

Larvae of the green lacewing *Mallada desjardinsi* (Neuroptera: Chrysopidae) protect themselves against aphid-tending ants by carrying dead aphids on their backs

Masayuki Hayashi · Masashi Nomura

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Abstract Larvae of the green lacewing *Mallada desjardinsi* Navas are known to place dead aphids on their backs. To clarify the protective role of the carried dead aphids against ants and the advantages of carrying them for lacewing larvae on ant-tended aphid colonies, we carried out some laboratory experiments. In experiments that exposed lacewing larvae to ants, approximately 40% of the larvae without dead aphids were killed by ants, whereas no larvae carrying dead aphids were killed. The presence of the dead aphids did not affect the attack frequency of the ants. When we introduced the lacewing larvae onto plants colonized by ant-tended aphids, larvae with dead aphids stayed for longer on the plants and preyed on more aphids than larvae without dead aphids. Furthermore, the lacewing larvae with dead aphids were attacked less by ants than larvae without dead aphids. It is suggested that the presence of the dead aphids provides physical protection and attenuates ant aggression toward lacewing larvae on ant-tended aphid colonies.

Keywords Ant–aphid mutualism · Defensive behavior · *Mallada desjardinsi* · *Tetramorium tsushimae* · *Aphis craccivora*

Introduction

Many ants tend myrmecophilous homopterans such as aphids and scale insects, and utilize the secreted honeydew as a sugar resource; in return, the homopterans receive beneficial services from the tending ants (Way 1963; Breton and Addicott 1992; Nielsen et al. 2010). These mutualistic interactions between ants and homopterans reduce the survival and abundance of other arthropods, including non-honeydew-producing herbivores and other predators (Bristow 1984; Buckley 1987; Suzuki et al. 2004; Kaplan and Eubanks 2005), because the tending ants become more aggressive and attack arthropods that they encounter on plants (Way 1963). Hence, natural enemies of homopterans such as predators and parasitoids are heavily attacked and excluded by homopteran-tending ants (Bristow 1984; Vinson and Scarborough 1991; Itioka and Inoue 1996). However, the exclusion by ants is not effective against all predators and parasitoid species; some predators and parasitoids are able to utilize aphids that ants are guarding to avoid ant aggression through behavioral, morphological and/or chemical adaptations (Völkl 1992, 1995; Liepert and Dettner 1993, 1996; Völkl and Vohland 1996; Sloggett et al. 1998, 2002; Sloggett and Majerus 2003; Kaneko 2002; Godeau et al. 2009; Schwartzberg et al. 2010). Some species of predators are reported to avoid being attacked by ants tending homopterans by covering their backs with wax structures. Coccinellid species, such as *Scymnus* spp. and *Azya orbigera* Mulsant, were reported to feed on ant-tended homopterans by producing and covering their back with wax (Völkl and Vohland 1996; Kaneko 2002, 2007; Liere and Perfecto 2008; Schwartzberg et al. 2010). The wax produced by larvae of *Scymnus louisianae* J. Chapin has been shown to attenuate ant aggression against the larvae (Schwartzberg et al. 2010). On the other hand, although

M. Hayashi (✉) · M. Nomura
Laboratory of Applied Entomology, Faculty of Horticulture,
Chiba University, Matsudo, Chiba 271-8510, Japan
e-mail: kichomen_h@hotmail.com

Present Address:
M. Hayashi
Graduate School of Horticulture, Chiba University, Matsudo,
Chiba 271-8510, Japan

larvae of the green lacewing *Chrysopa slossonae* Banks are reported to exploit ant-tended aphids by similarly covering their back with wax, the larvae do not produce the wax by themselves. The larvae of *C. slossonae*, which are specialist predators of the woolly alder aphid *Prociphilus tessellates* Fitch, steal and place the wax secreted by their prey on their own back (Eisner et al. 1978; Milbrath et al. 1993). Eisner et al. (1978) reported that the larvae carrying wax are ignored, or are bitten but immediately released by ants guarding the aphids, and they suggested that the wax prevents recognition by ants and that its stickiness provides physical protection.

The larvae of *C. slossonae* are not the only chrysopid species that place extraneous materials on their backs. Many species of chrysopid larvae carry not only aphid wax like *C. slossonae* but also various debris, such as dead aphids, aphids' exuviae, pieces of plants, etc. (Tsukaguchi 1995). When the chrysopid larvae of debris-carrier species prey on aphid species that do not secrete wax, the larvae necessarily place debris such as dead aphids other than aphids' wax. The debris on the back of chrysopid larvae is reported to reduce intraguild predation by larvae of ladybirds (Nakahira and Arakawa 2006) and green lacewings of other species, as well as cannibalism (Anderson et al. 2003; Mochizuki et al. 2006). In an ant-tended aphid colony, however, the intraguild predators are likely to be excluded by guarding ants. Therefore, carrying debris may protect the lacewing larvae against guarding ants rather than intraguild predators. We observed that chrysopid larvae carrying debris live near aphids that are tended by ants and prey on the aphids. Debris other than the aphid wax carried by chrysopid larvae is similarly suspected of having some defensive effects against aphid-tending ants and providing advantages for exploiting ant-tended aphids. However, there is no report about the role of the debris on the back of lacewing larvae in ant–aphid mutualisms.

We tested this possibility using the green lacewing *Mallada desjardinsi* Navas in laboratory experiments. Although larvae of *M. desjardinsi* are known to feed on several aphid species, including the myrmecophilous aphid *Aphis craccivora* Koch, they do not use ants as a food source under natural conditions (Tsukaguchi 1995; personal observations). The larvae carry debris such as dead aphids (Tsukaguchi 1995; Mochizuki et al. 2006; Nakahira and Arakawa 2006), and we observed that the larvae of *M. desjardinsi* carrying dead aphids live near ant-tended aphids and prey on the aphids under natural conditions. In this study, we elucidated the defensive function of the dead aphids carried by the larvae of *M. desjardinsi* against ants and the advantage of the dead aphids to the larvae on ant-tended aphid colonies. First, to investigate whether the dead aphids on the back of the lacewing larvae function as a defense, we exposed the larvae to ants. Second, to

elucidate whether the dead aphids on the back provide advantages for the lacewing larvae on ant-tended aphid colonies, we introduced the lacewing larvae onto plants colonized by aphids that ants were tending.

Materials and methods

Insects and plants

Adult females of the green lacewing *M. desjardinsi* were collected in Matsudo City, Japan (35°77'N, 130°06'E) from June to August 2010. The lacewings were maintained in plastic cups (120 mm in diameter, 90 mm in depth) and provided with an artificial diet (honey and dry yeast) as a food source for the adults and water-saturated cotton wool. Each egg laid by a female on a cup was individually transferred to a plastic case (12 mm in diameter, 12 mm in depth). Newly hatched larvae were reared by supplying them with eggs of the flower moth *Ephestia kuehniella* Zeller (Entofood; Arysta Lifescience Corp., Tokyo, Japan) as a food source in a climate-controlled room (25 ± 1°C, 16L8D). We used the third instar larvae of the lacewing in all experiments.

A. craccivora are myrmecophilous aphids that provide honeydew to several ant species (Katayama and Suzuki 2003a). We collected the aphids from the locust tree *Robinia pseudoacacia* L. in Matsudo City in July and September 2010 and used them in all experiments.

It is known that workers of the ant *Tetramorium tsushimae* Emery prefer sugars such as honeydew of homopterans. Under natural conditions, workers of *T. tsushimae* are often observed on plants colonized by *A. craccivora* (Katayama and Suzuki 2003a; personal observations). The ant colonies were collected in Matsudo City from May to August 2010. Each ant colony was composed of some queens, over 100 broods and over 300 workers. The ants were supplied with the mealworm *Tenebrio molitor* Linnaeus, and were colonized in glass test tubes (12 mm in diameter and 120 mm length). The colonies were maintained in a climate-controlled room (25 ± 1°C, 16L8D).

The broad bean plant *Vicia faba* L. is a host of *A. craccivora*. Seeds were individually sown in plastic pots (90 mm in diameter, 45 mm in depth) filled with vermiculite, and then the pots were kept in a climate-controlled room (25 ± 1°C, 16L8D). We used seedlings that reached 17–20 cm in height.

Treatments of green lacewing larvae

The third-instar larvae of *M. desjardinsi* were individually transferred into a plastic square Petri dish (25 mm × 25 mm, 10 mm in depth) and kept with 25–30 *A. craccivora*

for 24 h. Although some individual aphids were not preyed upon, we observed that all lacewing larvae preyed on aphids and placed the remains of aphids on their backs. As a control, we carefully removed dead aphids from lacewing larvae with a fine paintbrush without damaging the larvae (Fig. 1).

Exposure of the lacewing larvae to ants

Ten foraging workers of *T. tsushimae* were randomly selected from each ant colony and transferred to a plastic Petri dish (90 mm in diameter, 12 mm in depth). We coated the side of the Petri dish with Fluon® to prevent the ants and lacewing larvae from escaping. Ants were left in the Petri dish for 15 min to settle, then a lacewing larva with or without dead aphids was introduced into the same dish. Their behavior was recorded with a digital video camera (Sony, HDR-XR550V). The maximum duration of each observation was 15 min. When the lacewing larva was killed by the ants, we stopped recording the behavior of the ants. We measured how many times the lacewing larvae were contacted and attacked by ants during the experiments, and the survival of the larvae. Biting behavior was measured as an indicator of attack against the lacewing larvae. To adjust for differences in the duration of observation, we compared the numbers of larvae contacted and attacked by ants per minute. When ants attacked the lacewing larvae carrying dead aphids, we distinguished whether the ants bit the bodies of the larvae or the dead aphids on their back, and calculated the ratio of attacks to the bodies of the larvae (number of attacks to the bodies of the larvae by ants divided by the number of all attacks by ants). We repeated the experiment 19 times. The number of contacts and attacks by ants per minute and the survival of lacewing larvae were compared between the two treatments using the

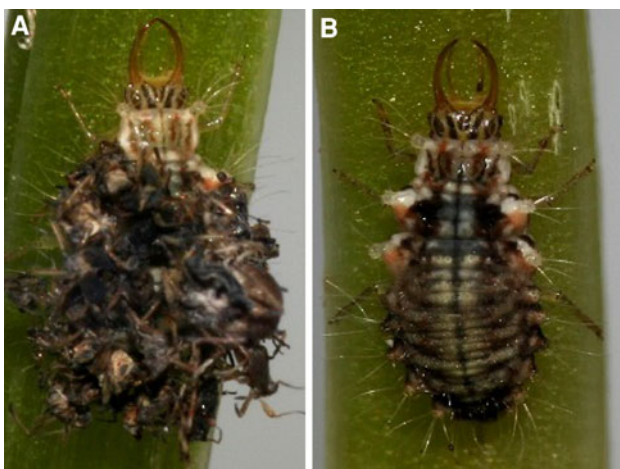


Fig. 1a–b Preparation of *Mallada desjardinsi* larvae. Larva with dead aphids (a) and larva without dead aphids (b)

Mann–Whitney *U* test and Fisher’s exact probability test, respectively.

Foraging of the lacewing larvae on plants colonized by ant-tended aphids

We put a broad bean plant into a plastic pot (90 mm in diameter, 45 mm in depth) filled with water. Branching shoots were removed with scissors to observe the behavior of ants and lacewing larvae on the plant clearly. Each plastic pot was covered with a Petri dish with a hole in the center to pass the stem through. The hole was closed with cotton wool to prevent ants from escaping. The seedling was then placed on an experimental arena made of plaster (45 mm in depth) in a plastic container (23 cm in length, 16 cm in width, 8.5 cm in depth). The inside of this arena was coated with Fluon® (Fig. 2). We placed one hundred aphids on the broad bean plant and an ant colony composed of a queen, 300 workers and about 100 broods nested in a glass test tube on the arena. Under these conditions, the ants could freely visit the aphid colony and feed on honeydew secreted by the aphids as the only available food resource. The ants and aphids were left on the experimental arenas for 4 days to settle.

We prepared lacewing larvae that had been starved for 24 h with and without dead aphids. Each larva was placed on the stem of a seedling. We measured the number of contacts and attacks by ants against the lacewing larva, the number of aphids preyed upon by the lacewing larva, and the residence time of the lacewing larva on the plant. The maximum duration of each observation was 30 min. When the lacewing larvae dropped from broad bean plants, we stopped the observation. To adjust for differences in the duration of observation, we compared the numbers of

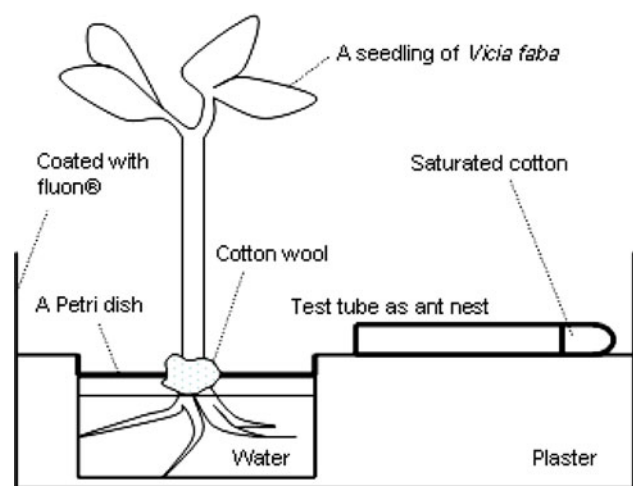


Fig. 2 Illustration of the experimental arena. *Aphis craccivora* were placed on a seedling of *Vicia faba* and *Tetramorium tsushimae* were transferred into this arena to enable the ants to freely visit the seedling colonized by aphids

larvae contacted and attacked by ants per minute. We repeated the experiment 16 times.

The number of contacts and attacks by ants per minute was analyzed using the Mann–Whitney U test; the number of aphids preyed upon by the lacewing larva was also analyzed by the Mann–Whitney U test; while the residence time of the lacewing larva was analyzed by the log rank test.

Results

Exposure of the lacewing larvae to ants

The survival rate of the lacewing larvae with dead aphids was significantly higher than that of the larvae without dead aphids in the presence of ants (survival rate: with dead aphids 100%, without dead aphids 58%, $P < 0.01$) (Fig. 3). Dead aphids on the back of lacewing larvae did not affect the number of contacts of lacewing larvae with ants (the number of contacts per min, mean \pm SE: with dead aphids 2.8 ± 0.30 , without dead aphids 3.0 ± 0.32 , $U = 176.5$, $P = 0.91$). There was no significant difference in the number of attacks by ants against lacewing larvae between lacewing larvae with and without dead aphids (number of attacks per min, mean \pm SE: with dead aphids 0.36 ± 0.09 , without dead aphids 0.41 ± 0.13 , $U = 167.5$, $P = 0.71$) (Fig. 4). When ants attacked the lacewing larvae with dead aphids, 29% of the attacks involved biting the bodies of the larvae.

Foraging of the lacewing larvae on plants colonized by ant-tended aphids

The residence time of the larvae with dead aphids on plants colonized by ant-tended aphids was significantly longer

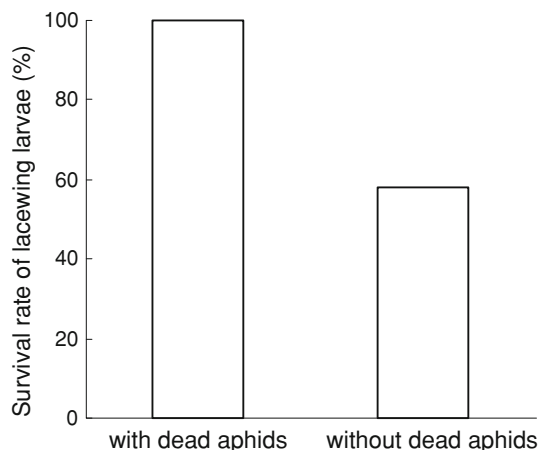


Fig. 3 Survival rate of *Mallada desjardinsi* larvae with and without dead aphids when exposed to *Tetramorium tsushimae*

than that of the larvae without dead aphids ($df = 1$, $\chi^2 = 11.1$, $P < 0.001$) (Fig. 5). Lacewing larvae with dead aphids preyed on significantly larger numbers of aphids than the control larvae (number of preyed-upon aphids, mean \pm SE: with dead aphids 3.8 ± 0.53 , without dead aphids 2.1 ± 0.64 , $U = 65$, $P < 0.05$) (Fig. 6).

The presence of dead aphids on the back of lacewing larvae did not affect the number of contacts of the larvae with ants (number of contacts per min, mean \pm SE: with dead aphids 0.67 ± 0.10 , without dead aphids 0.81 ± 0.13 , $U = 102.5$, $P = 0.35$). The number of attacks by ants against the larvae with dead aphids was significantly lower than that against the larvae without dead aphids (number of attacks per min, mean \pm SE: with dead aphids 0.05 ± 0.02 , without dead aphids 0.12 ± 0.02 , $U = 71$, $P < 0.05$) (Fig. 7).

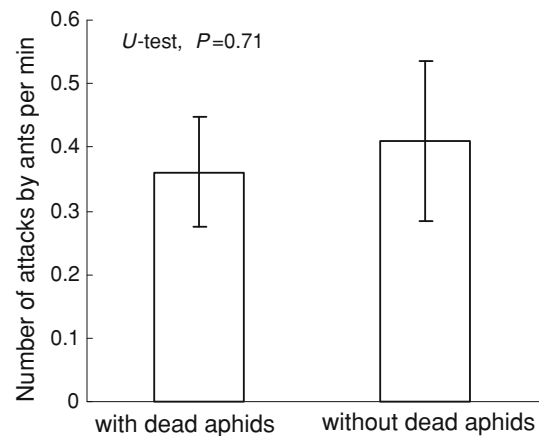


Fig. 4 Number of attacks by *Tetramorium tsushimae* against *Mallada desjardinsi* larvae with and without dead aphids per minute during exposure to ants. Bars show SE

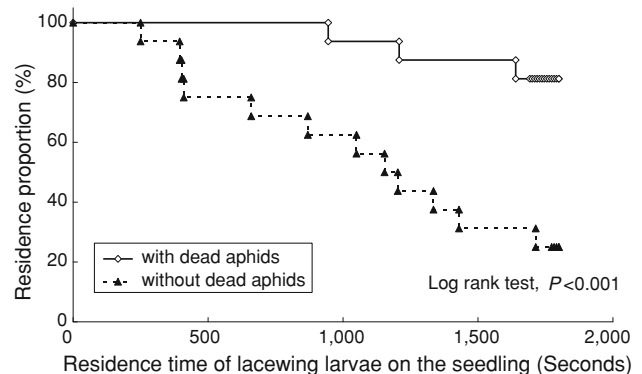


Fig. 5 Residence times of *Mallada desjardinsi* larvae with and without dead aphids on the seedling. The maximum duration of an observation was 1,800 s

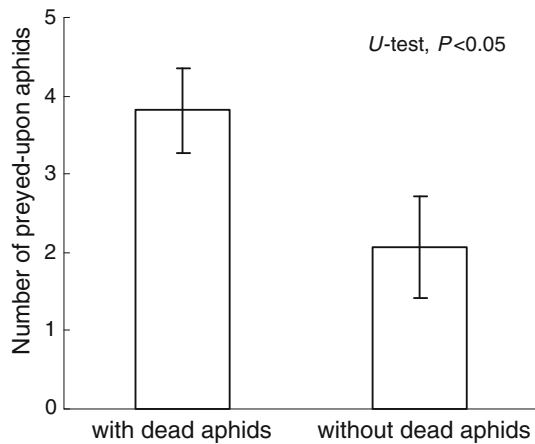


Fig. 6 Number of *Aphis craccivora* preyed upon by *Mallada desjardinsi* larvae during the experiments on plants colonized by ant-tended aphids. Bars show SE

Discussion

When exposed to ants, approximately 40% of the lacewing larvae were killed. However, all of the lacewing larvae carrying dead aphids on their backs survived (Fig. 3). Although the carrying of dead aphids did not affect the frequency of contact and attack by ants (Fig. 4), it did reduce attacks to the bodies of lacewing larvae. These results suggest that dead aphids on the backs of lacewing larvae function as a physical barrier against ants, resulting in increased survival.

When placed on plants colonized by ant-tended aphids, the lacewing larvae with dead aphids stayed on the plant for a longer time than those without dead aphids (Fig. 5). As a result, the larvae with dead aphids consumed more aphids (Fig. 6). These results suggest that carrying dead aphids on the back provides advantages to the lacewing larvae on ant-tended aphid colonies. On the other hand, there was no difference in the frequency of contact of ants with the lacewing larvae with and without dead aphids, although the frequency of attack by ants on the lacewing larvae with dead aphids was lower than that on the larvae without dead aphids (Fig. 7). This result suggests that dead aphids on the back provide protection by altering the behavior of aphid-tending *T. tsushimae*. In the experiments, we observed that the lacewing larvae, regardless of the presence or absence of dead aphids on their back, usually turned their backs toward the ants when the ants contacted the larvae. When there were dead aphids on the back of the larvae, the ants usually antennated the dead aphids. In previous studies, ants were found to use the suite of hydrocarbon compounds in their cuticular wax as a label to recognize nestmates and distinguish among castes (Bonavita-Cougourdan et al. 1993; Lahav et al. 1999; Thomas et al. 1999; Wagner et al. 1998, 2000). Identification of ants is considered to rely on contact

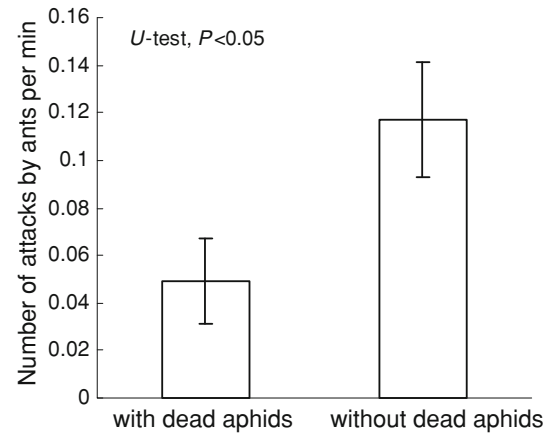


Fig. 7 Number of attacks by *Tetramorium tsushimae* against *Mallada desjardinsi* larvae with and without dead aphids per minute during the experiments on plants colonized by ant-tended aphids. Bars show SE

stimulus using chemical signatures. The cue for the ant's recognition of honeydew-producing homopterans may be associated with the cuticular chemistry of the homopterans (Glinwood et al. 2003; Choe and Rust 2006). Thus, predators and parasitoids that exploit ant-tended aphids without being attacked by ants chemically mimic the cuticular hydrocarbons of their aphids (Liepert and Dettner 1993, 1996; Lohman et al. 2006). In this study, although the presence of dead aphids on the lacewing larvae attenuated aggression by aphid-tending ants, it remains unclear how ants recognize dead aphids on the lacewing larvae and why ants attack less frequently. The dead aphids may prevent ants from recognizing lacewing larvae as a natural enemy of aphids.

However, the reduction in attacks against lacewing larvae with dead aphids was observed only when the larvae were placed on plants colonized by aphids (Figs. 4, 7). Differences in experimental conditions (i.e., the presence of alternative food for ants, the starvation of lacewing larvae, and the experience of the ants with aphids) may explain the reduced attack rate. Since it is reported that ants are less aggressive toward honeydew-producing insects due to their experience of receiving honeydew (Sakata 1994; Choe and Rust 2006), the presence of aphids may affect aggression toward lacewing larvae with dead aphids.

A. craccivora are commonly tended by several ant species such as *T. tsushimae*, *Pristomyrmex punctatus* Smith and *Lasius japonicus* Santschi (Katayama and Suzuki 2003a; personal observations). The exclusion and aggression of ants differ among ant species (Bristow 1984; Itioka and Inoue 1999; Katayama and Suzuki 2003b). Although *T. tsushimae* and *L. japonicus* show similar aggressiveness against enemies of aphids, *L. japonicus* is considered to exclude enemies more effectively than *T. tsushimae* (Katayama and Suzuki 2003b). On the other

hand, *P. punctatus* is less aggressive than *L. japonicus* (Itioka and Inoue 1999). Further studies are needed to clarify whether the dead aphids on the backs of lacewing larvae function as a defense against these ant species.

In the family Chrysopidae, many species are reported to carry debris and feed on myrmecophilous aphid species (Tsukaguchi 1995), and it is predicted that other chrysopid larvae are able to exploit ant-tended aphids like *M. desjardinsi*. Further research to verify this is required.

The results of this study suggest that the larvae of *M. desjardinsi* are able to exploit ant-tended aphids by carrying dead aphids. It is considered that the adaptation of aphidophagous predators and parasitoids to ant–aphid interactions provides some advantages. When ant-unattended resources are scarce, the adapted enemies are able to exploit ant-tended aphids that unadapted enemies cannot prey upon. Additionally, aphid-tending ants provide the adapted enemies with protection from predators, parasitoids or hyperparasitoids (Völkl 1992, 1995; Kaneko 2002; Majerus et al. 2007; Liere and Perfecto 2008). Chrysopid larvae are reported to be preyed upon by a wide range of insect generalist predators, including Anthocoridae, Coccinellidae, Syrphidae, Hemerobiidae and other Chrysopidae, and attacked by parasitic wasps (Canard et al. 1984). It is predicted that aphid-tending ants exclude these enemies of chrysopid larvae. The adaptation of the larvae of *M. desjardinsi* to aphid-tending ants by carrying dead aphids may have these benefits.

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