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REVIEW

Diet and chemical defence in ladybird beetles (Coleoptera: Coccinellidae)*

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Abstract. In this paper, I review the effects of the diet of ladybirds on chemical defence in this group of beetles. The tendency to reflex bleed and the diversity of autogenously produced alkaloids in different taxa may be evolutionarily related to diet and the likelihood of food limitation. Within predatory species, both prey quantity and quality have been shown to affect autogenous alkaloid production. A few ladybird predators have been suggested to adaptively sequester toxins from their prey for their own defence. However, in most cases the evidence for this is limited, with questions remaining about the costs of accumulated toxins and their defensive value, especially over and above pre-existing autogenous defence. Only a single case (*Hyperaspis trifurcata* and carminic acid) is well supported. In the case of ladybird predators acquiring pyrrolizidine alkaloids from the ragwort aphid *Aphis jacobaeae*, I show that toxin accumulation is not very costly and the aphid is even an essential prey for some ladybirds. However, the defensive value of pyrrolizidine alkaloids to ladybirds is still not investigated. Intraspecific diversity in autogenous chemical defence could be reinforced further if chemical protection is conferred via sequestered chemicals. However, to understand better how ladybird diet and chemical defence interact, we need a clearer grasp of how the defensive chemicals of food are resisted or tolerated by ladybirds.

INTRODUCTION

One of the significant achievements of Ivo Hodek, to whom this paper is dedicated, was his contribution to our understanding of ladybird beetle diets. His work developed into a categorisation of prey for insects as essential (supporting development and oviposition), alternative (maintaining survival), toxic and rejected prey (Hodek, 1962, 1967, 1973, 1996). As a student doing an undergraduate research project on ladybird diets, I well remember reading *Biology of Coccinellidae* (Hodek, 1973) and my surprise at finding that aphids were not all the same, but in fact varied in their palatability and suitability as food and that this in its turn varied across ladybird species. I knew that this was the case for plants and insect herbivores, as any budding entomologist who had kept caterpillars would, but the idea that this was also true for insect prey and their predators was new. Today, we talk about essential and alternative prey less than we used to, as new ideas and further refinements have come to the fore (Hodek & Evans, 2012), but the concepts remain a valuable way of understanding the relationship between ladybirds and their food.

Hodek's categorisation of prey focuses on their effect on predator life history, notably reproduction, development and survival; it also concentrates on the chemical and nutritional characteristics of prey over other factors, such as prey density, size or behaviour, which may also affect their suitability to predators in the field (Hodek & Evans, 2012). Researchers on ladybirds often extend Hodek's concepts to compare different prey against each other in their effects on ladybird fecundity, development and mortality, and studies have also measured related traits especially weight, but also size and fat content (e.g., Blackman, 1965; El-Hariri, 1966; Richards & Evans, 1998; Ware et al., 2009; Ungerová et al., 2010; Rounagh-Ardakani et al., 2020). There are of course other traits largely unrelated to life history that are potentially linked to insect diet, as well. In ladybirds, one such trait is their chemical defence. The adults and larvae of ladybirds, and sometimes the pupae, are able to secrete distasteful or toxic haemolymph by a process called reflex bleeding (e.g., Happ & Eisner, 1961; Kendall, 1971; Majerus, 2016). These secretions are laced with defensive chemicals, which are found in all life history stages of ladybirds, including eggs (Tursch et al., 1975; Daloze et al., 1994). The chemicals are predominantly autogenously produced alkaloids, as well as pyrazines that provide a warning odour (Moore et al., 1990; Daloze et

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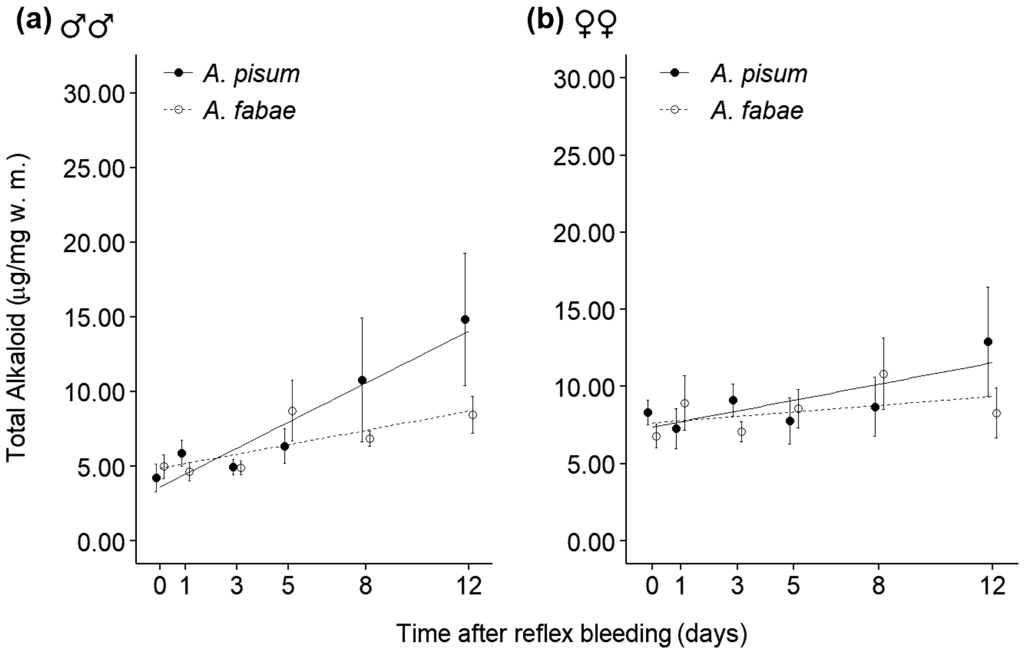

Fig. 1. Recovery in alkaloid concentration after reflex bleeding (measured as mass per unit wet body mass) in adult *Adalia bipunctata* (a) males and (b) females on two different aphid diets: a good quality diet (*Acyrthosiphon pisum*) and a poorer diet (*Aphis fabae*). Ladybirds were reflex bled on Day 0 and individuals frozen after reflex bleeding, on Day 0, or later, after 1, 3, 5, 8 or 12 days. Bodily alkaloid concentration was subsequently estimated using a gas-chromatograpic technique. Recovery on the *A. pisum* diet was more rapid. Alkaloid levels in males rose more quickly, likely because they do not invest a substantial proportion of the alkaloid they synthesise in eggs. From Oudendijk & Sloggett (2022).

al., 1994; King & Meinwald, 1996); however potentially other compounds might be used for defence (e.g., Frazer & Rothschild, 1960) including compounds obtained directly from food.

In this paper, I discuss the effects of ladybird diet on chemical defence. I begin by considering the effects of dietary variation on the autogenous alkaloid defences of ladybirds. I then revisit the idea that ladybirds might sequester compounds directly from food for their defence. The food of ladybirds could play a large role in qualitatively and quantitatively determining the nature of ladybird defensive chemistry. In considering that subject, this paper aims to provide a grounding for future researchers to build further on Ivo Hodek's legacy in the field of ladybird dietary studies.

EFFECT OF DIET ON AUTOGENOUS ALKALOID DEFENCES

Across the Coccinellidae, over evolutionary time, the diet of different ladybird taxa might have affected the range of alkaloid defences that they synthesise. Predatory ladybirds are often prey limited; by contrast, ladybird herbivores are less likely to be limited by their food. It is therefore interesting that members of the herbivorous subfamily Epilachninae have the most complex autogenous alkaloid defences, exhibiting a wider diversity of compounds per species that are also often ontogenetically variable (e.g., Proksch et al., 1993; Schroeder et al., 1998; Camarano et al., 2006). This high complexity could have arisen because epilachnine ladybirds are less food limited than predatory taxa (Sloggett, 1998; Majerus et al., 2007). There is also some evidence that herbivorous ladybirds reflex bleed more readily than aphidophagous species, suggesting that the costs may be less critical for the non-food limited herbivores, if indeed they are unconstrained by their food (Sloggett, 1998; Majerus et al., 2007).

Within species, diet does not appear to show a major effect on the mass of reflex blood produced by ladybirds (Lee et al., 2018), but food quantity or quality does place limitations on the synthesis of alkaloid. As part of a study linking chemical defence to aposematic colour, Blount et al. (2012) found that *Coccinella septempunctata* L. apparently synthesized less of the alkaloid free base precoccinelline, though not the corresponding N-oxide, coccinelline, when reared on a restricted aphid diet. More recently, Steele et al. (2020) showed that *Adalia bipunctata* (L.) reared on aphids provided every 2–3 days had lower levels of the alkaloid adaline than those reared on aphids provided daily. This effect was largely eliminated if the larvae were infected with a microsporidian, *Nosema adaliae* Steele & Bjørnson, because infection increased the amount of adaline in the less frequently fed larvae (Steele et al., 2020).

The work described above has focused on food quantity and on larval rearing conditions as a determinant for alkaloid in the resulting adults. In a recently published study, we have focused on the species of aphid prey (i.e. dietary quality) and on alkaloid synthesis in ladybird adults (Oudendijk & Sloggett, 2022). We used one of the best-known and -studied systems, the ladybird *Adalia bipunctata* and its prey *Acyrthosiphon pisum* (Harris) and *Aphis fabae* Scopoli, both reared on *Vicia faba* L. (broad bean). The former aphid is a high quality prey for *A. bipunctata* and the latter a low quality prey based on numerous other studies, largely of reproductive parameters (Hodek & Evans, 2012). In our study, after reflex bleeding, alkaloid levels in *A. pisum*-fed *A. bipunctata* increased more rapidly than those of conspecifics fed *A. fabae* (Oudendijk & Sloggett, 2022; Fig. 1). Interestingly, alkaloid increased in males (Fig. 1a) more rapidly than in females (Fig. 1b), likely because females also utilise alkaloid in eggs. The effect of diet on alkaloid investment in eggs appeared to be weak (Oudendijk & Sloggett, 2022), but might repay further investigation. Considered overall, the study suggests that alkaloid levels in adult ladybirds could be very dynamic, with differing prey species or other types of food playing an important role in this dynamism (Oudendijk & Sloggett, 2022).

SEQUESTERED CHEMICAL DEFENCE

Sequestered chemical defence in ladybirds has only been proposed in four studies (Table 1): in all cases they involve predatory species obtaining chemical compounds from prey, mostly aphids or scale insects, which in turn obtain them from their host plants. The ecology of defensive chemical sequestration, which has been best investigated in herbivorous insects, is undoubtedly very complex (Brown & Trigo, 1994), but a basic framework for further discussion of the ladybird examples is given here. At its most fundamental, the term "sequestration" means the accumulation of chemicals within an organism's body and only excludes material transiently passing through the gut (Duffey, 1980; Opitz & Müller, 2009). In the context of naturally produced chemicals, the term often comes associated with a presumption of some form of benefit, such as enhanced communication or defence (Duffey, 1980; Nishida, 2014). Possession of sequestered defensive chemicals might confer an ecological or physiological cost (but see Zvereva & Kozlov, 2016); however, the defensive benefit should be greater (e.g., Reudler et al., 2015; Züst et al., 2018).

Using this framework, there are three components that can be readily examined when looking at whether chemicals in ladybirds originating from food genuinely constitute adaptive sequestration of chemical defence. The first is whether the compound is truly sequestered, i.e. passes from the gut to the body. The second is whether sequestered chemicals confer a defensive advantage. This is of particular interest due to the autogenous alkaloids that ladybirds possess, perhaps rendering sequestered compounds excess to requirements. The third is whether the prey from which the compound is obtained is suitable food for the ladybird predator (i.e. that the physiological costs of predation are not too great). Studies of ladybird feeding (Hodek & Evans, 2012) can throw light on that.

The earliest proposed case of ladybird sequestration of chemical defences may fail the first test, because the compound may not be transferred to the body of the ladybird. Cardiac glycosides (cardenolides) from the prey aphid *Aphis nerii* Boyer de Fonscolombe from oleander were detected in *Coccinella undecimpunctata* L., possibly as a result of sequestration; however, the authors themselves stated that further work was needed to eliminate gut content as the source of the cardiac glycosides (Rothschild et al., 1973). Pupae of another ladybird, *Coccinella septempunctata*, feeding on *A. nerii* on the same hostplant did not contain cardiac glycosides (Rothschild et al., 1970). Clear evidence for sequestration of cardiac glycosides from *A. nerii* by ladybirds is thus wanting, although it is worthy of further investigation. *Aphis nerii* appears to be toxic to some ladybirds, but will support some development in others (Hodek & Evans, 2012).

A second doubtful case of adaptive sequestration of chemical defences involves the interaction between chemical accumulation and cost, the third criterion. *Harmonia axyridis* (Pallas) is an intraguild predator that consumes many other ladybird species with diverse alkaloid defences (e.g. Cottrell, 2007; Ware & Majerus, 2008; Sloggett et al., 2009a). Hautier et al. (2008) showed that adaline from *Adalia bipunctata* prey could be detected in the body of *H. axyridis* predators, including pupae and adults that had been fed *A. bipunctata* as larvae (up to 216h later): they thus suggested this as a case of sequestration of chemicals for defensive purposes. However, the situation is more complex than that. Alkaloids from intraguild prey certainly do enter the body from the gut in *H. axyridis* (Sloggett & Davis, 2010), fulfilling one criterion for defensive sequestration. However, adaline, which is apparently partially toxic to *H. axyridis* (Sato & Dixon, 2004), probably persists for a long time within its body because *H. axyridis* is not adapted to break it down metabolically: this

Table 1. Summary of proposed examples of sequestration of defensive chemicals by ladybirds from food (prey). In the case of herbivorous prey (aphids and scale insects), the chemicals originate in their host plant.

Ladybird species and life history stage	Chemicals	Prey	Prey hostplant	Reference
Coccinella undecimpunctata L. adults	Cardiac glycosides (cardenolides)	*Aphis nerii* Boyer de Fonscolombe (aphid)	*Nerium oleander* L. (oleander)	Rothschild et al., 1973
Coccinella septempunctata L. adults	Pyrrolizidine alkaloids	*Aphis jacobaeae* Schrank (aphid)	*Jacobaea vulgaris* Gaertner syn. *Senecio jacobaea* L. (ragwort) *Senecio inaequidens* de Candolle (South African ragwort)	Witte et al., 1990
Hyperaspis trifurcata Schaeffer larvae	Carminic acid	*Dactylopius confusus* (Cockerell) (coccid)	*Opuntia* sp. (cactus)	Eisner et al., 1994
Harmonia axyridis (Pallas) larvae, pupae, adults	Adaline and other ladybird alkaloids	*Adalia bipunctata* (L.) (ladybird) larvae	—	Hautier et al., 2008

is most likely due to a lack of a long coevolutionary history between the invasive *H. axyridis* and *Adalia* species (Sloggett & Davis, 2010). Unlike adaline, prey ladybird alkaloids with which *H. axyridis* has apparently coexisted for longer are lost within tens of hours, probably due to metabolic breakdown (Sloggett et al., 2009b; Sloggett & Davis, 2010). Adaline is also lost over time (Hautier et al., 2008; Sloggett & Davis, 2010), but its much slower loss compared to other alkaloids appears to be a side effect of toxicity, or at least metabolic incompatibility rather than an adaptation of *H. axyridis* for defence.

In contrast to these two examples, acquisition of repellent carminic acid by larvae of the ladybird *Hyperaspis trifurcata* Schaeffer from cochineal scale insect prey (*Dactylopius confusus* (Cockerell)) does appear to constitute adaptive sequestration of chemical defence (Eisner et al., 1994). Carminic acid is red, making it easy to trace in the bodies of predators: in *H. trifurcata* larvae fed *D. confusus*, it was visible in the reflex blood, so it is clearly transferred from the gut to the haemolymph of the larva (Eisner et al., 1994). *Hyperaspis trifurcata* are specialised predators on *Dactylopius* scale insects (e.g., Vanegas-Rico et al., 2016) suggesting this sequestration has evolved in the context of a close predator-prey relationship, and largely eliminating questions of dietary cost that arise when species with a broader dietary range consume prey with defensive chemicals.

The remaining criterion, apart from bodily acquisition and low cost, has also been confirmed. Both the reflex blood of *H. trifurcata* larvae and carminic acid at a similar concentration to that found in the reflex blood were repellent to ants: thus, possession of carminic acid does confer a defensive advantage to the larvae (Eisner et al., 1994). This is the only putative case of ladybird sequestered defence where this has been tested. It remains unknown whether carminic acid is the sole chemical defence of *H. trifurcata* larvae or interacts with autogenous alkaloid defence, which generally has not been investigated in *Hyperaspis* larvae (but see Lebrun et al, 2001 for an adult alkaloid). It would be worth examining if carminic acid replaces autogenous defence in this species. Interestingly, the carminic acid is lost towards the end of development and the reflex blood of resulting adults is white, indicating it is not present (Eisner et al., 1994), perhaps replaced with autogenous adult alkaloid defence.

Pyrrolizidine alkaloids and ladybirds: A test of dietary suitability

One further case of chemical sequestration from prey attracted the attention of Ivo Hodek himself. In this case, pyrrolizidine alkaloids (PAs) were transferred from ragwort aphids, *Aphis jacobaeae* Schrank to adults of *Coccinella septempunctata* (Witte et al., 1990). The qualitative and quantitative alkaloid patterns in ladybirds were generally similar to those in their aphid prey; however, these varied according to the species or chemotype of the ragwort host plant of the aphids, these being the ultimate source of the alkaloids. Interestingly, in both aphid and ladybird they were stored as tertiary alkaloids, rather than N-oxides, as occurs in other insects (Witte et al., 1990): this is notable as the autogenous alkaloid of *C. septempunctata* is mainly stored as the N-oxide coccinelline (Tursch et al., 1971). Witte et al. (1990) estimated the PA content of *C. septempunctata* adults as being up to 50% of the autogenous alkaloid content and suggested an adaptive function, although they did not test either this or the effect of an *A. jacobaeae* diet on the ladybird (i.e. cost of consumption).

Both Hodek (1996) and Hodek & Evans (2012) treated *A. jacobaeae* as a toxic aphid, but suggested that its relationship with ladybirds apparently differed to that of other toxic aphids due to the sequestration by ladybirds of PAs. They did note, however, that there was no data on the effect of eating the aphid on ladybird development and reproduction. In the light of this discussion, I recently made observations on *A. jacobaeae* as a diet of ladybirds in Eindhoven in the Netherlands. In north-west Europe, including this region, *A. jacobaeae* generally only reaches peak levels after *C. septempunctata* reproduction has ended; the majority of new *C. septempunctata* do not reproduce again until they have diapaused over winter (Hodek, 2012; Roy et al., 2013; J.J. Sloggett, pers. obs.). This was likely also true for the ladybirds of Witte et al.'s study (from Brauschweig, northern Germany). Thus, to maintain ecological realism I therefore focused on the effect of an *A. jacobaeae* diet on ladybird survival rather than reproduction.

I compared the survival of ten wild collected and recently eclosed *C. septempunctata* fed on *A. jacobaeae* with ten similar conspecifics fed on *Aphis fabae cirsiiacanthoidis* Scopoli, which is apparently a suitable prey for *C. septempunctata* (Hodek & Evans, 2012). Ladybirds were maintained individually in ventilated plastic boxes of dimensions 11 × 11 × 6 cm. Ladybirds were provided with wild-collected aphids on cut parts of the plants on which they were collected (*Jacobaea vulgaris* Gaertner for *A. jacobaeae* and *Cirsium arvense* (L.) Scopoli for *A. f. cirsiiacanthoidis*) on a daily basis for ten days in early July 2021. It was hypothesised that *A. jacobaeae* might prove toxic to the ladybirds when provided as the sole food over such a long period of time. However, this proved not to be the case and all ladybirds were alive after 10 days had elapsed (although a larva of the parasitoid wasp *Dinocampus coccinellae* (Schrank) emerged from one *A. jacobaeae*-fed *C. septempunctata* towards the end of the experiment).

Field observations provided further information about the relationship between *A. jacobaeae* and ladybirds. In collecting *A. jacobaeae* for the feeding experiment, approximately 100 *J. vulgaris* plants were visited (including some plants with few or no aphids). In most cases when *A. jacobaeae* were present they were tended by ants (cf. Vrieling et al., 1991) and due to this protection appeared to be inaccessible to ladybirds (cf. Majerus et al., 2007). However, in the absence of ants, one *C. septempunctata* adult and one *Harmonia axyridis* adult were found associated with *A. jacobaeae*. Furthermore, on a single untended plant with *A. jacobaeae*, seven *Adalia bipunctata* were found, including mating pairs, as well as a clutch of 13 eggs subsequently identified as *H. axyridis* after they had all hatched. After mating, *A. bipunctata* laid eggs rapidly when transferred to the lab and maintained on an *A. jacobaeae* diet. It thus appears to be the case that *A. jacobaeae* is not excessively poisonous to ladybirds and can even constitute an essential prey, for oviposition at least.

The costs of alkaloid sequestration to *C. septempunctata* and other species, if they also sequester PAs, seem to be minimal; however, ant protection may limit ladybird consumption of this aphid. It does still remain to be examined whether PAs confer additional protection to ladybirds over and above their autogenous defences. It might be that a higher level of protection is provided against important natural enemies by the additive effect of autogenous and sequestered defences together, or that the compounds are synergistic in protecting against different natural enemies.

CONCLUSIONS

It is increasingly clear that diet interacts with ladybird chemical defence in a diversity of ways. The finding that different aphid diets can affect autogenous alkaloid production, suggests that generalist ladybirds feeding on different aphid species could be differentially chemically defended. This intraspecific diversity in chemical defence could be further reinforced if certain foods confer chemical protection via sequestered chemicals. However, at the present time, it remains uncertain how prevalent such sequestration may be, as well as its ecological relevance given the autogenous defences of ladybirds. Surprisingly, considering the general prevalence of sequestered chemical defence in insect herbivores, there has been no such sequestration documented in herbivorous or mycophagous ladybirds. A closer examination of sequestration in these groups would also be worthwhile.

At a physiological level, an understanding of how the chemicals of different foods are resisted or tolerated by ladybirds is also important to understand the effect of diet on both autogenous and sequestered defence. However, this is a small subsection of a much wider research area addressing the underlying physiology of ladybird feeding. That is an important challenge for the future, lying beyond traditional studies of foraging and consumption of food and the ultimate effects of ladybird diet on different species' biological parameters. The pioneering studies of Ivo Hodek and his peers have provided many valuable insights into ladybird feeding, especially in respect of chemical content, but a challenge for the future still exists, in understanding of how ladybirds digest and process their food after eating it.

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