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<th>論文題名（外国語の場合は、その和訳を併記）</th>
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| Studies on the defensive strategy of the green lacewing *Mallada desjardinsi* against aphid-tending ants |
| (和訳：アブラムシ随伴アリに対するカオマダラクサカゲロウの防御戦略に関する研究) |
Mutualism is defined as an interaction between organisms of different species that is reciprocally beneficial for both species, and is widespread in nature. A well-known example of mutualism is the relationships between ants and honeydew-producing insects such as aphids. Many ants tend mutualistic aphids and utilize the secreted honeydew as a sugar resource, and in return, the aphids receive several beneficial services from the tending ants. The most important service offering to aphids by ants is the exclusion of other arthropods from aphid colonies. Because the tending ants heavily attack other arthropods including natural enemies and competitors of aphids, the aphids are provided with a safe habitat by the tending ants.

Hence, natural enemies of aphids such as predators and parasitoids are excluded by aphid-tending ants. However, the exclusion by ants is not effective against all predator and parasitoid species; some predators and parasitoids are able to utilize aphids that ants are guarding, by avoiding ant aggression through behavioral, morphological and/or chemical adaptations. For example, some species of predators are reported to avoid being attacked by ants tending aphids, by covering their back with wax structures. Ladybeetle species such as Scymnus spp. and Azya orbigera were reported to feed on ant-tended aphids by producing and covering their back with wax. The wax produced by Scymnus larvae has been shown to function as mechanical protection against ants and attenuate ant aggression toward the larvae. On the other hand, the parasitoid female of the aphidiid wasp Lysiphlebus cardui also does not release aggressive behavior in aphid-tending ants when searching for its host aphids. This lack of attacks is explained by reduced aggressiveness of the ants toward the wasps due to similarity in cuticular chemicals between the wasps and host aphids. Thus, the natural
enemies that can consume ant-tended aphids may have evolved to have adopted traits in order to avoid ant aggression. However, there are few studies demonstrating the mechanism that the natural enemies consume ant-tended aphids and avoid ant aggression in detail.

I observed that the green lacewing *Mallada desjardinsi* (Neuroptera: Chrysopidae) utilized ant-tended aphids in the field. Many species of chrysopid larvae including *M. desjardinsi* prey on aphids and show a unique behavior; they have numerous barbed bristles on their dorsal surface that allow the larvae to affix extraneous materials such as aphid carcasses to their backs. These materials carried on the backs of lacewing larvae are considered to function as protection against their predators. Furthermore, the eggs of most chrysopid species also have a unique trait; they are laid at the tip of a thin hyaline stalk. The egg stalks are also considered to have a role in protection against their enemies. Thus, it was predicted that the green lacewing *M. desjardinsi* can utilize ant-tended aphids by avoiding ant aggression by the traits of the larval and embryonic stages.

The aim of the present study is to clarify how the green lacewing *M. desjardinsi* utilizes ant-tended aphids and avoids exclusion by ants. First, I elucidated the defensive function of the aphid carcasses carried by *M. desjardinsi* larvae against ants and the advantage of the aphid carcasses for the larvae on ant-tended aphid colonies (Chapter 1). Second, I investigated the function of chemical substances from aphid carcasses carried by *M. desjardinsi* larvae against aphid-tending ants by performing behavioral assays and chemical analyses (Chapter 2). Third, I tested whether the behavior of ants toward aphids and *M. desjardinsi* larvae depends on the aphid-tending...
experience of the ants (Chapter 3). Finally, I investigated whether egg stalks of *M. desjardinsi* provide a defense function against ants and intraguild predators, and whether eggs of *M. desjardinsi* are protected from predation by aphid-tending ants (Chapter 4). Based on these results, I discussed the benefits obtained by *M. desjardinsi* from utilizing ant-tended aphids with avoiding ant aggressions.

In Chapter 1, to clarify the protective role of aphid carcasses against ants and the advantages of carrying them for lacewing larvae on ant-tended aphid colonies, I carried out some laboratory experiments. In experiments that exposed lacewing larvae to ants, approximately 40% of the larvae without aphid carcasses were killed by ants, whereas no larvae carrying aphid carcasses were killed. The presence of the aphid carcasses did not affect the attack frequency of the ants. When I introduced the lacewing larvae onto plants colonized by ant-tended aphids, larvae with aphid carcasses stayed for longer on the plants and preyed on more aphids than larvae without aphid carcasses. Furthermore, the lacewing larvae with aphid carcasses were attacked less by ants than larvae without aphid carcasses. It is suggested that the presence of the aphid carcasses provides physical protection and attenuates ant aggression toward lacewing larvae on ant-tended aphid colonies.

In Chapter 2, I tested whether cuticular hydrocarbons (CHCs) of aphid carcasses affected the aggressiveness of aphid-tending ants. Aphid carcasses were washed with *n*-hexane to remove lipids. Lacewing larvae with washed aphid carcasses were attacked by aphid-tending ants more frequently than those with untreated aphid carcasses. I measured the aggressiveness of aphid-tending ants to lacewing larvae that were either carrying a piece of cotton wool (a dummy aphid carcass) treated with CHCs
from aphids or lacewing larvae, or carrying aphid carcasses. The rates of attack by ants on lacewing larvae carrying CHCs of aphids or aphid carcasses were lower than that of attack on lacewing larvae with conspecific CHCs. Chemical analysis by gas chromatography/mass spectrometry showed similarity of CHCs between aphids and aphid carcasses. These results suggest that aphid carcasses on the backs of lacewing larvae function via chemical mimicry to limit attacks by aphid-tending ants.

In Chapter 3, I examined whether the behavior of ants toward aphids and lacewing larvae, changed depending on their aphid-tending experience. The results indicate that the ability of ants to recognize mutualistic aphids is acquired by learning, because ants exhibited lower levels of aggressiveness towards aphids when they had previous experience of tending aphids. Ants also moderated their aggressiveness toward lacewing larvae carrying aphid carcasses if the ants had previously tended aphids, indicating that chemical mimicry by carrying aphid carcasses is dependent on ants having learned aphid chemical cues. Chemical mimicry by lacewing larvae is therefore considered to exploit the recognition systems of ants.

In Chapter 4, I examined whether the egg stalks of lacewings protect the eggs from ants and predators. When exposed to ants, almost all eggs with intact stalks were untouched, whereas 50-80% of eggs in which stalks had been severed at their bases were destroyed by ants. In contrast, most eggs were preyed upon by larvae of the lacewing *Chrysoperla nipponensis*, an intraguild predator of *M. desjardinsi*, regardless of whether their stalks had been severed. These findings suggest that egg stalks provide protection from ants but not from *C. nipponensis* larvae. To test whether *M. desjardinsi* eggs are protected from predators by aphid-tending ants, we introduced *C. nipponensis*
larvae onto plants colonized by ant-tended aphids. A significantly greater number of eggs survived in the presence of ants because aphid-tending ants excluded larvae of *C. nipponensis*. This finding indicates that *M. desjardinsi* eggs are indirectly protected from predators by ants in ant-tended aphid colonies.

A suite of studies suggested that the lacewing *M. desjardinsi* exploits ant-tended aphids by laying stalked eggs and carrying aphid carcasses. It is considered that adaptation of aphidophagous predators and parasitoids to ant-aphid interactions provides some benefits. Because natural enemies of aphids are usually attacked and excluded by aphid-tending ants, natural enemies without exclusion by aphid-tending ants would be able to exploit food sources that are largely free from other competitors. Furthermore, these adapted enemies are protected against their own natural enemies by the aphid-tending ants. Several other natural enemies of ant-tended aphids are also known to reduce their risk of predation or parasitism indirectly by presence of aphid-tending ants. In particular, chrysopid eggs and larvae are reported to be preyed by a wide range of insect generalist predators. Aphid-tending ants would exclude these enemies of the lacewings. Adaptation of the lacewing *M. desjardinsi* to ant-aphid interactions by laying stalked eggs and carrying aphid carcasses would have these benefits. What remains to be determined is whether there are any significant costs of the traits. For example, the lacewing larvae may reduce their mobility or greater energy expenditure during locomotion by carrying aphid carcasses. On the other hand, the lacewing females may reduce the number of egg production by investing egg stalks. Further studies are needed to clarify the costs of these traits of the lacewings.