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Reaction of Ants to, and Feeding Biology of, a Congeneric Myrmecophilous and Non-myrmecophilous Ladybird

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Abstract *Coccinella magnifica* Redtenbacher lives only in close contact with species of the *Formica rufa* group. Laboratory experiments were set up to determine how this species may be adapted to living with ants by comparing its behaviour with that of the closely related *Coccinella septempunctata L*. Eggs and larvae of *C. magnifica* placed on the foraging trails of ants were bitten significantly less often by the ants than those of *C. septempunctata*. However, the ants responded similarly to the adults of both species. For these two species, the presence of ants resulted in a significant decrease in predation efficiency. However, *C. magnifica* was more efficient at catching aphids in the presence of ants than *C. septempunctata*. The behaviour of this myrmecophilous species is discussed by taking into account that it is a generalist in terms of prey specificity.

Keywords Predation efficiency · ant-tended aphids · ant aggressiveness · myrmecophily

Introduction

Some species of ants occasionally feed on aphids but more usually they tend them and collect the honeydew they produce (e.g. Nixon 1951; Way 1963; Skinner 1980; Morales 2000). The majority of ladybird beetles (Family Coccinellidae) feed on

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either aphids or coccids during their larval development and as adults. They show various degrees of prey specificity (e.g. Iablokoff-Khnzorian 1982; Majerus 1994; Hodek and Honek 1996). Therefore, ants and ladybirds may compete for the same resources. Most studies on the interactions between aphids, ants and ladybirds are descriptive but the general picture that emerge is that ants rarely tolerate the presence of ladybird beetles in their surroundings (Lucas 2005; review in Majerus et al. 2007). However, among the 6,000 species of ladybird beetles (Slipinski 2007), seven are considered to be true myrmecophiles and four are suspected to at least live in association with ants. Each of these seven myrmecophilous ladybird species has developed a specific type of association with ants, which allows them to exploit the same resource as the ant (Majerus et al. 2007).

In Western Europe, there are two myrmecophilous ladybirds. The adults and larvae of these ladybirds feed on aphids, which normally benefit from the protection of ants (Völkl 1995; Majerus 1989). *Platynaspis luteorubra* Goeze measures 3.0 mm, is associated with small ants, mainly *Lasius niger* L., most often on thistle (*Cirsium arvense* (L.) Scopoli) or tansy (*Tanacetum vulgare* L.) and is morphologically well differentiated from its close relatives (Völkl 1995). The second species, *Coccinella magnifica* Redtenbacher, is much bigger (6.7 mm) and is only found in the immediate vicinity of *Formica rufa* L. and *Formica polyctena* Förster nests in Great-Britain and Belgium. It is very similar in appearance to *Coccinella septempunctata* L., which is a generalist predator found in a wide range of habitats but very occasionally associated with ants (Sloggett and Majerus 2000a). These two species of *Coccinella* are used here to investigate the mechanisms by which *C. magnifica* has adapted to living in close association with ants (Majerus 1989; Majerus et al. 2007).

Unlike *C. septempunctata*, *C. magnifica* is only found foraging in the territories of *F. polyctena* and *F. rufa* colonies (Majerus 1994; Sloggett and Majerus 2000a). This constraint on their distribution is probably counterbalanced by *C. magnifica* out-competing other ladybirds in ant-foraged habitats. Whether this conforms to the Enemy Free Space hypothesis (Jeffries and Lawton 1984) has not been tested experimentally (Sloggett et al. 2004). Another benefit might be a reduced risk of intraguild predation (Bristow 1983; Breton and Addicott 1992; Bishop and Bristow 2003) because *C. magnifica* is normally the only ladybird present in these ant-protected areas (Majerus 1989; Sloggett and Majerus 2000b; Godeau et al., personal observation). However, this also remains to be tested.

Colonies of aphids tended by ants are generally larger than unattended ones, they have a higher growth rate and last longer because winged forms appear and disperse later (e.g. El-Ziady and Kennedy 1956; Banks 1962; Way 1963; Kleinjan and Mittler 1975; Addicott 1979; Bristow 1984; Völkl 1992; Flatt and Weisser 2000; Sloggett and Majerus 2000b). It is suggested that the positive impact of ants on aphid colonies is the driving force in the evolution of myrmecophily in ladybirds (Sloggett and Majerus 2000a). Nevertheless, even in these rich food patches, *C. magnifica* still has to cope with or avoid inciting attack by the ants protecting these resources.

Species of ants belonging to the genera *Lasius* and *Formica* are the most common ants attending aphids in Europe (Hölldobler and Wilson 1990). They do not sting but can bite or spray formic acid (Hölldobler and Wilson 1990). Ants use their mandibles to kill eggs and larvae, which are easily seized and bitten (Bradley 1973;

Sloggett and Majerus 2003). Adult ladybirds, however, can easily escape ant attacks by ducking down or dropping off a plant (Bradley 1973; Sloggett et al. 1998). They are thought to be able to withstand attacks by ants thanks to their domed shape and smooth dorsal surface. When molested, ladybirds may also reflex bleed. The substances contained in this exudate are repulsive or distasteful to ants (Happ and Eisner 1961; Pasteels et al. 1973; Holloway et al. 1991).

Adults and larvae of *C. magnifica* are less frequently attacked by *Formica* workers than are those of *C. septempunctata* (Sloggett and Majerus 2000a, b; Sloggett and Majerus 2003) and, unlike this species, *C. magnifica* is more likely to remain in the vicinity of ant-tended colonies than to fly away (Sloggett et al. 1998). In our opinion this suggests that myrmecophilous species have evolved chemical and/or behavioural adaptations for living with ants. For example, chemicals on the body surface or in the droplets of haemolymph produced by *C. magnifica* when it reflex bleeds might reduce the aggressiveness of ants toward this species of ladybird. Despite the indications that *C. magnifica* is adapted to living in aphid colonies tended by ants, the mechanism(s) by which they achieve this is(are) unknown.

The objective of this study was to determine how *C. magnifica,* unlike *C. septempunctata,* is able to successfully coexist with ants. The foraging behaviour of these ladybirds in the presence of ants was studied in the laboratory, in particular (a) the intensity of aggression shown by ants to the eggs, larvae and adults of both species and (b) the impact of ants on the foraging efficiency of these ladybirds.

Material and Methods

The Ant Colony

A *F. polyctena* nest was collected from the field in Belgium (Mons) and maintained for 5 years in the laboratory (20±1°C, LD 16:8) in a large plastic container (70×50×50 cm). This fully-functional nest contained several hundred workers and some queens and produced brood every year. Wooden bridges linked the nest to foraging trays where the workers had access to dead cockroaches and to several glass tubes filled with a sugary solution and plugged with a piece of cotton wool. Fresh cockroaches and supplies of sugar were provided every week. Other bridges connected the nest to garbage and experimental arenas. Fluon® was painted around the rim of the plastic container and the various trays to prevent ants from escaping.

Ladybird Culture

Adults of *C. magnifica* and *C. septempunctata* were collected in the field and used to set up two laboratory cultures. They consisted of adults kept at 20±1°C under LD conditions of 16:8 h, in 5-l plastic boxes, which contained a piece of corrugated filter paper on which the females laid eggs. Three times a week the ladybirds were fed an excess of pea aphids, *Acyrthosiphon pisum* Harris reared on broad beans, *Vicia faba* L. Two stems of broad bean were added to each box to improve the survival of the aphids. Eggs were taken from the stock culture and incubated in 175-cm^3 plastic boxes kept under the same conditions as the stock culture. After hatching the larvae were fed three times a week with an excess of pea aphids until pupation.

Experiment 1: Response of ants to ladybird eggs and larvae

Strips of corrugated filter paper with batches of *C. septempunctata* eggs were taken from the stock culture. The filter paper around each egg batch was carefully cut with fine scissors. Then, a batch of eggs (average batch size for *C. septempunctata*: 45.5 eggs) was stuck to the bottom of an ant-foraging tray with a piece of adhesive tape. The access point to this tray was opened to the ants and the number of times they palpated the eggs with their antennae and bit the eggs was counted over a period of 2 min. The number of antennal contacts with eggs was recorded in order to estimate the level of ant activity. This was repeated ten times and the same experiment was repeated ten times using *C. magnifica* eggs (average batch size for *C. magnifica*: 28.2 eggs). The trials were conducted when eggs from our ladybird culture were available, i.e. throughout 2 and 4 weeks, for *C. septempunctata* and *C. magnifica* respectively. For each species, the results were subsequently divided into two equal periods to check for any effect of time on the behaviour of ants during the experiment. The numbers of times the ants bit the eggs were compared using an ANCOVA, with a model including the periods of time and the species of ladybirds as fixed factors. The number of times the ants palpated the eggs was used as covariate to control for the ant activity. The values were square-root transformed prior to the analysis (Sokal and Rohlf 1995).

A first instar larva of *C. septempunctata* was taken from the stock culture, put on a piece of filter paper and gently placed in the experimental arena. Then, the ants were given access to the arena. The number of times the ants bit the larvae was recorded over a period of 5 min. This was repeated ten times. The same experiment was then performed using successively 15 second or third larvae and 15 fourth instar larvae. Larvae of *C. magnifica* were then similarly treated. The numbers of times the ants bit the larvae of the two species of ladybirds were compared using non-parametric Mann–Whitney tests.

Experiment 2: Response of ants to ladybird adults

An adult of *C. septempunctata* was taken from the stock culture and placed in an arena where ants from the colony foraged. Care was taken not to stress the ladybird and so avoid reflex bleeding. Four categories of interaction were observed, ranging from low to high aggressiveness:

Level 0 (very low aggressiveness) = ants approach, walk, self groom, interact with another worker and ignore the ladybird; level 1 = ants palpate the ladybird with their antennae or their labial mouthparts; level 2 = ants try to bite the ladybird and simultaneously often straddle the ladybird; level 3 (high aggressiveness) = ants bite the ladybird, bend their abdomen and spray formic acid or pull at the beetle after biting. The interactions between the ants and the ladybird were observed for 10 min and the number of each type of interaction counted. This was repeated ten times with *C. septempunctata*. Ten adult *C. magnifica* were then similarly treated. The frequencies of the four types of interactions recorded for both species of ladybird were compared using a G-test (Sokal and Rohlf 1995).

Experiment 3: Predation efficiency of ladybird adults in the presence and absence of ants

Two saplings of *Betula pendula* L., measuring about 1.5 m, were dug up from a plot of land colonized by birches in autumn 2001 and planted individually in 30 cm diameter pots filled with standard compost. These saplings were kept outside during winter. The next spring they were placed in the laboratory; wooden bridges connected the pots to the nest of *F. polyctena*. In April 2002, ten twigs of birch infested with small colonies (<50 individuals) of *Symydobius oblongus* (von Heyden) were collected from the field and transferred to the laboratory. This aphid is always tended by ants (Heie 1982). Aphids readily moved from the twigs to the branches of the potted birches and formed new colonies. There were more than ten aphid colonies on each sapling in July 2002 when they were used for the experiments on predation efficiency.

An adult of *C. septempunctata* was taken from the stock culture and kept for 24 h without food in a Petri dish. At the end of this period it was gently transferred to the base of a birch branch on which ants were foraging. The number of aphids eaten by the ladybird, the predation success (= aphid eaten/aphid attacked) and the number of aphids leaving the colonies attacked by the ladybird were recorded over a period of 10 min. At the same time it was also noted whether the ladybird ducked down, reflex bled or fled when it encountered ants. This was repeated 17 times and a new aphid colony used for each replicate. During the ten first replicates of this experiment, the aggressive behaviour of the ants was also recorded using the four categories defined in experiment 2. Seventeen other adults of *C. septempunctata* were similarly treated, except that ants were excluded by a ring of glue round the base of the branch 24 h prior to the experiment.

The behaviour of 20 adults of *C. magnifica* was similarly recorded on birch saplings with ants and 20 other adults were observed on birch saplings without ants.

The number of aphids eaten, the predation success and the number of aphids dislodged by the ladybirds were analysed using two way ANOVA, with species and the presence/absence of ants as independent fixed variables. Prior to these analyses, the distributions of frequencies and the variances of the data were respectively normalized and equalized respectively by a log, arcsine and square-root transformation. The number of times the ladybirds ducked down, reflex bled or flew away when encountered by ants were log transformed prior to being analysed using a two way ANOVA, with behaviours and ladybird species as fixed variables, followed by post-hoc Tukey's tests (Sokal and Rohlf 1995). The numbers of behaviour of the different levels of aggression exhibited by the ants encountering ladybirds were divided by the total time of interaction of each repetition. They were then analysed using a two way ANOVA with levels of aggression and ladybird species as fixed variables.

Results

Experiment 1: Response of ants to ladybird eggs and larvae

The activity of the ants did not change during the experiments performed with the eggs of one or the other ladybird species (covariate: $F_{[1,\ 15]}=1.67$; $P=0.216$; Fig. 1

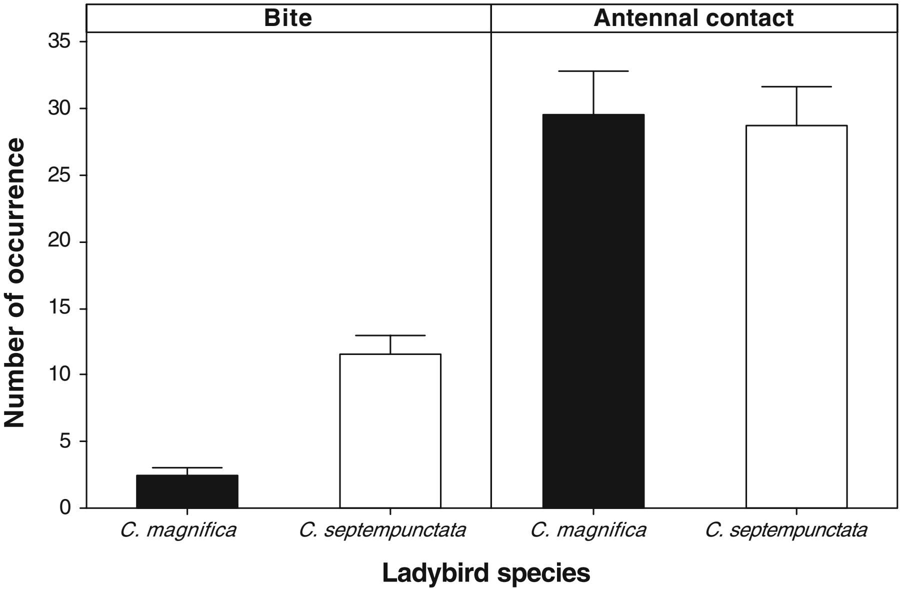

Fig. 1 The mean number (+1 SE) of times ants bit (*left*) or palpated with its antenna (*right*) the cluster of eggs of *C. magnifica* or *C. septempunctata* attached to the bottom of the ant-foraging tray.

(right)). After controlling for the effect of the covariate, *C. magnifica* eggs were bitten significantly less often than those of *C. septempunctata* (Species: $F_{[1,\ 15]}=48.73$; $P=0.000$; Fig. 1 (left)). There was no difference in the number of bites on eggs between the first and the second period of experimentation (Period: $F_{[1,\ 15]}=0.62$; $P=0.444$), and no combined effect of the time and the ladybirds species (Species × Period: $F_{[1,\ 15]}=0.83$; $P=0.377$).

Similarly, *C. magnifica* larvae were bitten significantly less often than those of *C. septempunctata* at all instars (Table 1).

Experiment 2: Response of ants to ladybird adults

The ants responded to the adults of both species of *Coccinella* similarly. The most aggressive types of interaction (level 3) were rather rare and *C. septempunctata* was not subjected to more attacks than *C. magnifica* ($G=2.6$; $df=3$; N.S.; Fig. 2).

Table 1 The Mean Number of Times *F. polyctena* Workers Bit the Larva of *C. septempunctata* and *C. magnifica* Placed in the Foraging Tray (*N*=the Number of Replicates)

Stage	Number	*C. magnifica*	*C. septempunctata*	Mann–Whitney (W)	*P*-value
Instar 1	10	1.3	4.4	136.0	0.0184
Instar 2 and 3	15	4.2	12.8	326.5	0.0001
Instar 4	15	4.5	8.3	290.5	0.0166

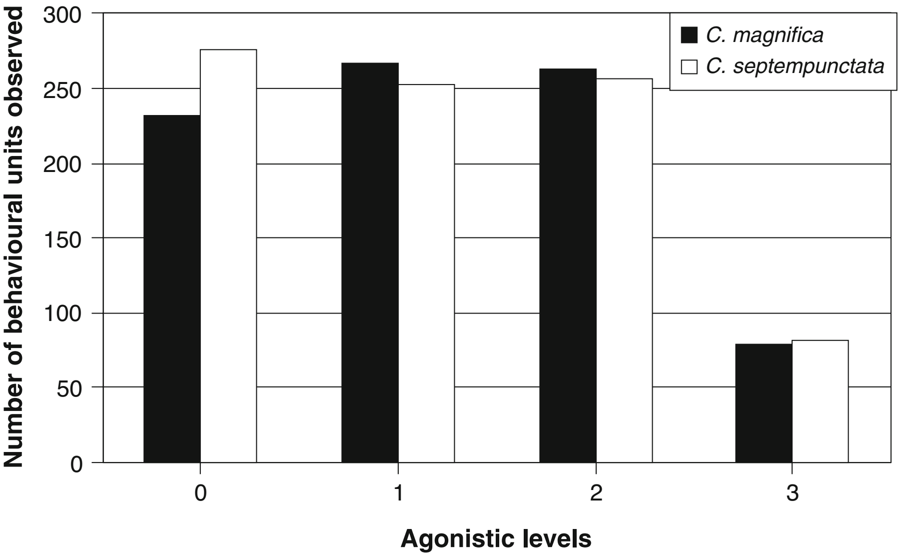

Fig. 2 The distribution of frequencies of the behaviours of increasing aggressiveness displayed by *F. polyctena* workers towards *C. magnifica* or *C. septempunctata* adults placed on ant foraging trails in the laboratory.

Experiment 3: Predation efficiency of ladybird adults in the presence and absence of ants

Ladybird Predation

In terms of the number of aphids eaten, predation success and number of aphids escaping from ladybirds, there was no significant interaction between the presence/absence of ants and the ladybird species (number of aphids eaten: $F_{[1,\ 70]} = 0.04$; P=0.848; predation success: $F_{[1,\ 70]}$=3.10; P=0.083; number of aphids escaping: $F_{[1,\ 70]}$=4.07; P=0.051).

For both species of ladybirds, the presence of the ants resulted in a significant decrease in the number of aphids eaten and of aphids leaving colonies attacked by ladybirds compared to when ants were absent (number of aphids eaten: $F_{[3,\ 70]}$= 6.96; P=0.000; number of aphids leaving the colony: $F_{[3,\ 70]}$=6.77; P=0.001). *C. magnifica* tended always to eat more aphids, dislodged fewer aphids and had a higher predation success than *C. septempunctata* (Fig. 3). The highest difference in the performances among the treatments was found between *C. magnifica* and *C. septempunctata* in the presence of ants (Tukey comparisons: number of aphids eaten: T=−2.711; P=0.041; predation success: T=−4.45; P=0.000).

Ladybird Behaviour

The two ladybirds differed significantly in their reactions to ant attacks (interaction: $F_{[2,\ 99]}$=15.72; P=0.000; Fig. 4). The most common reaction of *C. septempunctata* was to move away from ants, which they did significantly more often than *C. magnifica* (Tukey comparison: T=−5.47; P=0.000; Fig. 4). When attacked by ants

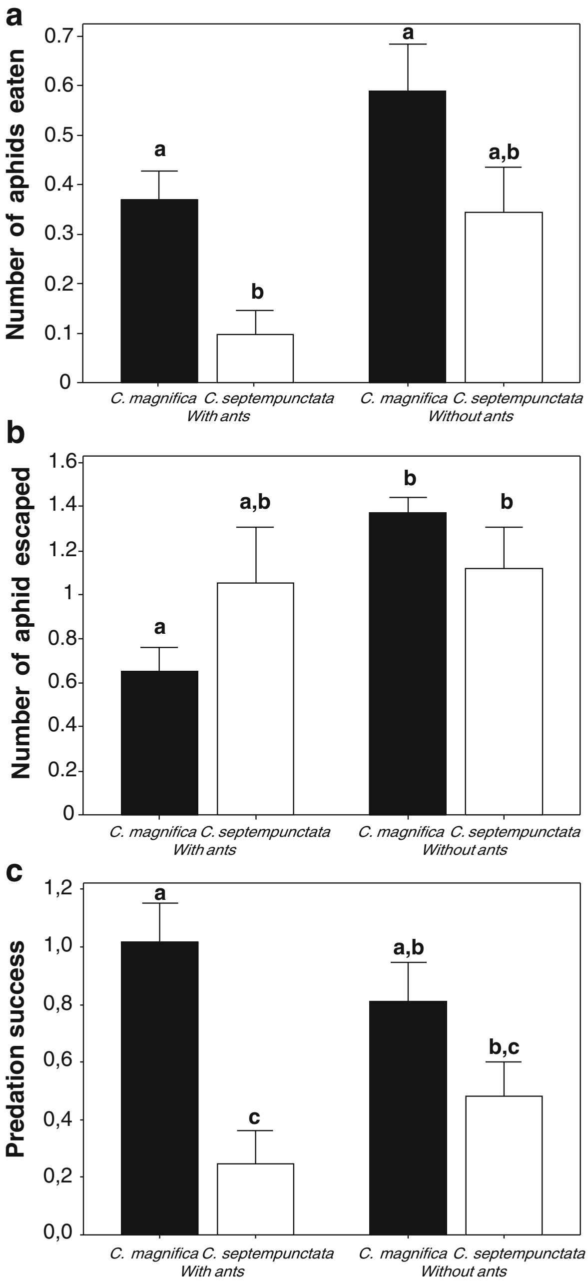

Fig. 3 The mean number (+1 SE) of aphids eaten (**a**), escaped (**b**) and the mean value of the predation success (**c**) of adults of *C. magnifica* and *C. septempunctata* preying on the aphid *S. oblongus* on potted birch saplings in the presence or absence of ants. *Bars* with the same *letter* are not statistically different at $P=0.05$ (Tukey's post-hoc comparisons).

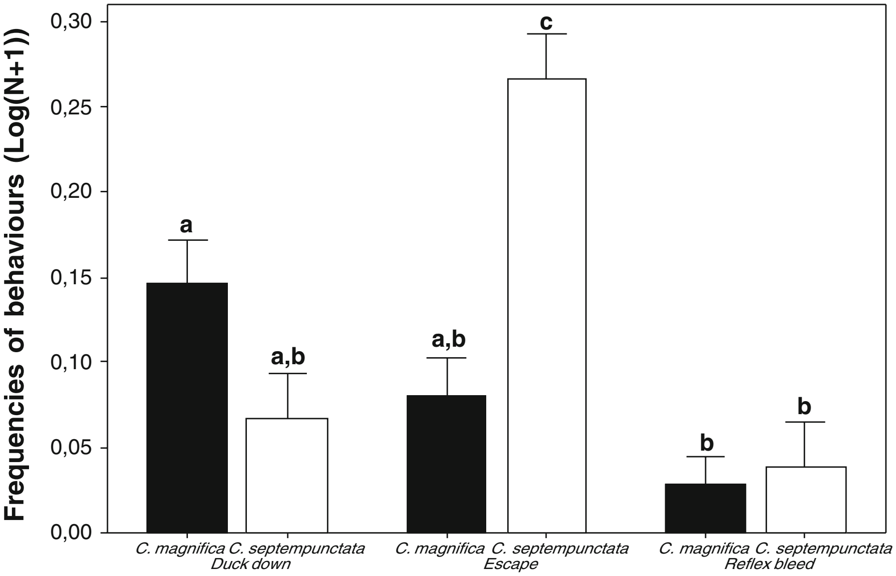

Fig. 4 The frequencies of the behaviours (duck down, escape or reflex bleed) of adults of *C. magnifica* and *C. septempunctata* when attacked by ants defending *S. oblongus* colonies on potted birch saplings in the laboratory. *Bars* with the same *letter* are not statistically different at $P=0.05$ (Tukey's post-hoc comparisons).

C. magnifica tended to stay in or next to an aphid colony and duck down more often than *C. septempunctata* (Tukey comparison: $T=2.32$; $P=0.190$; Fig. 4). Reflex bleeding occurred less frequently than either ducking down (Tukey comparison: $T=-3.04$; $P=0.008$) or moving away (Tukey comparison: $T=-5.83$; $P=0.000$) and to a similar extent in both ladybirds (Tukey comparison: $T=-0.323$; $P=0.990$; Fig. 4). As a consequence, *C. magnifica* spent on average significantly more time in an aphid patch than *C. septempunctata* (496 versus 114.5 s; $W=60$; $P=0.001$).

Ant Behaviour

The number of the behaviours per second shown by the ants toward *C. septempunctata* was higher than toward *C. magnifica* (Ladybird species: $F_{[1,\ 94]}=12.65$; $P=0.001$; Table 2). The ants showed a low level of aggression ('Contact' and 'Ant tries to bite'), which rarely involved biting (Level of aggression: $F_{[4,\ 94]}=3.97$; $P=0.005$; Table 2), but this pattern was similar for both ladybird species (Interaction: $F_{[4,\ 94]}=2.09$; $P=0.090$; Table 2).

Discussion

The results of the experiments in which ladybird eggs, larvae and adults were presented to ants suggest that two different but complementary mechanisms account for the relative immunity of *C. magnifica* from *F. polyctena* attack. This ladybird may be protected chemically and/or behaviourally.

Table 2 The Number of the Behaviours of the Different Levels of Aggression Exhibited per Second by Ants Encountering Adults of *C. magnifica* and *C. septempunctata* in or Close to an Aphid Colony of *S. oblongus* on Potted Birch Saplings in the Laboratory

Level of aggression	*C. septempunctata*[a]	*C. magnifica*
Contact (level 1)	0.107	0.015
Ant tries to bite (level 2)	0.136	0.028
Bite elytra (level 3)	0.032	0.010
Bite leg (level 3)	0.000	0.000
Abdomen bending (level 3)	0.050	0.009

[a] There were only nine replicates because on one occasion there was no interaction between an adult of *C. septempunctata* and the ants

The eggs and larvae of ladybirds are easily killed by ants biting them. Therefore, it would be adaptive if these stages of *C. magnifica* were protected by cuticular chemicals that reduce ant aggression. When placed on ant trails in the laboratory, eggs and larvae of *C. magnifica* were less frequently attacked than those of *C. septempunctata*. The latter were often destroyed by ants. That is, workers of *F. polyctena* are able to distinguish between the immature stages of these two ladybirds. Cuticular hydrocarbons are a good candidate as they are known to play a role in the communication between ladybirds (Hemptinne et al. 1996, 1998). Moreover, nestmate recognition in ants is also mediated by cuticular hydrocarbons and fatty acids (Dettner and Liepert 1994; Lenoir et al. 2001) and the hydrocarbon profiles of myrmecophilous guests are similar to those of their host ants (Vander Meer and Wojcik 1982; Akino 2002; Orivel et al. 2004).

Adults of both *C. magnifica* and *C. septempunctata* are attacked when dropped on ant nests (Donisthorpe 1920a, b), and on foraging trails and on ant-tended aphid colonies in the field (Sloggett et al. 1998; Sloggett and Majerus 2003). This is confirmed by our experiments in the laboratory on foraging trays and on birch saplings infested with *S. oblongus*. The experiment using potted birches points to another aspect of the interactions between ants and ladybirds. *C. septempunctata* has a natural tendency to leave aphid patches when it is attacked by ants whereas *C. magnifica* tended to assume a defensive position and to stay longer in ant-tended aphid colonies. The adults frequently ducked down and on several occasions moved their elytra to shield themselves and fend off ant attacks. *C. magnifica* can even continue eating an aphid when it crouches closely against the substrate or when ants try to bite it (personal observation; Sloggett et al. 1998). Sometimes *C. magnifica* grasps an aphid and retreats some distance from the colony to escape ant attacks (personal observation; Sloggett and Majerus 2003). This behaviour is not only known for *C. magnifica* but is also proposed as the mechanism by which *C. septempunctata* is able to reduce aphid disturbance when foraging on *Centaurea sp.* (Stadler 1991). Although chemicals probably play a role in the protection of immature stages of *C. magnifica* from ant aggression, the behaviour of the adults allows this ladybird to forage in the territories of *F. rufa* and *F. polyctena*.

The predation success of *C. magnifica* and *C. septempunctata* foraging on potted birches in the absence of ants differed with the former species eating more aphids than the latter. This advantage of *C. magnifica* is greater when ants have access to the birches. *C. magnifica* also disturbed the aphids less in ant-attended colonies. As ladybirds often experience difficulties in eating aphids in the presence of ants it is not surprising that *C. septempunctata* and other ladybird species are rarely found with *C. magnifica* in the field.

The results of the laboratory experiments reported here indicate that ants have a negative effect on ladybird foraging success, as is recorded for the hyperparasitoid *Alloxysta brevis* (Thomson) (Hübner 2000). The number of aphids eaten by both ladybirds decreased when ants were present. Probably, the ants disturbed these ladybirds and therefore increased their prey handling time. *C. magnifica* stayed in ant-tended aphid colonies, whereas *C. septempunctata* left when ants were present. This difference in behaviour enables *C. magnifica* to exploit a rich source of food, which is not available to many other aphidophagous insects.

In another experiment, we found that two non-myrmecophilous (*Metopolophium dirhodum* (Walker) and *A. pisum*) and an obligatory myrmecophilous aphid (*S. oblongus*) are equally suitable food for *C. magnifica* (Godeau et al., in prep). Thus *C. magnifica* is not a strongly prey specific species, which is consistent with its large set of preferred prey (Sloggett et al. 2002).

The two myrmecophilous ladybirds, *C. magnifica* and *P. luteorubra*, strongly differ in prey specificity, with the former being a generalist like *C. septempunctata,* but restricted to particular habitats, and the latter being oligophagous, and feeding on aphids infesting common plants like *C. arvense* or *T. vulgare*. These two examples suggest that myrmecophily evolved independently several times in the Coccinellidae and, as a result, is likely to take different forms. Comparisons with other myrmecophilous eating Hemiptera are needed for a better understanding of these complex interactions.

The degree of protection of mutualistic Hemiptera by ants is highly variable in space and time, depending on the densities of the colonies (Breton and Addicott 1992; Bishop and Bristow 2003) or honeydew composition (Völkl et al. 1999; Fischer et al. 2002; Woodring et al. 2004). Similarly, two species of aphids can compete for ant protection in the same habitat yet be unequally protected because of their species specific characteristics. Mutualistic interactions therefore are very variable, which could explain the diversity of ant-associated mutualist predators.

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