

# Interactions between ants and aphidophagous and coccidophagous ladybirds

Michael E. N. Majerus · John J. Sloggett ·  
Jean-François Godeau · Jean-Louis Hemptinne

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**Abstract** Aphidophagous and coccidophagous coccinellids come into conflict with homopteran-tending ants for access to food. Antagonistic interactions between coccinellids and ants may be competitive or non-competitive. Competitive interactions occur when coccinellids attack aphids or coccids that are being tended by ants for honeydew. Non-competitive interactions include all interactions away from ant-tended homopteran colonies. We here review observations and studies of such interactions. We note that most competitive interactions occur at times when untended aphids/coccids are scarce. We describe the chemical and physical defences that coccinellids use against ant aggression and consider whether these have evolved as general anti-predator deterrents or specifically in response to ants. Myrmecophilous coccinellids are then

considered, with particular focus on the two most studied species, *Coccinella magnifica* and *Platynaspis luteorubra*. We note that the myrmecophily of the two species has the same adaptive rationale—to enable the ladybirds to prey on ant-tended aphids at times of aphid scarcity—but that it is based on different traits to facilitate life with ants. Finally, we consider the role of ants in the evolution of habitat specialisation in some coccinellids.

**Keywords** Coccinellidae · Myrmecophily · Aphids · Coccids · Optimal forage theory · Chemical defence

## Introduction

Insects that are associated with ants are called myrmecophilous (*myrmex* = ant: Greek). Myrmecophilous aphids and coccids show behavioural and structural modifications to life with ants. When an ant encounters such an insect, it usually strokes it with its antennae. This induces the aphid or coccid to suppress its usual defensive behaviour of kicking out, running away, dropping off the plant or clamping down. Instead, it raises its abdomen and exudes droplets of honeydew, which the ants then imbibe. Ants gain food from the association, for honeydew is rich in carbohydrates and also contains amino acids, amides, proteins, minerals and B-vitamins (Way 1963; Carroll and Janzen 1973; Hölldobler and Wilson 1990). At times, ants also gain protein, by preying on aphids or coccids. Benefits to the aphids or coccids include improved hygiene via removal of caste skins, dead aphids and honeydew (Way 1954; Banks 1958; Seibert 1992); direct increases in development rate, adult body size, fecundity and

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M. E. N. Majerus (✉)  
Department of Genetics, University of Cambridge,  
Downing Street, Cambridge CB2 3EH, UK  
e-mail: m.majerus@gen.cam.ac.uk

J. J. Sloggett  
Department of Entomology, University of Kentucky,  
S-225 Agricultural Science Center North, Lexington,  
KY 40546-0091, USA

J.-F. Godeau  
Biodiversity Research Centre,  
Université Catholique de Louvain,  
Place Croix du Sud, 4-5,  
1348 Louvain-la-Neuve, Belgium

J.-L. Hemptinne  
Evolution et Diversité Biologique,  
Ecole Nationale de Formation Agronomique,  
UMR 5174 CNRS/Université Toulouse III/ENFA,  
2, route de Narbonne, BP 22687,  
31326 Castanet-Tolosan Cedex, France

reproductive rate (El-Ziady and Kennedy 1956; Banks 1958; El-Ziady 1960); and protection from enemies (Bartlett 1961; Banks 1962; Jiggins et al. 1993).

By protecting homopterans from predators and parasitoids, ants come into conflict with such species (Rosen 1990; Dixon 1998). Evolutionary and ecological responses of parasitoids to antagonism from ants include more rapid ovipositing (Bartlett 1961), avoidance behaviour (Völkl 1997) and various chemical adaptations (Liepert and Dettner 1996; Völkl 1997). Evolutionary and ecological responses of homopteran predators to ant attendance of their prey has received less attention. Although many attributes of aphidophages and coccidophages have been suggested to result from interactions with Homoptera-tending ants, evidence supporting such suggestions is sparse, scattered back over a century, and is often contradictory.

In this report, we briefly review literature on interactions between one group of homopteran predators—the ladybirds (Coccinellidae)—and ants. We consider when and why ladybirds feed on ant-tended Homoptera, describe two case studies of myrmecophilous coccinellids and speculate on the evolution of responses to ants and the evolution of myrmecophily.

### Interactions between ants and ladybirds

Ant–ladybird interactions are of three types. First, and most importantly, ants that tend Homoptera compete with aphidophagous or coccidophagous ladybirds for resources. Second, ladybirds may feed on ants, although only one ladybird is known to specialise on ants (Harris 1921). Third, ants may prey on ladybirds. The most useful separation of these interactions is into competitive and non-competitive.

#### Competitive ant–ladybird interactions involving homopterans

There is considerable evidence that Homoptera-tending ants are more aggressive towards coccinellids in the vicinity of tended colonies than elsewhere. This has been described as ownership behaviour (Way 1963). This aggression is aimed at both adult and larval coccinellids. Adults are usually chased from homopteran colonies (Bradley 1973; McLain 1980; Itioka and Inoue 1996; Sloggett 1998), while soft-bodied larvae may be picked up and carried away from the colony, dropped off the plant, or killed (Bradley 1973; Vinson and Scarborough 1989; Bach 1991; Jiggins et al. 1993; Sloggett and Majerus 2003).

Studies comparing the density of ladybirds in the presence and absence of ants have usually shown that ants reduce ladybird numbers on ant-tended colonies of both aphids and coccids (natural presence/absence of ants: Mariau and Julia 1977; McLain 1980; Völkl and Vohland 1996; ant absence due to artificial barriers: Bradley 1973; Reimer et al. 1993; Itioka and Inoue 1996; or poisoning: Mariau and Julia 1977; Jutsum et al. 1981). Exclusion of coccinellids from homopteran colonies by ants is beneficial to both tended aphids (Banks 1962; Mariau and Julia 1977; Reimer et al. 1993) and tended coccids (Bradley 1973).

#### Coccinellid predation of ant-tended Homoptera

A few coccinellids are considered myrmecophilous. While such species habitually live near ant nests, most non-myrmecophilous coccinellids only feed on ant-tended Homoptera when untended Homoptera are scarce (Sloggett and Majerus 2000a). That said, differences in the size, aggressiveness and density of tending ants, and in the size, behaviour and defensive capabilities of coccinellids, undoubtedly affect the level and outcome of ladybird/ant interactions.

The most detailed work on coccinellid predation of tended and untended Homoptera has involved aphidophagous species in temperate regions. Aphidophagous coccinellids usually breed in periods of aphid abundance, when adults are feeding on untended prey (Majerus 1994; Hodek 1996; Sloggett 1998). Consequently, immature coccinellids (excepting myrmecophiles) rarely come into conflict with ants tending aphids. Only in years with a general scarcity of aphids will coccinellid larvae try to attack ant-tended aphids and so be under selection for adaptations to enable them to feed on such prey (Sloggett 1998).

In contrast, adult coccinellids come into conflict with aphid-tending ants annually in late summer when feeding up prior to overwintering. Due to aphid scarcity at this time, they feed on alternative foods, such as pollen, nectar, sap, honeydew, non-homopteran invertebrates and conspecifics (Hodek 1996; Sloggett and Majerus 2000b). Some also attack ant-tended aphids (Sloggett 1998; Sloggett and Majerus 2000a). The tolerance of adult ladybirds to ant aggression then becomes critical, as those with little tolerance are then forced to feed on non-homopteran food. Unfortunately, few studies allow an assessment of the relative tolerances of different coccinellids to ants. Most studies of the effects of ants on coccinellids have involved a single target species of ladybird (Bradley 1973; Itioka and Inoue 1996) or have clumped results of all coccinellids together (Banks and Macaulay 1967; Bristow 1984). However, two studies

showed that coccinellids vary in their tolerance to ants, even if the myrmecophiles are excluded.

DeBach et al. (1951) observed that 66% of *Rhizobius lophanthae* was found in the presence of the ant *Iridomyrmex humilis* tending the coccid *Aonidiella aurantii*, on citrus, but only 15% of a *Chilocorus* species occurred in the same situation.

In a study in an English pine forest, the numbers of six species of coccinellid, two types of aphid, and ant presence or absence were monitored from spring to autumn (Sloggett 1998; Sloggett and Majerus 2000a). The ladybirds comprised four conifer specialists—*Myrrha 18-guttata*, *Anatis ocellata*, *Myzia oblongoguttata* and *Harmonia 4-punctata*—the generalist *Coccinella 7-punctata* and the myrmecophile *Coccinella magnifica*. The aphids were *Schizolachus pineti*, which are not tended by ants, and two *Cinara* species, present at two adjacent sections, one containing several *F. rufa* nests (ant plot), while the other was free of *F. rufa* (control plot). *Cinara* aphids on *Pinus sylvestris* in the ant plot were regularly tended by *F. rufa*, while those in the control plot were not.

Analysis of the patterns of abundance of the various ladybirds in the two plots through the summer allows determination of the ant-tolerance. *Myrrha 18-guttata* and *A. ocellata* had little tolerance of ants, these species only occurring in the ant plot after ants had disappeared in September. A third species, *H. 4-punctata*, exhibited low ant tolerance, being much less abundant in the ant plot than in the control plot. *Coccinella 7-punctata* showed a similar pattern but with a slightly higher tolerance. *M. oblongoguttata* were found significantly more in the control than in the ant plot during early summer, when aphids were abundant. However, once aphids became scarce, their abundance was similar in the two. That it increased in the ant plot once aphids became scarce strongly suggests that it moved into this area to feed on *Cinara* aphids even though these were ant-tended. *M. oblongoguttata* are highly specialised in their diet, only breeding when feeding on conifer aphids, particularly *Cinara* spp. (Majerus 1993). This specialisation towards a few aphid species, most of which elicit ant attendance, will have imposed selection pressure for *M. oblongoguttata* to be ant tolerant. The main defence observed was physical, the ladybird dropping the elytra down to the substrate on the side being assailed by ants. Occasionally, *M. oblongoguttata* have been observed to run from ants, but rarely dropped from the pines and was not observed to fly away. The sixth species of ladybird, *C. magnifica*, was more abundant in the ant area than in the area lacking ants throughout the study, confirming its myrmecophile status (see below).

Larvae of five species were found on *P. sylvestris*, those of *C. 7-punctata* not being found. No larvae of *M. 18-guttata* were found in the ant area. Larvae of *A. ocellata*, *H. 4-punctata* and *M. oblongoguttata* were much more abundant in the ant-free area than in the ant area. Larvae of *C. magnifica* were confined to the ant area.

From these results, Sloggett and Majerus (2000a) drew up an order of ant tolerance for these six ladybirds: *M. 18-guttata* + *A. ocellata* < *H. 4-punctata* < *C. 7-punctata* < *M. oblongoguttata* < *C. magnifica*. They concluded that *C. magnifica* is a true myrmecophile, while *M. oblongoguttata* has some defence against ants, both as an adult and as larva. Adult *C. 7-punctata* coexists with *F. rufa* at moderate levels when aphids are scarce, but does not breed in the presence of *F. rufa*.

Most work on ladybird–ant interactions have involved ant-tended aphids. However, the levels of predation of ant-tended aphids and ant-tended coccids by ladybirds might be quite different. As most coccinellids mainly attack ant-tended Homoptera when non-tended Homoptera are scarce, the probability of finding untended Homoptera becomes critical. Several factors may cause differences in the likelihood that coccinellids will encounter ant-tended aphids when compared with ant-tended coccids. First, at higher latitudes, aphids are much more common relative to coccids than in the tropics. Ant diversity and abundance is much greater in the sub-tropics and tropics than in more temperate climes. Thus, untended colonies of coccids will be less common than untended colonies of aphids. Second, and conversely, aphids are renowned for the ephemerality of their colonies, particularly in seasonal climes: coccids less so (Dixon 2000). In part, aphid ephemerality is due to eradication of colonies by predators and parasitoids, although other factors, such as the concentration of soluble sap available in plant sap (Dixon 1970; Strong et al. 1984), are also important. The “boom and bust” cycle seen in aphids means that their predators often face a dearth of non-ant-tended aphids that have been protected from this predation/parasitoid pressure. Ant-tended colonies of aphids persist for longer than untended colonies of the same species (Addicott 1979; Bristow 1984; Mahdi and Whittaker 1993; Sloggett and Majerus 2000a). Foraging theory predicts that aphidophagous coccinellids are most likely to feed on ant-tended aphids when untended aphids are scarce, i.e., when untended aphids are of greater relative value (Stephens and Krebs 1986). In temperate regions, untended aphids become scarce in late summer, while ant-tended colonies often remain abundant at this time (Mahdi and Whittaker 1993; Sloggett and Majerus 2000a).

It is not clear whether overall aphidophagous coccinellids or coccidophagous coccinellids are under greater pressure to feed on ant-tended prey. What is clear is that the pressure will vary with both coccinellid species and prey species. Moreover, this pressure will vary greatly in seasonal habitats (*sensu* Southwood 1977), which will be more pronounced in temperate regions than in the tropics. Work on the relative availabilities of untended and tended aphids and coccids through the year in a variety of climate zones is urgently needed, and may shed light on both similarities and differences in the interactions between coccidophagous and aphidophagous coccinellids and Homoptera-tending ants.

#### Non-competitive interactions

Non-competitive interactions include all those away from ant-attended homopteran colonies, plus instances of predation of ladybirds by ants (or the reverse). Such interactions are important as they influence habitat preferences and ladybird distributions within an environment. Away from homopteran colonies, ants that encounter ladybirds either attack them or ignore them, depending usually on the species of ant. Thus, several ants that attack coccinellids in the vicinity of tended homopterans, including *Lasius niger* (El-Ziady and Kennedy 1956; Banks 1962), *Formica fusca* (Rathcke et al. 1967), *I. humilis* (Dechene 1970) and *Myrmica ruginodis* (Jiggins et al. 1993), are indifferent to ladybirds elsewhere. Conversely, some ants that are prey on insects attack ladybirds whenever they encounter them, and so exclude many coccinellids from their forage range. Examples are few because most empirical evidence is based on introducing coccinellids to captive, starved ant colonies, and interactions do not reflect what happens in the field, and because it is difficult to disentangle the effects of ant predation of coccinellids from ant attendance of Homoptera. Thus, Hays and Hays (1958) found that captive, starved *Solenopsis invicta* would kill and eat five species of coccinellid, yet Wilson and Oliver (1969) found only one coccinellid among 4,056 prey items taken by this ant, and Sterling et al. (1979) found that *S. invicta* presence did not reduce coccinellid numbers in cotton fields. Such difficulties mean that separating ant-coccinellid interactions into competitive and non-competitive may be overly simplistic. However, despite this artificiality, it is likely that highly aggressive predatory ants have a greater effect on coccinellid distributions in a habitat than do ants that only attack ladybirds near homopteran colonies.

#### Coccinellid defences against ants

The tolerance of ladybirds to ants depends, at least in part, on the defensive capabilities of the ladybirds. Coccinellids use various mechanisms when faced with ant aggression (Pasteels et al. 1973; Richards 1980, 1985; Majerus 1994). These defences may be behavioural, physical or chemical, with some being shown at specific periods of the life cycle, and others shown at both adult and immature stages.

##### Behavioural defences

Most coccinellids exhibit defensive behaviours when attacked by ants. Most commonly, larvae escape by running away or dropping to the ground, while adults may fly (Banks 1962; Bradley 1973; Itioka and Inoue 1996) in addition to using these tactics. For adults, an alternative to fleeing is to “clamp down”, retracting their legs under the body, pulling their heads close to the thorax and attaching firmly to the substrate (Bradley 1973; Jiggins et al. 1993; Majerus 1994). Members of the sub-family Chilocorinae have a very flat ventral surface and a lip around the elytral edge, so that the contact made when they clamp is very tight and prevents ants from gaining access to the vulnerable ventral surface of the ladybird. Conversely, many Coccinellinae species do not clamp down completely, but adopt a rolling motion, dropping the side being attacked to make close contact with the substrate (Jiggins et al. 1993; Sloggett 1998).

Many coccinellid pre-pupae and pupae can rapidly raise their anterior end in response to tactile stimuli. This “pupal flicking” behaviour (Majerus 1994) may be repeated many times. Eisner and Eisner (1992) suggested that this is a defence against ants, with the joints between abdominal segments acting as “gin-traps” that damage ant appendages. However, a more likely explanation of this behaviour is that it reduces oviposition by pupal parasitoids, such as scuttle flies (Diptera: Phoridae) (Disney et al. 1994).

It is unclear whether these behavioural defences evolved as specific responses to ant aggression or are general anti-predator/parasitoid devices, although Sloggett (1998) suggests that some of these behaviours are more extensively developed in species that encounter ants frequently.

##### Physical defences

The chorion of ladybird eggs is relatively thin and is unlikely to be effective against ant mandibles. The exoskeleton of coccinellid larvae is soft and easy to

pierce. However, many coccinellid larvae are covered by spines (Richards 1980), which may provide some protection against ant attack, although this has not been demonstrated experimentally (Sloggett 1998).

The exoskeletons of coccinellid pupae are relatively hard and, although not impregnable to predators or parasitoids, will provide some protection against ant attack. Moreover, except in the Coccinellinae, Stictolotinae and a few species from other sub-families, the pupa gains some protection from the final larval skin (Richards 1980), which is not shed back, but simply splits along the dorsal mid-line during pupation. This additional layer, which is sometimes spiny or waxy, should be considered a general defensive adaptation.

Some coccinellid larvae are covered on the ventral surface by a network of wax filaments. Pope (1979) proposed that this wax covering was an adaptation against ant attack. First, it may be difficult for ants to bite into. Second, as some waxes are sticky, it may cause ants to break off attacks to clean their mouthparts. The defensive efficiencies of wax coverings of two species of *Scymnus* were examined by Völkl and Vohland (1996). They showed that mortality of normal larvae (waxy) of *S. nigrinus* and *S. interruptus*, caused by attacks from *Formica polyctena* and *L. niger*, respectively, was lower than that of larvae from which the wax had been removed. Although some normal larvae were killed, the ants that attacked these larvae frequently broke off attacks to clean their mouthparts. Moreover, Völkl and Vohland (1996) found that numbers of *S. nigrinus* larvae were significantly higher closer to *F. polyctena* than in its absence, while numbers of *S. interruptus* were similar in the presence and absence of *L. niger*.

A third adaptive function of larval wax may be mimetic. Some species with wax coverings feed on mealy aphids and resemble their prey closely. It is thus possible that mealybug-tending ants ignore such coccinellid larvae because the larvae are not recognised as a threat to the homopterans. Support comes from observations of *Cryptolaemus montrouzieri* larvae being ignored by *Pheidole megacephala* when on colonies of waxy mealybugs tended by this ant, but attacked by the same ant on tended colonies of the waxless *Coccus viridis* (Bach 1991). The wax coverings of coccinellids are secreted by the larvae themselves. Interestingly, some chrysopid (Neuroptera), larvae harvest wax from their homopteran prey and stick it to their dorsal surface (Eisner et al. 1978). These larvae frequently feed on ant-tended aphids. As the wax coverings of the aphids and chrysopid larvae are indistinguishable, the ants do not attack the larvae.

Some coccinellid pupae also have wax coverings. The larva of *Scymnodes lividigaster* smears wax onto the surface of the substrate where it attaches before pupation (Richards 1980). The pupa that is formed is both wax-covered and spiny. Richards (1980) has proposed that both the wax smear and the pupal covering act to deter aphid-tending ants and other predators. If so, it is not clear whether deterrence is from the physical barrier of the pupal covering, the texture of the wax, its chemical composition, its colour or a combination of these (Richards 1980; Sloggett 1998).

The pupa of *Rodatus major* has a very dense wax covering, which, in addition to being a physical barrier against ant aggression, may have a mimetic function. The species feeds mainly on eggs of the coccid *Monophlebulus pilosior*, which are often tended by *Iridomyrmex* ants. Richards (1985) has proposed that the wax gives *R. major* larvae a resemblance to the ovisac of this coccid.

The main physical defence of adult coccinellids against ant attack is its hard dorsal surface. Coupled with the clamping and rolling behaviours, the dorsal surface provides a stout barrier to injury from ants. The fine hairs that cover the elytra of some coccinellids may provide additional protection against ant attack, but this has yet to be demonstrated.

#### Chemical defences

Coccinellids are well known for their bright coloured patterns, which are generally considered to be aposematic, advertising unpalatability (Brakefield 1985; Majerus 1994). This unpalatability is largely chemical in nature. Coccinellids reflex bleed, secreting a foul-smelling, distasteful fluid from the tibio-femoral joints of adults or the dorsal surface of larvae and pupae.

At the centre of coccinellid defence lies an array of alkaloids (Daloze et al. 1995) and pyrazines (Moore et al. 1990). The variety of defensive chemicals in the coccinellids and the variation in concentrations of the substances present in these cocktails indicate that these insects were some of the first to use combinatorial chemistry in their defence (Schröder et al. 1998).

Many, but not all, of the defensive chemicals found in ladybirds are synthesised by the ladybirds themselves (Tursch et al. 1976; Jones and Blum 1983). However, some coccinellids also have the ability to store and use defensive chemicals from their prey. *Coccinella undecimpunctata* and *Hippodamia variegata* both sequester cardiac glycosides from *Aphis nerii* (Rothschild and Reichstein 1976). *Hyperaspis trifurcata* gain a major weapon by storing anthraquinone carminic acid from its main prey, cochineal insects of

the genus *Dactylopius*. Similarly, *C. septempunctata* sequester pyrrolizidine alkaloids when feeding on *Aphis jacobaeae* (Witte et al. 1990). In these latter two cases, the defensive chemicals are manufactured by the plants on which the aphids feed, so the ladybirds get these defensive elements third hand.

The defensive chemicals of many coccinellids are distasteful or toxic to many predators (Morgan 1896; Pasteels et al. 1973; Brakefield 1985; Marples et al. 1989), but not to all (Muggleton 1978; Majerus 1994; Majerus and Majerus 1997). The general consensus is that reflex blood is distasteful to ants (Stäger 1929; Happ and Eisner 1961; Pasteels et al. 1973; Sloggett 1998). Furthermore, ants contaminated by reflex blood may have their mobility impaired by it as it dries (Stäger 1929; Bhatkar 1982).

The extent to which adult coccinellids reflex bleed in response to ant attacks varies between species and circumstances. Some observers have reported that ladybirds rarely reflex bleed, even under sustained attack by ants (Marples 1993; Jiggins et al. 1993), while others have observed ladybirds reflex bleeding readily when attacked (Banks 1962; Bhatkar 1982). Majerus (1994) argued that reflex bleeding is used by adult coccinellids against ants as a last defence, when other defences, including fleeing, have failed. Reflex bleeding is costly due to energy expended in chemical synthesis and in fluid loss (de Jong et al. 1991; Holloway et al. 1991, 1993) and is therefore only deployed when other strategies have failed and the ladybird is in severe jeopardy (Majerus 1994).

Sloggett (1998) used the cost-benefit argument to conclude that reflex bleeding did not evolve initially as a defence against ants. He noted that coccinellids most often come into conflict with homopteran-tending ants at times of ant-untended homopteran scarcity. At such times ladybirds will have low resource reserves and so reflex bleeding would incur a relatively high cost. It is notable that the phytophagous coccinellid *E. varivestis* reflex bleeds readily when attacked by ants (Happ and Eisner 1961). This species synthesises a vast array of defensive alkaloids (Eisner et al. 1986; Attygalle et al. 1993a, b; Proksch et al. 1993; Shi et al. 1997; Radford et al. 1997). Sloggett argued that this complexity may be a consequence of the plant diet of *E. varivestis*, so that, unlike homopteran predators, it will rarely be food limited and thus be able to devote more resources to chemical defence and reflex bleeding.

The evidence that coccinellid larvae reflex bleed when attacked by ants is clear (El-Ziady and Kennedy 1956; Happ and Eisner 1961; Bradley 1973; Sloggett 1998). This is because larvae are at greater risk of suffering injury from ants than are adult ladybirds

(Majerus 1994). It may also be that as larvae usually occur at times of prey abundance, they are less resource limited than adults (Sloggett 1998).

Ant aggression probably played little role in the initial evolution of reflex bleeding in coccinellids. However, it may have a role in shaping the precise balance of defensive capabilities of coccinellids to a variety of predators, parasites and pathogens. In coccinellids that frequently encounter ants, more resources may be devoted to defences against ants (and less against other enemies) than in species that rarely interact with ants. In addition, ants may reduce the density of potential coccinellid predators and parasitoids occurring within ant forage ranges, producing enemy-free space (Jeffries and Lawton 1984). If so, ladybirds that commonly co-occur with ants, including myrmecophiles, may invest fewer resources in defences against predators/parasites that are excluded by ants than would ladybirds that rarely occur with ants (Sloggett 1998).

Coccinellid eggs and some pupae also have chemical defences. The eggs of aphidophagous coccinellids contain defensive chemicals that deter some predators (Agarwala and Dixon 1992; Majerus 1994; Hemptinne et al. 2005), including ants (Godeau 1997; Sloggett 1998). For example, *F. rufa* workers find the eggs of *C. septempunctata* repellent, although they may still destroy the eggs (Sloggett 1998). Some coccinellid pupae (e.g., Chilocorini) reflex bleed and this blood has some deterrent effect against ants. Pupae of *E. varivestis* have a covering of glandular hairs, each hair producing a droplet of alkaloid that is repellent to ants (Attygalle et al. 1993a).

## Myrmecophily

The extent of myrmecophily among coccinellids

A small number of coccinellids are regularly associated with one or more species of ant and may be myrmecophilous (Berti et al. 1983; Sloggett 1998). These associations are listed in Table 1, together with the evidence on which their suggested myrmecophily is based. Of the 11 taxa listed, myrmecophily should be considered unproven in 4. The suggestion of myrmecophily in the tribe Monocorynini is based only on antennal morphology, and records of associations between these ladybirds and ants are lacking (Sloggett 1998). In *Scymnus fenderi* and *S. formicarius*, the possibility of myrmecophily emanates from a few records of adults and pupae being found with ants. The myrmecophily of *Hyperaspis acanthicola* is based on

**Table 1** Coccinellids that have been suggested as being myrmecophilous

Coccinellid	Associated ant(s)	Evidence of myrmecophily	References
Subfamily: Coccidulinae Tribe Monocorynini Various species	Unknown	Adults have compact antennal clubs. Myrmecophily unproven	Kovár (1996)
Subfamily: Scymninae <i>Scymnus fenderi</i>	<i>Pogonomyrmex subnitidus</i>	One adult recorded from <i>P. subnitidus</i> nest. Ant is gramnivorous and does not tend Homoptera. Myrmecophily unproven	MacKay (1983) and Hölldobler and Wilson (1990)
<i>Scymnus formicarius</i>	<i>Formica rufa</i>	Little known. Adults apparently found with ants	Wasmann (1894)
<i>Brachiacantha quadripunctata</i>	<i>Lasius umbratus</i> <i>Formica subpolita</i> (= <i>F. camponoticeps</i> )	Waxy larvae prey upon tended coccids and adelgids within ant nests. Closely related species are probably also myrmecophilous. Other ant hosts are probable	Mann (1911), Wheeler (1911), Gordon (1985), and Montgomery and Goodrich (2002)
<i>Brachiacantha ursina</i>	<i>Lasius</i> spp.	Probably the same behaviour as <i>B. quadripunctata</i>	Smith (1886) and Montgomery and Goodrich (2002)
<i>Hyperaspis reppensis</i>	<i>Tapinoma nigerrimum</i>	Larvae apparently feed on ant-tended fulgorids in ants' nests. Adults are attacked by ants	Silvestri (1903)
<i>Hyperaspis acanthicola</i>	<i>Pseudomyrmex ferruginea</i>	Larvae found in hollow spines of <i>Acacia</i> spp. abandoned by ants. Myrmecophily unproven	Chapin (1966)
<i>Ortalia pallens</i>	<i>Pheidole punctulata</i>	Myrmecophilous larvae feed on ants. Adult habits unknown	Harris (1921)
<i>Thalassa saginata</i>	<i>Hypoclinea bidens</i>	Pupae found with ants. Chemical mimicry demonstrated for larvae, pupae and adults. Production of chemical attractant. Myrmecophily probable. Diet unknown, hypothesis of ant brood predation by larvae and/or adults	Berti et al. (1983), Corbara et al. (1999), and Orivel et al. (2004)
Subfamily: Chilocorinae <i>Platynaspis luteorubra</i>	<i>Lasius niger</i> <i>Myrmica rugulosa</i> <i>Tetramorium caespitum</i>	Multiply recorded with a variety of ant species. Larvae, and pupae show myrmecophilous morphology	Pontin (1959), Majerus (1994), and Völkl (1995)
Subfamily: Coccinellidae <i>Coccinella magnifica</i>	<i>Formica rufa</i> group	All stages found with ants	Donisthorpe (1919–1920), Wasmann (1912), Majerus (1989), Sloggett (1998), Sloggett et al. (1998), and Sloggett and Majerus (2003)

Adapted from Sloggett (1998)

larvae being found in hollow Acaci spines abandoned by ants and may also be unsound. For all these species, further observations to determine the extent of associations with ants are needed. Experimental work to test whether these coccinellids benefit from any associations found with ants would be even more valuable.

The myrmecophily of the remaining seven taxa is more certain, but in some little is known of the precise

nature of the association with ants. In *Brachiacantha quadripunctata*, *B. ursina*, *Hyperaspis reppensis* and *Ortalia pallens*, myrmecophily may be limited to the larvae. In each species, larvae have been found in ants' nests feeding on ant-tended fulgorids or coccids, and in *O. pallens* on the host ants. The predation of ants by *O. pallens* probably results from a dietary shift after it had developed a myrmecophilous habit (Sloggett

1998). The larvae and pupae of *Thalassa saginata* develop in the nests of *Dolichoderus bidens* (Berti et al. 1983). The larvae mimic cuticular lipids of the ants' brood, although whether they feed on the brood is not known (Orivel et al. 2004).

In *Coccinella magnifica* and *Platynaspis luteorubra*, adaptations to a myrmecophilous existence are seen in the larvae and in some other life-history stages. The myrmecophily of both species has been studied in some detail and consideration of these cases sheds light not only on the ecology and evolution of myrmecophily, but on interactions between ants and insects that prey on Homoptera more generally.

#### The case of *Coccinella magnifica*

*Coccinella magnifica* is a known myrmecophile (Sloggett et al. 2002 and references therein). It occurs through much of the Palaearctic, its local distribution resulting from its association with ants. In northwestern Europe, it occurs in the foraging areas of ants of the *F. rufa* group.

The obligate myrmecophily of *C. magnifica* was confirmed in Britain during a general survey of coccinellids. Samples of all seven spotted ladybirds of appropriate size were collected at 26 sites in southern England, without consideration of the presence or absence of *F. rufa*. A total of 5,971 ladybirds were collected. Of these, only 49 were *C. magnifica*, all found along with *F. rufa*, and the remainder was *C. septempunctata* (Majerus 1989).

Donisthorpe (1919–1920) placed *C. magnifica* and *C. septempunctata* on *F. rufa* nests, the former being only slightly attacked while the latter were “vigorously assailed”. Pontin (1959) and Majerus (1989) recorded similar observations. Some workers have recorded that adult *C. magnifica* reflex bleed freely when attacked by ants (Donisthorpe 1919–1920), while others have observed that its relative immunity to attack by ants was rarely associated with reflex bleeding (Majerus 1989; Jiggins et al. 1993).

Various hypotheses have been put forward to explain the low levels of aggression of ants towards *C. magnifica*. Possibly, *C. magnifica* secrete a pheromone that deters ants (Majerus 1989; Sloggett 1998) by advertising distastefulness or toxicity. Alternatively, the ladybird may secrete chemicals that mimic the ants' own scent or, possibly, the odour of aphids (Majerus 1989). Third, *C. magnifica* may exude a chemical that is harmful to ants (Donisthorpe 1919–1920). Field and laboratory studies of the interactions of *C. magnifica* and other ladybirds that occur with *F. rufa* in conifer and mixed woodland were used to test these hypoth-

eses (Sloggett et al. 1998; Sloggett and Majerus 2003). Of particular note are experiments on the behaviour of *F. rufa* towards *C. magnifica* and *C. septempunctata* introduced onto ant foraging trails and ant-tended aphid colonies. On trails, *C. magnifica* were attacked occasionally, but very much less than *C. septempunctata*. This finding is important, as Godeau et al. (2003) have shown that *C. magnifica* follow ant trails to locate aphid colonies. Moreover, on ant-tended aphid colonies, *C. magnifica* stayed on the colony longer and were more successful in feeding on aphids than *C. septempunctata*. Although ants attacked both species, the degree of aggression towards *C. septempunctata* was greater than that towards *C. magnifica*. In response to attacks, *C. septempunctata* dropped off plants or flew away significantly more often than *C. magnifica*. *C. septempunctata* adults occasionally responded to ant attacks by reflex bleeding, in contrast to *C. magnifica* which never did. Larvae of both species were seen to reflex bleed when attacked by ants. Although *C. magnifica* larvae reflex bled much less often than *C. septempunctata*, ants were more deterred from attacking *C. magnifica* larvae than *C. septempunctata* larvae when they reflex bled (Sloggett and Majerus 2003). The soft-bodied *C. magnifica* larvae were also frequently found in situations that minimised ant aggression, feeding on aphids dislodged onto ant trails or on untended aphids. Indeed, *C. magnifica* appear to lay eggs away from ant-tended aphids, but close to untended aphids (Sloggett and Majerus 2003). Finally, none of the defensive behaviours of *C. magnifica* in interactions with *F. rufa* was unique to *C. magnifica*. All were also seen in *C. septempunctata*, with differences between species being of the degree to which the various behaviours were used. Thus, *C. magnifica*'s defence against ants may have evolved by gradual adaptation of *C. septempunctata* behaviours.

Sloggett (1998) also considered the chemistries of *C. magnifica* and *C. septempunctata*. He showed that dead *C. septempunctata* were more frequently attacked on ant trails than were *C. magnifica*, whether whole corpses, corpses without elytra or wings, or just elytra were used. He deduced that the low level of aggression shown by ants to *C. magnifica* has a chemical basis. Analysis of the cuticular lipids of the two species showed little difference, and little similarity to the surface lipids of *F. rufa* (G. Lognay, J.J. Sloggett and J-L. Hemptinne in Sloggett 1998). Due to the lack of similarity between the surface lipids of *C. magnifica* and *F. rufa*, Sloggett (1998) argued that *C. magnifica*'s immunity to ant attacks was not due to chemical mimicry of the ants. Moreover, the similarity in the cuticular lipids of *C. magnifica* and *C. septempunctata*



make it improbable that *C. magnifica* gains immunity by mimicking another element in the habitat. Transfer experiments showed that *C. magnifica*'s defence is not *F. rufa* nest specific (Sloggett 1998). Sloggett concluded that *C. magnifica*'s defence is probably based on repellent chemistry and that the chemicals involved are alkaloids, and possibly pyrazines. Interestingly, while the predominant alkaloids produced by most *Coccinella* species are coccinelline and precoccinelline, those of *C. magnifica* are hippodamine and convergine (Dixon 2000; Sloggett 2005). Convergine is more repellent to ants than coccinelline (Pasteels et al. 1973).

#### The case of *Platynaspis luteorubra*

Larvae of *P. luteorubra* occur with various ants tending aphids, including *L. niger*, *Myrmica* spp. and *Tetramorium caespitum*, in both underground galleries and on plants (Pontin 1959; Völkl 1995; Godeau 2000). The larvae and pupae have shapes unlike those of most ladybirds, but similar to other myrmecophilous larvae, such as those of some lycaenid butterflies and *Micron* hoverflies.

Völkl (1995) has shown that *P. luteorubra* is a true myrmecophile, and larvae are frequently found in association with ant-tended aphids. Intensive field studies on various plants showed that *P. luteorubra* larvae occurred significantly more in ant-tended than unattended colonies. The species has a range of morphological and behavioural adaptations to life with ants, thereby giving them access to ant-attended resources. Ants do not recognise larvae of *P. luteorubra* as a threat to their attended aphids. This may be due to the larva's unusual coccid-like shape and its slow inconspicuous movements. Völkl also assumed that the larvae produces "camouflage" chemicals. Studies in Germany have shown that when larvae of *P. luteorubra* were moved between colonies of the ant-tended aphids, *A. fabae* and *Metopeurum fuscoviride*, the response of ants towards them changed. Larvae moved to a new colony of conspecific aphids were not attacked, while those moved to a colony of the other species were (Oczenascheck 1997). Analysis of the larval cuticular lipids showed that these were similar, both in type and quantity, to those of their prey. As the cuticular lipids of these two aphids differ both qualitatively and quantitatively, a change in prey led to a change in the cuticular lipids and so the effectiveness of the larvae's chemical mimicry. This is a very efficient form of scent mimicry because the larvae do not have to manufacture different cocktails of mimetic chemicals when feeding on different prey species.

Völkl (1995) found that *P. luteorubra* pupae were frequently attacked by *L. niger*, but were protected from injury by dense long hairs. The chemical mimicry of the larvae is not carried forward into the pupal stage, probably because alcohols rather than lipids dominate the cuticular compounds of pupae. In Belgium, adult *P. luteorubra* frequently feed on *A. fabae* tended by *L. niger* on *Cirsium arvense* (Godeau 2000). Adults are often attacked by *L. niger* and respond either by fleeing or by clamping down.

The myrmecophily of *P. luteorubra* is adaptive. Larvae in ant-tended aphid colonies have higher prey capture than those in unattended colonies, and adults that develop in ant-tended colonies are larger than those that develop in unattended colonies (Völkl 1995).

#### Habitat specialisation and the evolution of myrmecophily in coccinellids

There are striking differences in the adaptations that the two best-studied myrmecophilous coccinellids have evolved to enable them to live with ants. *Platynaspis luteorubra* larvae chemically mimic aphids, sequestering mimetic chemicals from their prey. *Coccinella magnifica* appears to use ant-repellent chemicals, as well as physical and behavioural defences. Despite these different adaptations, the main reason for myrmecophily is probably the same in the two species: to enable them to feed on ant-tended aphids when other aphids are scarce.

Comparative work on *C. magnifica* and *C. septempunctata* allows speculation on the evolution of myrmecophily. Sloggett and Majerus (2000a) showed that *C. septempunctata* has some tolerance of *F. rufa* during periods of aphid scarcity. Donisthorpe (1919–1920) also wrote of *C. 7-punctata* "experimenting in a myrmecophilous existence". Furthermore, Bhatkar (1982) observed large groups of this ladybird with *F. polycytana*, and other *Coccinella* species (*C. undecimpunctata*, *C. transversoguttata*, *C. trifasciata*) have been reported with ants, particularly in late summer (Bradley and Hinks 1968; Bhatkar 1982). This suggests that *Coccinella* species often facultatively coexist with ants. Members of this genus are intolerant of low aphid densities, and this may have driven them to evolve some tolerance to ants when aphids are scarce (Sloggett and Majerus 2000a). It seems feasible, then, that the non-myrmecophilous ancestors of *C. magnifica* occasionally had to prey upon ant-tended aphids, and thus selection was imposed on them to evolve some tolerance to ants. Additional selective advantages to myrmecophily may have enhanced the behaviour over time. These may have included more efficient use of

ant-tended prey species, reduced energetic costs associated with prey switching (Hattingh and Samways 1992), reduced requirement for migrations, reduced competition with other aphidophages and reduced densities of ladybird predators and parasitoids (Sloggett and Majerus 2000a).

Living in the forage range of aggressive ants may give myrmecophilous ladybirds an advantage from “enemy-free space”. Little work has been conducted on the role of enemy-free space in the evolution of habitat preferences in coccinellids, although it appears to be weak when compared with food-related factors (Sloggett and Majerus 2000b). In *P. luteorubra*, living with ants greatly reduces the levels of infection by the host-specific parasitoid wasp *Homalotylus platynaspidis* (Völkl 1995). Similarly, Majerus (1994) and Sloggett et al. (2004) found lower levels of parasitism by *Dinocampus coccinellae* in *C. magnifica* than in *C. septempunctata* in the same habitat. However, in captivity, in the absence of ants, *D. coccinellae* parasitism of *C. magnifica* is negligible. Thus, the low parasitism of *C. magnifica* by this wasp may be due to factors intrinsic to the ladybird, possibly its highly repellent defensive chemistry, rather than being directly attributable to ants.

In research on habitat or host plant preferences, two questions should be addressed. First, and obviously, why does a species live in certain habitats or on certain plants? The second question, which is often forgotten, is why does a species not live in other habitats or on other plants? Species with highly specialised ecologies, such as myrmecophiles, are easiest to interpret.

In *C. magnifica*, we have some idea of why they live with ants and not elsewhere. They do so to utilise a food source protected from other predators by an aggressive guardian, against whom they are themselves well defended. But why does *C. magnifica* not live anywhere else? Here we must speculate. Possibly *C. magnifica* are poor competitors or lack efficient defences against some predators and parasites. However, if this is so, more fundamental questions must then be asked: why are they bad competitors and their defences inadequate?

One possibility may follow from *C. magnifica*'s specialisation to life with ants. Production of repellent alkaloids is costly, reducing resources for other functions, such as toxin production, or fighting ability. This is a direct cost of immunity. A more indirect cost is that when living with aggressive ants, the selection pressures to maintain strong defences against a range of predators and parasites are reduced, because ants exclude these. If these ancestral defences have any cost, the systems will be lost. In the early 1990s, Dr John

Barrett (personal communication) devised an interesting analogy. If *C. magnifica* are the populace of the United States, then the ants could be seen as a Reaganesque Star Wars system, spreading a powerful defensive umbrella over an area surrounding their territory. Presence of this defensive system negates the need for more conventional defences, and the costs of these can be saved. One is safe as long as one stays under the umbrella, but not if one strays.

## Conclusion

Many predatory coccinellids encounter homopteran-tending ants regularly because they both use resources provided by Homoptera. Ants are thus important in the ecology of many coccinellids. However, caution should be taken when investigating the interactions between coccinellids and ants. Perhaps too often the reactions of coccinellids to ants have been viewed in isolation. In reality, many of the defences used by coccinellids when faced with aggressive ants are simply modifications of general defences. So, it is those few species of coccinellid that have the closest association with ants, the myrmecophiles, that may be most illuminating. Here, the closeness of the association means that many coccinellid behaviours to ants have evolved specifically because of the association. The two best studied myrmecophilous coccinellids, *C. magnifica* and *P. luteorubra*, have already given insights into not only specific inter-species interactions, but also the roles of enemy free space, resource utilisation, inter-specific competition and the evolution of habitat specificity. Moreover, studies on these two species show both illuminating similarities and differences. It is striking that so little is known about ladybird–ant relationships, with the paucity of knowledge about such interactions in the tropics being most extreme. Certainly, other myrmecophilous coccinellids await discovery. If other ladybirds with close associations with ants are identified, then close scrutiny will surely provide novel insights into a range of phenomena.

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