Chemical defence, offence and alliance in ants-aphids-ladybirds relationships

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Introduction

Thirty years ago, I used a trophic web centred on aphids to illustrate the aims and scope of Chemical Ecology (Pasteels, 1976). The fashion in Ecology was to quantify the energy fluxes between trophic levels, whereas Chemical Ecology planned to investigate the chemicals controlling these fluxes. Chemical mediators appeared to act as negative or positive feed back loops regulating energy flow rates, sometimes passing through the proximate level to act on the next level. They were classified as pheromones, allomones, kairomones or synomones, according to whether or not the partners were the same species, and to cost-benefit criteria (e.g. Dicke and Sabelis, 1988). However, chemicals themselves cannot be classified univocally in this way, as the same compound released by the same organism would receive different labels depending on the partners and the context (Pasteels, 1982). It is not the chemical signals that must be classified, but the interactions between the organisms.

Here, I will review some of the recent advances in the understanding of how chemicals regulate interactions between aphids, ladybirds and ants, illustrating the astonishing refinement of some mechanisms. This review does not aim at being exhaustive, but lays stress on pending questions that deserve further investigation.

Defence and chemical piracy

A straightforward way to avoid being eaten is to be toxic or at least unpalatable, and chemical defence was reported in all trophic levels. No further comment is needed on chemical defence in plants (e.g., Arnonson et al., 2004) and ants (review in Leclercq et al., 2000), and only aphids and ladybirds will be considered here.

The siphuncular wax is the most obvious chemical defence of many aphids against parasitoids or small predators, including ladybird larvae (Dixon, 1958; Edwards, 1966). Other defence can be plant-derived. All aphids are not equally suitable as food for ladybirds (review in Hodek, 1973). It seems most unlikely that this could be the result of different nutrient balances in their aphid prey, but it is more likely due, at least in part, to the aphid host-plant secondary chemistry (e.g., Francis et al., 2000). Sequestration of plant toxins by herbivores for their own defence, here called chemical piracy, is widespread. Sequestration by aphids of plant alkaloids, cardenolides or isothiocyanates derived from glucosinolates has been reported several times (Rothschild et al., 1970; Malcom, 1990; Witte et al., 1990; Wink and Witte, 1991; Mendel et al, 1992, Francis et al 2001). Spectacular adverse effects were observed on ladybird development, reproduction or survival, when feeding on sequestering aphids (Pasteels, 1978; Wink et al., 1991; Mendel et al., 1992; Francis et al., 2001). As expected, specialized aphids are more efficient pirates than generalists (Francis et al., 2001). Specialized aphids probably stored the plant toxins in their body, but the site of storage remains unknown. Even excreted plant toxins negatively affect parasitoids that feed on honeydew (Mendel et al 1992). The cost-benefit balance when feeding on toxic plants deserves further investigation in both specialist and generalist aphids.

Many ladybirds display warning colours and odours (i.e., pyrazines, Moore et al., 1990, also used as aggregation pheromone by the 7-spot ladybird, Al Abassi et al., 1998). They are protected against ants and birds by accumulating autogenous alkaloids in their blood, that are released by reflex bleeding when attacked (Pasteels et al., 1973; Marples et al., 1989). The diversity of alkaloids synthesized by ladybirds is astonishing: azaphenolenes, homotropanes, aliphatic and aromatic amines, pyrrolidines, piperidines, azamacrolides, macrocyclic polyamines … (reviews in Daloze et al., 1995; King and Meinwald, 1996). The selective pressure, if any, leading to such diversity remains obscure. Possibly, different alkaloids evolved in response to different predator pressures (Dixon, 2000), but there are little evidence supporting this assumption. Actually, the similarity of the alkaloids shared by different ladybird species appears more function of the ladybird taxonomic relatedness than of them facing the same potential natural enemies while living in sympatry.

Alkaloids do not protect ladybirds from cannibalism and indeed they should be immune to their own toxins. However, intraguild predation could offer a significant pressure for alkaloid diversity in species living in micro-sympatry. Intraguild predation between ladybirds was reported, but with reluctance and at nutritive cost for the predator (Hemptinne et al., 2000 a, and references therein). Closely related species sharing the same alkaloids are expected to occupy different niches with little opportunity of encounters. The possible importance of intraguild predation in the evolution of ladybird chemical defence is further illustrated by the observation that ladybird larvae are far more reluctant to feed on eggs of other species than on their own eggs. Alkanes covering the eggs are used as cue to recognize conspecific eggs from those of other species (Hemptinne et al., 2000 c). Intraguild predator avoidance between a parasitoid and a ladybird was recently reported. The aphid parasitoid, *Aphidius ervi*, avoid alkanes in chemical trails deposited on leaf surface by both larvae and adults of *Coccinella septempunctata* (Nakashima et al., 2004).

Any chemical defence can be circumvented. The ladybird parasitoid, *Dinocampus coccinellae*, is attracted by the ladybird alkaloids, precoccinelline and myrrhine (Al Abassi et al., 2001). Chemical piracy was also reported in ladybirds. Cardenolides are sequestered by *Coccinella 11-punctata* feeding on *Aphis nerii*, which itself sequestered them from their oleander host-plant (Rothschild et al., 1973). The 7-spot ladybird sequesters from *Senecio inaequidens*, via *Aphis jacobaeae*, up to 4.9 mg/g fresh weight of pyrrolizidine alkaloids, which represents an increase of nearly fifty % of their average load of autogenous alkaloids (Witte et al., 1990). These ladybirds seem to tolerate some plant toxins. However, the cost-benefit balance when feeding on aphids developing on toxic plants remains to be assessed in ladybirds apparently able to tolerate the plant toxin.

Offence

Foraging behaviour of coccinellids has been the topic of detailed, fascinating studies (see Dixon, 2000 for an excellent review). The ability to locate and recognize aphids is critical for successful predation. Eggs must also be laid in numbers, and at times that will optimize larval survival and development by avoiding food depletion, cannibalism and intraguild predation since patches of prey are ephemeral and limited in size. This foraging strategy is partly regulated by chemical cues.

It is well known that honeydew induces searching behaviour in many aphidophagous species. The 7-spot ladybird is attracted by an aphid alarm pheromone (*E*)-*β*-farnesene, and this attraction is inhibited by (-)-*β*-caryophyllene. Both terpenes are common plant volatiles, and ladybirds would be attracted only when concentration of the farnesene is high relative to that of the caryophyllene, allowing the ladybirds to detect their prey over common plant odour background (Al Abassi et al., 2000). Young larvae of the 2-spot ladybird attracted by the odour of ß-farnesene subdue large aphids by group attack (Hemptinne et al., 2000b). Chemical cues for prey recognition are unknown, but cuticular hydrocarbons seem obvious candidates (Dixon, 2000). In the coccidophagous ladybird, *Cryptolaemus montrouzieri*, oviposition is stimulated by wax filament produced by their prey or their ovisac (Merlin et al, 1966a).

Ovipositing female 2-spot and 7-spot ladybirds avoid aphid patches already occupied by conspecific larvae, limiting the risks of early patch depletion and cannibalism. The oviposition deterrent pheromone is a mixture of alkanes laid by larvae as tracks on the substrate. These pheromones are species-specific and do not prevent risk of intraguild predation (Doumbia et al., 1998, Hemptinne et al., 2001). A similar strategy is used by *Cryptolaemus montrouzieri*, where the oviposition deterring pheromone is present in the filament wax of their larvae (Merlin et al, 1996b). Pheromones, that deter oviposition, are secreted also by larvae of other aphidophagous insects, i.e., *Chrysopa* spp, but these pheromones appear less species-specific (Rüzica, 1997 a and b).

Alliance and sneak thieves

Plants and natural enemies of herbivores share common interests in defence or offence against herbivores. Alliances between the first and third trophic levels against the second level are thus expected. There are now convincing evidence that plants recruit parasitoids or predators by odours induced by herbivory (e.g. Turlings and Wäckers, 2004). Such recruitment is often specific. The specificity in the quality or quantity of volatiles emitted in response to different herbivores, and the specific attraction of natural enemies to these induced volatiles suggest that this indirect plant-defence has been shaped by a coevolutionary process among the three trophic levels, presently a very active and fascinating topic of research.

Phloem feeders usually induced smaller amounts of plant volatiles than chewing insects (Turlings et al., 1998; W. Boland, pers. com.), but recruitment of parasitoids of aphids or mealybugs by plant-induced volatiles has been demonstrated. The aphid parasitoid, *Aphidius ervi*, is specifically attracted by 6-methyl-5-hepten-2-one, released by bean plant, *Vicia faba*, infested with the parasitoid host, *Acyrthosiphon pisum*. The non-host aphid, *Aphis fabae*, does not induced such indirect plant-defense (Du et al., 1998; Powell et al., 1998). Encirtid parasitoids are attracted by cassava plant volatiles, induced by the mealybugs, *Phenacoccus manihoti* and *P. herreni* (Souissi et al., 1998; Bertschy et al., 2001).

Conflicting results were obtained with ladybirds. The 7-spot ladybird was reported being attracted by plant volatiles induced by aphids feeding on *Hordeum vulgare* or on tea shoots (Ninkovitc et al., 2001; Han and Chen, 2002). Negative results were reported by Francis et al. (2004) with the 2-spot ladybird, which responded to crushed aphids releasing alarm pheromone (see above), and not to intact aphids feeding on various cruciferous plants, possibly because the amounts of volatiles induced in their experimental set up were too low. Possible attraction of ladybirds by plant-induced volatiles needs further research. Associative learning is an expected requirement for effective attraction of polyphagous ladybugs by aphid plant-induced volatiles (see Vet and Dicke, 1992). Such learned odours could offer useful cues for quickly selecting new suitable patches when the ladybird had to move from one aphid colony to another.

Aphid-ant interactions are usually considered as mutualistic, but see Stadler and Dixon (1999). In truly mutualistic association, as well as when ants exploit the aphids, alliance is expected between ants and aphids against aphid predators and parasitoids. Indeed it has been reported many times that ants actively protect the aphids from their natural enemies (e.g. Way, 1963). Parasitoid cuticular hydrocarbons are recognition cues for the ants, releasing aggressive behaviour toward most parasitoids. However, some parasitoids and one ladybird can avoid attacks and sneak into aphid colonies attended by ants. These sneaky parasitoids either mimic recognition cues present in the cuticular lipids of aphids or lack releasers of aggressive behaviour in ants (Dettner and Liepert, 1994). This demonstrates once again the importance of cuticular hydrocarbons as recognition cues at nearly all levels of the food web. The myrmicophilous ladybird, *Coccinella magnifica*, follows the trails of wood ants to reach aphid colonies (Sloggett et al., 1998). The ants largely ignored the larvae and eggs of the ladybird, but not the adults. Possibly cuticular hydrocarbons are involved in protecting ladybird's juveniles.

Conclusion

Progresses in our understanding of how chemical communication regulates the interactions between partners in aphid trophic-webs have been spectacular during the past 30 years. No doubts that these interactions will prove in the near future to be even more complex and subtle than presently recognized, as many questions remain open. Some were raised above and will not be repeated here. However, two avenues of research look especially promising to me.

The first avenue concerns the influence of the aphid host-plant on ladybird foraging behaviour and fitness. Aphid-plant interactions could offer cues for ladybirds in their search and recognition of suitable food patches. Plant-volatiles induced by aphids could offer cues, not for primary attraction to aphid patches, but by associative learning for feeding on similar rewarding food sources. Plant secondary compounds excreted in the honeydew could provide additional cues influencing ladybird selection of appropriate resources. To what degree are ladybird responses to these various potential cues innate or learned? Recent experiments suggest that patch assessment by ladybirds is influenced by experience (Frechette et al., 2004). Besides protecting the aphids in degrees depending on their level of host specialisation, plant secondary-compounds can be sequestered by the ladybirds. Do they incorporate the plant toxins in their eggs, as do other sequestering insects? Does plant-derived defence increase in significant ways the diversity of chemical defence of ladybirds, and does it influence the rate of cannibalism or intraguild predation? Finally very little is known about how aphids and ladybirds handle plant toxins: excretion, detoxification, transformation, transport and storage…

The second avenue concerns cues used by the aphid-web partners for their mutual recognition. Cuticular hydrocarbons appear prominent in this role. In ladybirds, the same alkanes, but in different proportions, are used for mate recognition, to deter ovipositing females from preoccupied aphid patches, and to flag their eggs (Hemptinne and Dixon, 2000). This multiple used of alkanes was considered as an example of semiochemical parsimony. Does it mean that the ladybirds respond to the same signal in a context dependent way, or do they differentiate mixtures of alkanes in different proportions, or both? Where is the signal in a mixture and what is the discriminatory capacity of the ladybirds? How much are ladybirds olfactory neurones tuned for perceiving peculiar hydrocarbons, as they are for detecting (*E*)-*ß*–farnesene and (-)-*ß*-cariophyllene (Al Abassi et al., 2000)? Again to what degree are the responses to recognition cues innate or learned, in particular during interspecific interactions?

Raising questions is an easy task, biased by the author's personal interests. But it is a privilege granted authors writing this type of overview.

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