation of ladybirds are too sparse to allow any such inferences to be made (e.g. Majerus 1994; Ceryngier and Hodek 1996). There have been a number of studies of spider–ladybird interactions: it is evident that spiders are sometimes deterred from eating ladybirds and that this deterrence varies with both predator and prey taxon (Nentwig 1983, 1986; Young 1989; Yasuda and Kimura 2001). However, the rationale underlying this interspecific variation remains poorly understood. In the biological control of aphids, spiders can potentially complement more specialised predators such as ladybirds, but spider predation can also be detrimental if it is intense (Sunderland 1999). Conversely, spider interactions with pest phytophagous ladybird species might potentially reduce their damaging effects (Hlivko and Rypstra 2003; Beyene et al. 2007). The ecological complexity of the spider–ladybird interaction and its variable effects on biological control make further studies of spider interactions with ladybirds particularly desirable.

In this paper, the garden cross spider, *Araneus diadematus* Clerck (Araneae: Araneidae), is considered as a potential predator of ladybirds. This orb-web spider is a large species that is native to Europe and introduced to North America (Roberts 1995; Dondale et al. 2003). It occurs in tree- and shrub-dominated habitats, which provide the most suitable sites for construction of its webs (Hänggi et al. 1995). The spider has an annual or, in northerly regions, biennial life cycle (Johannesen and Toft 2002). Adulthood is reached in late summer or autumn and after oviposition in the autumn the adults die; the spiderlings hatch the following spring (Vanuytven 2005). *Araneus diadematus* is polyphagous: Ludy (2007) found that in crop field margins, it consumed primarily Diptera, but also Heteroptera, Hymenoptera and Coleoptera and crop pests such as Sternorrhyncha, which include aphids. This spider was chosen for this study for two reasons. First, it had been recorded feeding on ladybirds, but there was also an

observation of it being repelled by a ladybird caught in a web (Majerus 1994). These observations suggested that interactions with ladybirds do occur in nature. Second, it is common, including in agricultural habitats such as field margins. This increases its potential importance as an enemy of ladybirds, and also makes it easily observed and collected. In this study laboratory feeding experiments on *A. diadematus* with ladybird prey are combined with a field study on ladybirds in *A. diadematus* webs to deduce natural predation levels by this spider.

Materials and methods

Laboratory study of prey acceptability and suitability

Spiders

Adult *A. diadematus* were collected for laboratory experiments in the city of Groningen, The Netherlands (53°13'N, 6°33'E) in October. The spiders were housed individually in 250 ml clear plastic cups, with the mouth of the cup covered with netting material held in place with a rubber band (Sloggett *in press*). Although a larger area is required to allow the spiders to build proper webs (Zschokke and Herberstein 2005), this accommodation proved satisfactory. Spiders built rudimentary webs within the cups and exhibited no obvious signs of agitation, remaining immobile most of time. Prior to experiments spiders were provided with small house cricket nymphs, *Acheta domesticus* (L.), as food. They were sprayed with water every two days. They were maintained under ambient laboratory conditions (temperature 20–22.5°C, approx 14 h light per day).

Prey

There were four live prey feeding treatments: (1) a house cricket nymph, serving as a non-chemically defended control; (2) an adult of the native European ladybird *Coccinella septempunctata* L.; (3) a non-melanic adult of the exotic invasive ladybird *Harmonia axyridis* (Pallas), and (4) a melanic adult of *H. axyridis*. House cricket nymphs were approximately the same size as the ladybirds in the other treatments. Like the spiders, all ladybirds were

collected in Groningen. *Coccinella septempunctata* was chosen for testing as the commonest native ladybird in Groningen. *Harmonia axyridis*, which originates in Asia, has now colonised Europe, Africa and America (Koch et al. 2006; Stals and Prinsloo 2007; Brown et al. 2008). It is now the dominant ladybird species in Groningen, as in many of the new regions that it now occupies. In its native and introduced ranges, *H. axyridis* is unpalatable and poisonous to intraguild predators, such as other ladybirds and chrysopids (e.g. Phoofolo and Obrycki 1998; Yasuda and Ohnuma 1999; Cottrell 2004) and its larvae are avoided by the Japanese spider *Misumenops tricuspidatus* (Fabricius) (Yasuda and Kimura 2001). *Harmonia axyridis* was chosen for this study to test the possibility that it benefits from enemy release (Colautti et al. 2004) from *A. diadematus* in its European range i.e. that the spider is unable to exploit this prey, or suffers a cost when it does so, due to the novel chemical defence that *H. axyridis* possesses. Non-melanic and melanic *H. axyridis* were given as different treatments as it has been suggested that non-melanics may have higher levels of harmonine alkaloid chemical defence than melanics, making them better defended (Bezzerides et al. 2007). Thus a further aim of the study was to test whether non-melanic *H. axyridis* were better defended against *A. diadematus* than melanics.

Experimental procedure

Experimentation began 4–8 days after spiders were collected. At the start of the experiment the prey item (live ladybird or cricket) was introduced into the cup with the spider. Prey were left with the spiders for two days, after which all prey that remained uncaptured were removed. Spiders were checked every 12 h and any prey captured by the spiders (i.e. wrapped in silk) recorded. Preliminary experiments with spiders in the field indicated that spiders often did not feed on prey immediately after capture, even when the prey was palatable. Thus captured prey was left with a spider for a further two days after capture was recorded, and then removed and the remains examined for signs of feeding. *Araneus diadematus* can be starved for long periods of time (Vollrath and Samu 1997) and even under standard laboratory conditions only need to be fed 1–2 times a week

(Zschokke and Herberstein 2005). It is therefore unlikely that the experimental time period with no access to other prey would make spiders sufficiently hungry to consume ladybirds if they were disfavoured as prey.

On the basis of these observations prey were divided into three groups: uncaptured prey, captured prey that were not eaten and eaten prey. Captured prey that were not eaten included prey of which a small part had been eaten. By contrast the soft parts of prey scored as eaten were entirely consumed. After prey had been examined, spiders that had eaten prey were returned to a cricket diet for a further week and monitored for mortality or other evidence of prey toxicity.

Trials were matched, with equal numbers of all four treatments being tested at the same time on spiders that had been in the laboratory for the same period of time. In total 39 matched replicates were tested (i.e. a total of 156 spiders).

Spider predation of ladybirds in the field

Between 16th October and 30th October 2007 and 12th October and 21st October 2009, inhabited *A. diadematus* webs in Groningen were examined for the presence of ladybird cadavers. The majority of webs examined were in shrubs and bushes and on buildings. At this time, ladybirds, mainly *H. axyridis* and *C. septempunctata*, were observed dispersing to overwintering sites, which included many of the habitats where *A. diadematus* webs were examined.

If ladybird cadavers remain in spiders' webs for long periods of time, this can result in an overestimate of the extent of spider predation. To deduce for how long ladybirds were likely to remain in *A. diadematus* webs, ten non-melanic *H. axyridis* were killed by freezing. They were introduced, one per web, into ten inhabited *A. diadematus* webs, in close proximity to the spider occupant, on 14th October 2009. The webs used were in a privet hedge (*Ligustrum ovalifolium* Hasskarl) around a small municipal garden. Ladybirds were also aggregating there to overwinter. The ten *A. diadematus* webs into which the ladybirds had been introduced were examined 5 h later and then daily, at the same time as the ladybirds were introduced, until no cadavers remained in the webs.

Results

Laboratory study of prey acceptability and suitability

Results of the laboratory feeding experiment are shown in Fig. 1. Crickets were generally consumed completely, except sometimes for the legs. Spiders never ate the hard parts of ladybirds (head, pronotum, elytra, abdominal cuticle), but consumed the soft interior of the abdomen. In cases where prey were classified as caught but not eaten, at least a part of the prey had always been consumed. In many cases spiders were observed eating ladybirds in the same 12 h period in which they were captured.

Across all treatments there was no heterogeneity when caught (eaten and uneaten) and uncaught prey were compared ($\chi^2 = 5.31$, 3 d.f., $0.1 < P < 0.2$), or when eaten and uneaten (caught uneaten and uncaught) prey were compared ($\chi^2 = 6.26$, 3 d.f., $P = 0.1$). An independent 2×2 test on even the most extreme data (crickets vs. *C. septempunctata*), was only significant if eaten and uneaten data was compared, and then at the lowest level ($\chi^2 = 4.88$, 1 d.f., $0.02 < P < 0.05$).

Data for the two forms of *H. axyridis* clearly did not differ, nor did *H. axyridis* differ from any of the other treatments, even when data for the non-melanics and melanics were grouped together and tested against each other data set individually (caught/uncaught—vs. crickets $\chi^2 = 0.55$, vs. *C. septempunctata* $\chi^2 = 1.84$;

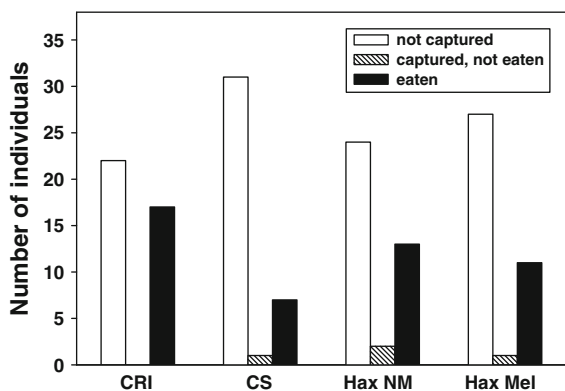


Fig. 1 Results of laboratory feeding experiments with live prey. CRI, crickets; CS, *C. septempunctata*; Hax NM, non-melanics *H. axyridis*; Hax Mel, melanics *H. axyridis*. $n = 39$ matched replicates

eaten/uneaten—vs. crickets $\chi^2 = 1.36$, vs. *C. septempunctata* $\chi^2 = 1.59$, all tests 1 d.f., for all $P > 0.15$).

None of the spiders classed as having eaten prey died in the week following prey consumption. Spiders that had consumed ladybirds appeared to behave normally and continued to feed during this period.

Spider predation of ladybirds in the field

In 2007, three (2.1%) of 146 webs examined contained ladybirds, of which two (1.4%) were *C. septempunctata* and one (0.7%) was a non-melanics *H. axyridis*. In 2009 only one (0.9%) of 110 webs examined contained a ladybird. This was also a non-melanics *H. axyridis*. In 2009 an unoccupied web was also observed containing a single elytron of a melanics *H. axyridis*, presumably eaten earlier by the then occupant.

The decline in the number of *H. axyridis* cadavers remaining in *A. diadematus* webs after artificial introduction is shown in Fig. 2. All ten of the ladybirds were wrapped in silk by spiders on being placed in the web. After 5 h all cadavers were still in the web. At this time spiders in all ten webs were observed feeding on them. By the following day most cadavers had disappeared, although a few remained, still being eaten by the spiders. The day after they had all disappeared. Based on these observations, spiders begin to feed on ladybirds within maximally 5 h of

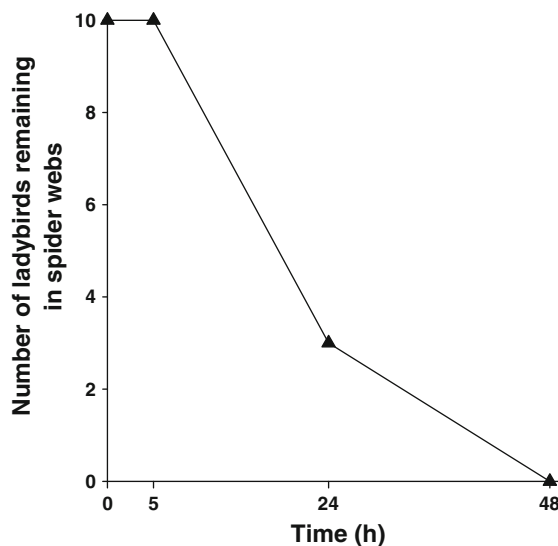


Fig. 2 Number of *H. axyridis* cadavers remaining in *A. diadematus* webs over time after artificial introduction (initial $n = 10$, one per web)

capture in the field, and, when they finish the remains are discarded from the web, in most cases within 24 h. Thus, measures of numbers of ladybirds in webs provide a good approximation to the proportion of spiders eating ladybirds on each day.

Discussion

Spiders may react in a number of different ways to potentially toxic prey: prey may be avoided or discarded after attack; spiders can acquire an aversion to prey, and in a few cases prey that are not avoided can subsequently prove toxic (Toft 1999). In the case of *A. diadematus*, the overall effects of ladybird chemical defences on the spider appear to be very weak. Although in all ladybird treatments fewer prey were both caught and completely eaten than in the cricket treatment, the differences observed between ladybird and cricket treatments were quantitatively very small. Using independent $2 \times 2 \chi^2$ tests only one cricket-ladybird comparison (prey eaten/uneaten, against *C. septempunctata*) was statistically significant, and even this significance disappears if the correct multiple-comparison procedure is used, in spite of a relatively large sample size. No spiders that ate ladybirds died or appeared to suffer any discomfort. It is unlikely that a decline in alkaloid content after prey capture or death but before consumption can explain the apparent tolerance of *A. diadematus* for ladybirds. The beetles retain their distasteful properties for some days after death, at least to humans (J.J. Sloggett pers. obs.), and times from ladybird capture to consumption were generally relatively short, both in the laboratory (where spiders were often observed to capture and eat ladybirds in the same 12 h time period) and most notably in the field (where all ten spiders were observed eating *H. axyridis* prey after 5 h). It remains possible that with a sufficiently high level of ladybird dietary content *A. diadematus* could exhibit an acquired aversion to ladybirds. However, this is unlikely because of the low level of natural ladybird predation by *A. diadematus*, particularly given the short persistence of acquired aversions to particular toxic prey in spiders (Toft 1999).

The finding that *A. diadematus* is largely unaffected by ladybird chemical defences is particularly

noteworthy for *H. axyridis* prey. The alkaloids of *H. axyridis* are harmonine and 3-hydroxypiperidin-2-one (Alam et al. 2002). The latter alkaloid is unknown from native ladybirds in the new regions colonised by *H. axyridis*. This is especially notable for Europe, where the alkaloids of native species have been intensively studied (Pasteels et al. 1973; Tursch et al. 1975; Daloze et al. 1995; Laurent et al. 2005). European predators are consequently not expected to be adapted to countering the deleterious effects of 3-hydroxypiperidin-2-one, which appear to be severe (Stocks and Lindsey 2008). Other studies have shown that predators are generally vulnerable to novel prey defensive chemistry when either the prey (Phillips et al. 2003; Suttle and Hoddle 2006) or the predator (Sloggett et al. 2009b) is an exotic. Most notably, significant mortality, attributed to prey chemical defence, was observed in native French Polynesian spiders after consumption of an invasive cicadellid (Suttle and Hoddle 2006). No such toxic effects, or strong effects on prey capture or consumption, are evident for *A. diadematus* preying on *H. axyridis*. Even the abdomen of a ladybird is a substantial meal for the spider and, was it to be toxic, it is likely that some effect would be evident after consumption. Consequently, the exotic ladybird does not appear to obtain enemy release from the spider by virtue of its novel chemical defences. As the spider is little deterred by *H. axyridis* chemistry in general, the comparison of non-melanic and melanic ladybirds throws little light on any potential differences in their chemical defence levels.

There are probably two components that render *A. diadematus* an effective predator of ladybirds. The first is related to prey capture: as with other prey, on catching ladybirds *A. diadematus* wrap them in silk. This behaviour has been suggested as providing orb-web spiders with protection against prey defensive secretions (Eisner and Dean 1976) and in the case of ladybird prey might allow the spiders to avoid being smeared with ladybird defensive secretions, which in addition to being repellent are sticky and difficult to remove. The second component is that which allows *A. diadematus* to readily eat ladybirds without apparently suffering any form of cost. The most likely explanation for this is that *A. diadematus* possesses strong toxin-resistance. This is probably capable of countering a broad spectrum of defensive chemicals, as it is effective against the chemical

defences of occasional prey such as ladybirds and even against wholly novel chemical defences, such as the 3-hydroxypiperidin-2-one of *H. axyridis*. Although resistance to prey chemical defences is unstudied in *A. diadematus*, such broad spectrum chemical resistance would be of considerable value to the polyphagous spider in dealing with the wide variety of insect prey that it consumes, much of which must be defended chemically.

In spite of *A. diadematus*' undoubted ability to catch and consume ladybirds, the spider does not consume a large number of them. In 2007, about 2% of *A. diadematus* webs contained ladybirds, while in 2009 it was less than 1%. Potentially ladybird cadavers could remain in spiders' webs for long periods of time (e.g. Majerus 1994). However, this study showed that at least for inhabited *A. diadematus* webs, this is not the case and ladybirds typically remained in the web for less than 24 h. Instantaneous counts of ladybirds in webs thus provide an accurate measure of the proportion of spiders preying on ladybirds each day. The low level of ladybird predation by *A. diadematus* probably arises because ladybirds move around plants more often by walking than flying, and thus infrequently become ensnared in webs. Behavioural avoidance of webs is also a possibility, as may be the case in the phytophagous ladybird *Epilachna varivestis* (Mulsant) (Hlivko and Rypstra 2003). Based on a daily proportion of 1–2% of *A. diadematus* preying on ladybirds, and even taking into account that smaller juvenile spiders would catch less ladybird prey than the adults studied here, a substantial proportion of *A. diadematus* would eat at least one ladybird during their lives. Given the overriding numerical dominance of ladybirds over the spider, this would not result in a very high level of ladybird mortality, however.

In crops, it is most likely that ladybirds and *A. diadematus* would exhibit complementary rather than antagonistic pest biocontrol effects. The occurrence of *A. diadematus* webs in crops or their near vicinity may reduce initial colonisation of crops by dispersive aphid morphs as well as protecting crops against other pests, while aphidophagous ladybirds will reduce aphids after they have colonised crops. Predation of ladybirds by *A. diadematus* in field crops, at least, is likely to be limited, because *A. diadematus* is more likely to reside in the near vicinity of crop fields, for example in field margins,

rather than in crops themselves. Additionally, at peak aphid densities, in spring and early summer, the spider is a smaller juvenile, making capture of ladybirds more difficult, although not excluding predation of smaller ladybird larvae. A more significant overall risk to ladybirds from the spider is likely to occur in the autumn during migration to overwintering sites. Ladybirds are more likely to encounter spiders in the more densely-vegetated overwintering habitats, as observed in this study, and in many cases at this time the spiders will be the larger adults.

It is not clear to what extent these results can be extended to other orb-web spiders. Majerus (1994) reports other araneid species eating ladybirds. However Nentwig (1983) found that *Zygiella x-notata* Clerck rejected unidentified coccinellid prey. Although ladybird alkaloids are more likely to confer strong protection against generalist predators than highly specialised natural enemies such as parasitoids and parasites, this study serves to emphasise that not all generalist predators are deterred by ladybird chemical defences. Consequently, overall losses to generalist predators could be much higher than is often supposed, especially amongst adult ladybirds, which have fewer other enemies than the immature stages. In addition to spiders, such predators could include certain types of bird, such as those that feed on the wing, insectivorous ants and beetles, and omnivores such as earwigs, which although unlikely to consume adults, may consume ladybird eggs (Majerus 1994, 1998; Majerus and Majerus 1997; Sloggett et al. 1999; Sloggett in press). Although individually their effects are likely to be outweighed by those of particular ladybird parasitoids, parasites or pathogens, the total combined effect of generalist predators on ladybird populations could still be substantial. Further studies like this one, combining laboratory and field elements, should be carried out to deduce to what extent this is actually the case.

Acknowledgements I thank Ilja Zeilstra and two anonymous referees for reading and commenting on this manuscript.

References

- Alam N, Choi IS, Song K-S, Hong J, Lee CO, Jung JH (2002) A new alkaloid from two coccinellid beetles *Harmonia axyridis* and *Aiolocaria hexaspilota*. Bull Korean Chem Soc 23:497–499

- Beyene Y, Hofsvang T, Azerefege F (2007) Population dynamics of tef epilachna (*Chnootriba similis* Thunberg) (Coleoptera, Coccinellidae) in Ethiopia. *Crop Prot* 26:1634–1643
- Bezzerides AL, McGraw KJ, Parker RS, Husseini J (2007) Elytra color as a signal of chemical defense in the Asian ladybird beetle *Harmonia axyridis*. *Behav Ecol Sociobiol* 61:1401–1408
- Brown PMJ, Adriaens T, Bathon H, Cuppen J, Goldarazena A, Hägg T, Kenis M, Klausnitzer BEM, Kovár I, Loomans AJM, Majerus MEN, Nedved O, Pedersen J, Rabitsch W, Roy HE, Ternois V, Zakharov IA, Roy DB (2008) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *BioControl* 53:5–21
- Ceryngier P, Hodek I (1996) Enemies of Coccinellidae. In: Hodek I, Honěk A (eds) *Ecology of Coccinellidae*. Kluwer, Dordrecht, pp 319–350
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecol Lett* 7:721–733
- Cottrell TE (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biol Control* 31:362–371
- Daloze D, Braekman J-C, Pasteels JM (1995) Ladybird defence alkaloids: structural, chemotaxonomic and biosynthetic aspects (Col.: Coccinellidae). *Chemoecology* 5/6:173–183
- Dondale CD, Redner JH, Paquin P, Levi HW (2003) The insects and arachnids of Canada. Part 23. The orb-weaving spiders of Canada and Alaska (Araneae: Uloboridae, Tetragnathidae, Araneidae, Theridiosomatidae). NRC Research Press, Ottawa
- Eisner T, Dean J (1976) Ploy and counterploy in predator–prey interactions: orb-weaving spiders versus bombardier beetles. *Proc Natl Acad Sci USA* 73:1365–1367
- Hänggi A, Stöckli E, Nentwig W (1995) Lebensräume Mitteleuropäischer Spinnen: Charakterisierung der Lebensräume der häufigsten Spinnenarten Mitteleuropas und der mit diesen vergesellschafteten Arten (Miscellanea Faunistica Helvetiae 4). Centre Suisse de Cartographie de la Faune, Neuchâtel
- Hlivko JT, Rypstra AL (2003) Spiders reduce herbivory: nonlethal effects of spiders on the consumption of soybean leaves by beetle pests. *Ann Entomol Soc Am* 96:914–919
- Johannsen J, Toft S (2002) A test for reproductive separation of alternate generations in a biennial spider, *Araneus diadematus* (Araneae, Araneidae). *J Arachnol* 30:65–69
- King AG, Meinwald J (1996) Review of the defensive chemistry of coccinellids. *Chem Rev* 96:1105–1122
- Koch RL, Venette RC, Hutchison WD (2006) Invasions by *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in the Western Hemisphere: implications for South America. *Neotrop Entomol* 35:421–434
- Laurent P, Braekman J-C, Daloze D (2005) Insect chemical defense. In: Schulz S (ed) *The chemistry of pheromones and other semiochemicals II*. Topics Curr Chem 240: 167–229
- Lucas É (2005) Intraguild predation among aphidophagous predators. *Eur J Entomol* 102:351–363
- Ludy C (2007) Prey selection of orb-web spiders (Araneidae) on field margins. *Agric Ecosyst Environ* 119:368–372
- Majerus MEN (1994) *Ladybirds (new naturalist series)*. HarperCollins, London
- Majerus MEN (1998) Predation of ladybirds (Coccinellidae) by other beetles. *Entomol Rec J Var* 110:27–30
- Majerus MEN, Majerus TMO (1997) Predation of ladybirds by birds in the wild. *Entomol Mon Mag* 133:55–61
- Marples NM (1993a) Is the alkaloid in 2spot ladybirds (*Adalia bipunctata*) a defence against ant predation? *Chemoecology* 4:29–32
- Marples NM (1993b) Toxicity assays of ladybirds using natural predators. *Chemoecology* 4:33–38
- Nentwig W (1983) The prey of web-building spiders compared with feeding experiments (Araneae: Araneidae, Linyphiidae, Pholcidae, Agelenidae). *Oecologia* 56:132–139
- Nentwig W (1986) Non-webbuilding spiders: prey specialists or generalists? *Oecologia* 69:571–576
- Pasteels JM, Deroe C, Tursch B, Braekman JC, Daloze D, Hootele C (1973) Distribution et activités des alcaloïdes défensifs des Coccinellidae. *J Insect Physiol* 19:1771–1784
- Phillips BL, Brown GP, Shine R (2003) Assessing the potential impact of cane toads on Australian snakes. *Conserv Biol* 17:1738–1747
- Phoofolo MW, Obrycki JJ (1998) Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomol Exp Appl* 89:47–55
- Roberts MJ (1995) *Spiders of Britain and northern Europe (Collins field guide)*. HarperCollins, London
- Sloggett JJ (in press) Colour pattern polymorphism and chemical defence in *Harmonia axyridis*. In: Babendreier D, Aebi A, Kenis M, Roy HE (eds) Study group “Benefits and risks of exotic biological control agents” at Engelberg (Switzerland), 6–10 September 2009. IOBC/WPRS Bull
- Sloggett JJ, Davis AJ (2010) Eating chemically defended prey: alkaloid metabolism in an invasive ladybird predator of other ladybirds (Coleoptera: Coccinellidae). *J Exp Biol* 213:237–241
- Sloggett JJ, Majerus MEN (2000) Aphid-mediated coexistence of ladybirds (Coleoptera: Coccinellidae) and the wood ant *Formica rufa*: seasonal effects, interspecific variability and the evolution of a coccinellid myrmecophile. *Oikos* 89:345–359
- Sloggett JJ, Manica A, Day MJ, Majerus MEN (1999) Predation of ladybirds (Coleoptera: Coccinellidae) by wood ants, *Formica rufa* L. (Hymenoptera: Formicidae). *Entomol Gaz* 50:217–221
- Sloggett JJ, Obrycki JJ, Haynes KF (2009a) Identification and quantification of predation: novel use of gas chromatography-mass spectrometric analysis of prey alkaloid markers. *Funct Ecol* 23:416–426
- Sloggett JJ, Haynes KF, Obrycki JJ (2009b) Hidden costs to an invasive intraguild predator from chemically defended native prey. *Oikos* 118:1396–1404
- Stals R, Prinsloo G (2007) Discovery of an alien invasive, predatory insect in South Africa: the multicoloured Asian ladybird beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *S Afr J Sci* 103:123–126
- Stocks IC, Lindsey DE (2008) Acute corrosion of the oral mucosa in a dog due to ingestion of multicoloured Asian lady beetles (*Harmonia axyridis*: Coccinellidae). *Toxicol* 52:389–391

- Sunderland K (1999) Mechanisms underlying the effects of spiders on pest populations. *J Arachnol* 27:308–316
- Suttle KB, Hoddle MS (2006) Engineering enemy-free space: an invasive pest that kills its predators. *Biol Invasions* 8:639–649
- Toft S (1999) Prey choice and spider fitness. *J Arachnol* 27:301–307
- Tursch B, Daloze D, Braekman JC, Hootele C, Pasteels JM (1975) Chemical ecology of arthropods-X. The structure of myrrhine and the biosynthesis of coccinelline. *Tetrahedron* 31:1541–1543
- Vanuytven H (2005) Spinnen—Leven op acht poten. Spinnen van België en Nederland onder de loep, Panaman, Antwerp
- Vollrath F, Samu F (1997) The effect of starvation on the web geometry of an orb weaving spider. *Bull Br Arachnol Soc* 10:295–298
- Yasuda H, Kimura T (2001) Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Entomol Exp Appl* 98:17–25
- Yasuda H, Ohnuma N (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomol Exp Appl* 93:63–67
- Yasuda H, Evans EW, Kajita Y, Urakawa K, Takizawa T (2004) Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia* 141:722–731
- Young OP (1989) Interactions between the predators *Phidippus audax* (Araneae: Salticidae) and *Hippodamia convergens* (Coleoptera: Coccinellidae) in cotton and in the laboratory. *Entomol News* 100:43–47
- Zschokke S, Herberstein ME (2005) Laboratory methods for maintaining and studying web-building spiders. *J Arachnol* 33:205–213

Author Biography

John J. Sloggett has been working with ladybirds for 16 years, in Britain, Germany, USA and the Netherlands, since studying for a Ph.D. under Dr. Mike Majerus in the 1990s. His interests include the evolution of habitat and dietary breadth, chemical defence and invasive species. This work is part of a wider study examining the role that predator and prey chemical defences play in the biology of invasive predators, most notably the ladybird *Harmonia axyridis*.