

The effects of attacks by the mutualistic ant, *Lasius japonicus* Santschi (Hymenoptera: Formicidae) on the foraging behavior of the two aphidophagous ladybirds, *Coccinella septempunctata brucki* Mulsant (Coleoptera: Coccinellidae) and *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae)

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Abstract

As difference in food requirements of aphidophagous ladybirds might have an influence on the strength of interactions between the ladybirds and mutualistic ants, the effects of ant attacks on the foraging behavior of the two ladybird species, *Coccinella septempunctata brucki* and *Propylea japonica*, were investigated in relation to their developmental stages (adults and larvae). Large-sized *C. septempunctata* adults preyed on more aphids and were more frequently attacked by the ants than another species and developmental stage. Escape rates of the ladybirds after attacking tended to be higher in adults than in larvae. The percentage of *C. septempunctata* adults remaining on the plant in the ant-present treatments was significantly lower than in ant-excluded treatments, while there was no significant difference in the proportion of *P. japonica* adults between the two treatments. The proportion of larvae of both species was high even in ant-present treatments. This study revealed that the effects of ant attacks on the ladybirds differed between the two species in relation to their developmental stages, suggesting that food requirement of ladybirds would be one of important factors to understand the relationship between aphidophagous ladybirds and mutualistic ants.

Key words: Predatory ladybird; aphid-attending ant; mutualism; foraging behavior; developmental stage

INTRODUCTION

In general, foraging behavior of arthropod predators is categorized into two groups, ambush and active foraging (e.g. New, 1991). Predatory ladybirds search actively for prey and they tend to switch their searching behavior from extensive to area-concentrated search after eating an aphid (Nakamuta, 1985). Foraging behavior also differs even among aphidophagous insect species (e.g. Lucas et al., 1998). Several species of aphidophagous insects including predatory ladybirds visit plants with many aphids and often attack the same colonies as the members of an aphidophagous guild (Rotheray, 1989). These predators sometimes compete with their prey, depending on the aphid abundance (Obrycki et al., 1998) and dif-

ference in foraging behavior influences on the encounter rate between aphidophagous species involved, which in turn would result in the relative strength of the interactions (Lucas et al., 1998; Snyder et al., 2004; Yasuda et al., 2004).

It is well known that honeydew-producing homopterans including aphids, coccids, and mealybugs are mutualistically able to associate with ant species, and that their honeydew is one of the food resources of these ants (Way, 1963; Hölldobler and Wilson, 1990). Ants protect homopterans from their natural enemies, and this protection is thought to provide important benefits to the population growth of ant-attendant homopterans (Cushman and Whitham, 1989, 1991; Müller and Godfray, 1999; Morales, 2000). For instance, ants negatively affect the abundance of homopteran predators

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(Cushman and Whitham, 1989, 1991; Dutcher et al., 1999) and prey consumption by aphidophagous insects (Vinson and Scarborough, 1989). Although the intensity and nature of these negative effects of ants may differ among homopteran predators (e.g. Kaneko, 2002, 2003a, b), our understanding of these interactions remains incomplete.

Ladybirds are thought to be an important predator of aphids because of their abundance and voracity (Obrycki and Kring, 1998; Müller and Godfray, 1999), and are often observed in aphid colonies with mutualistic ants in the fields (e.g. Kaneko, 2002, 2003a, b). As the morphology, size, and behavior of ladybirds greatly differ among species, these factors might have an influence on the vulnerability of ant attacks. For instance, a small-sized ladybird, *Scymnus posticalis* Sicard, tended to be ignored by ants, while ants often drove a large-sized ladybird, *Harmonia axyridis* (Pallas), from aphid colonies (Kaneko, 2002, 2003a). In addition, Völkl and Vohland (1996) revealed that wax cover on the ladybird, *Scymnus interruptus* (Goeze), functioned as a mechanical defense for ants attacking. These results suggested that the consequence of ants attacking would differ among ladybird species in relation to their development. However, the effects of mutualistic ant attacks on the foraging behavior of different ladybird species with different developmental stages are poorly understood.

In addition to the factors mentioned above, the aggressiveness of ants also influences the intensity of ants attacking predatory ladybirds (Kaneko, 2003a, b; Katayama and Suzuki, 2003). Furthermore, the amount of prey required by the predatory ladybirds could also be a possible factor that influences the difference in ant attacks among ladybird species since large ladybirds would tend to stay longer in an aphid colony because of the large food requirement. The longer stay probably results in a higher encounter rate of mutualistic ants, and as a result, large ladybirds are often expected to be more frequently attacked by ants than small-sized ladybirds. Although the food requirement of ladybirds is likely to be one of the important factors in the relationship between mutualistic ants and aphidophagous ladybirds, our understanding in this regard is not complete.

In the present study, we conducted field experiments to understand the difference in the effects of

ant attacks on the foraging behaviors of two species of aphidophagous ladybirds, *Coccinella septempunctata brucki* Mulsant and *Propylea japonica* (Thunberg), in relation to their developmental stages. As these ladybirds differ in food requirements because of the difference in their body size (Kurosawa et al., 1985), which in turn influences the strength of the interaction between the ladybirds and mutualistic ants, we address two hypotheses as follows: 1) Difference in food requirement between the two species and/or between developmental stages influences the intensity of being attacked by mutualistic ants because individuals with a large food requirement would tend to stay longer in the aphid colony, which would lead to a higher encounter rate with the ants; and 2) After ladybirds are attacked by mutualistic ants, adults escape more often than larvae because it seems easier for adults to leave plants occupied by mutualistic ants.

MATERIALS AND METHODS

Field experiments were conducted on the experimental farm of Yamagata University, Japan (38°43'N, 139°49'E), from 1 September to 27 October in 2000. Young broad beans, *Vicia faba* L., were planted on 9 July. To introduce black bean aphids, *Aphis craccivora* Koch, to each plant, two small seedlings of broad beans grown in a greenhouse and infected with aphids (mean \pm SE = 193 \pm 23 individuals per seedling) were attached onto the plant on 30 August. The aphids were attended by ants, *Lasius japonicus* Santschi. Each plant on which aphids were attended by the ants was covered with a plastic cylindrical cage with muslin at the top (20 cm in diameter, 40 cm in depth). In ant-excluded treatments, to prevent ant attendance, a tape (2.5 cm in width) with Tangle-foot (Fuji-Tangle, Fuji Chemical Industry Co., Ltd., Toyama, Japan) was attached to the base of the plant. The height of the experimental plants was measured and the number of leaves, ants, and aphids on the plants were counted before the start of the experiment.

Females of the two species of ladybird, *C. septempunctata* and *P. japonica*, were collected on broad beans at the study site from August to October. *Coccinella septempunctata* is larger in size than *P. japonica* (Kurosawa et al., 1985). Only re-

productive females were used in the experiment and this was confirmed by laying eggs when reared on *A. craccivora* in a laboratory. Each female was used in each treatment only once and the larvae produced were reared on *A. craccivora* in the laboratory until they became fourth instar larvae. The same number of these larvae that hatched from each clutch were assigned to each treatment. Adults and larvae were starved for more than 3 h prior to the experiments, then they were placed on a broad bean leaf using a paintbrush, and observations were commenced.

We recorded the following items for 5 min after the start of the experiments: (1) residence time of ladybird adults and larvae on the plant; (2) number of aphids eaten; (3) frequency of attacks by ants on a ladybird; and (4) escape frequency of the ladybird from the attack. The number of aphids eaten per residence time of ladybird (min) was calculated. An ant biting on a ladybird was regarded as an attack. The proportion of ladybirds attacked by the ants was indicated as the number of individuals being attacked divided by the total number of individuals used. Ladybird larvae and adults often dropped from the plants to escape from ant attacks. In addition, adults also flew away from the plants after being attacked by the ants. The escape frequency of ladybirds was measured as the proportion of individuals that left the plant following ant attacks. This was calculated as the number of individuals that left the plant after being attacked divided by the number of individuals being attacked.

In addition, locations of the ladybirds after 5, 30 and 60 min were recorded, and the percentage remaining on the plant was calculated as the number of individuals observed as being on the plant at each time period divided by the total number of ladybirds used.

Residence time and aphid consumption by the ladybirds were analyzed using the Mann-Whitney *U*-test. To compare the percentages being attacked and escaping between the two species and between adults and larvae, Fisher's exact test was used. In addition, the percentage of ladybirds remaining on the plant between ant-presence and ant-excluded treatments was analyzed by Fisher's exact test.

RESULTS

Prior to the experiment, we confirmed that there were no significant differences in the number of ants between the two treatments in adults of both species and in *C. septempunctata* larva (Table 1), while a slightly higher number of ants were found in the *P. japonica* larvae ant-present treatment compared to ant-excluded treatment (Table 1). In addition, the number of aphids did not significantly differ between the treatments, and plant structure (such as height and the number of leaves) was also similar in the two treatments and for all combinations analyzed.

Table 1. The numbers of ants and aphids on the plants, and the height and the numbers of leaves of the plant before the treatments were done^a

| Species | Treatment expected | <i>n</i> | No. ant | <i>U</i> | No. aphid | <i>U</i> | Plants | | | |
|--------------------------|--------------------|----------|---------|----------------------|-----------|----------------------|-------------|----------------------|----------|----------------------|
| | | | | | | | Height (cm) | <i>U</i> | No. leaf | <i>U</i> |
| Adult | | | | | | | | | | |
| <i>C. septempunctata</i> | ant-present | 16 | 7.5±1.4 |]111.5 ^{ns} | 83.3±24.5 |]113.5 ^{ns} | 31.5±2.1 |]74.5 ^{ns} | 16.9±1.3 |]87.0 ^{ns} |
| | ant-excluded | 16 | 8.6±1.4 | | 52.3±17.2 | | 33.3±1.8 | | 18.5±1.8 | |
| <i>P. japonica</i> | ant-present | 20 | 7.7±1.0 |]174.0 ^{ns} | 32.4±6.6 |]153.5 ^{ns} | 30.8±1.5 |]188.0 ^{ns} | 15.9±1.2 |]163.0 ^{ns} |
| | ant-excluded | 20 | 8.7±1.6 | | 43.7±6.7 | | 31.2±0.8 | | 17.1±0.9 | |
| Larva | | | | | | | | | | |
| <i>C. septempunctata</i> | ant-present | 17 | 5.7±0.8 |]102.0 ^{ns} | 53.7±12.7 |]126.5 ^{ns} | 25.5±1.4 |]108.5 ^{ns} | 13.6±0.5 |]96.0 ^{ns} |
| | ant-excluded | 17 | 4.5±0.6 | | 54.4±9.0 | | 27.3±1.3 | | 13.0±0.8 | |
| <i>P. japonica</i> | ant-present | 20 | 4.9±0.5 |]116.5* | 46.7±12.1 |]173.5 ^{ns} | 26.3±1.3 |]138.5 ^{ns} | 12.4±0.7 |]127.5 ^{ns} |
| | ant-excluded | 20 | 3.8±0.6 | | 35.0±6.9 | | 25.0±0.8 | | 13.1±0.7 | |

^a mean±SE.

ns: non-significant. *: $p < 0.05$.

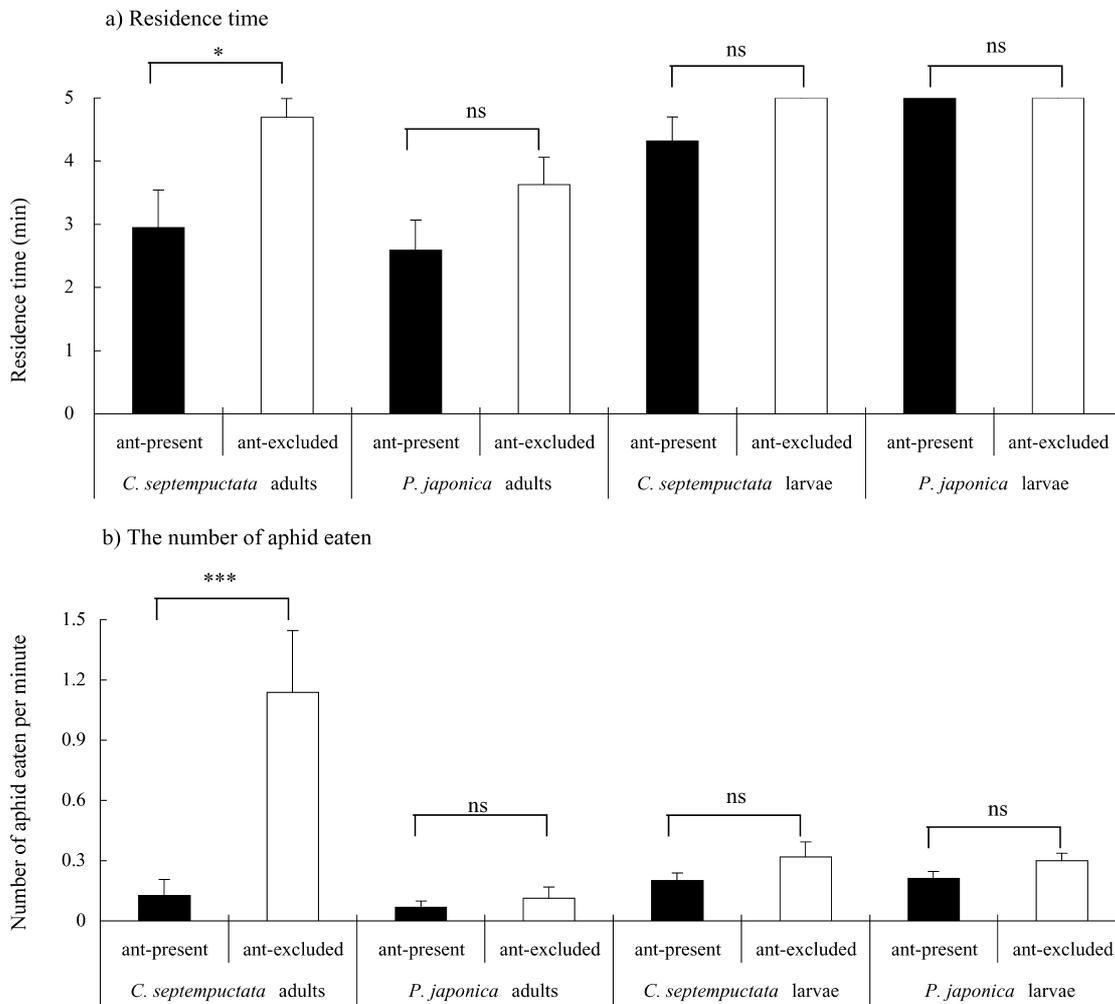


Fig. 1. a) Residence time and b) the number of aphids eaten by adults and larvae of the two ladybird species, *C. septempunctata* and *P. japonica*, in the two treatments (\pm SE) (ns: non-significant; * $p < 0.05$; *** $p < 0.001$).

Effects of ants on ladybird residence time and aphid consumption

Residence time of *C. septempunctata* adults in the ant-presence treatment was significantly shorter than that in the ant-excluded treatment (Fig. 1; $U = 85.0$, $p < 0.05$). However, residence times of adult *P. japonica* and the larvae of both species were not significantly different between the treatments (*P. japonica* adults, $U = 137.0$, $p > 0.05$; *C. septempunctata* larvae, $U = 119.0$, $p > 0.05$; *P. japonica* larvae, no emigration from the plants was observed in both treatments). In addition, once the individual left the plant, it was never observed to return to the plant during 5 min of observation.

The number of aphids eaten by *C. septempunctata* adults in the ant-present treatment was lower than that in the ant-excluded treatment ($U = 40.5$,

$p < 0.001$). The number of aphids eaten by *P. japonica* adults and by the larvae of both species tended to be lower in the ant-present treatments, but not significantly different (*P. japonica* adults, $U = 188.0$, $p > 0.05$; *C. septempunctata* larvae, $U = 116.5$, $p > 0.05$; *P. japonica* larvae, $U = 135.5$, $p > 0.05$).

Ant attack and the frequency of escape

Ants were more likely to attack adults of *C. septempunctata* than the larvae (Table 2). In *P. japonica*, however, there was no significant difference in the percentage of ant attack between adult and larval stages. The percentage of *C. septempunctata* adults being attacked was higher than that of *P. japonica* adults, but there was no significant difference in percentage of larvae being attacked

Table 2. Percentages of being attacked by ants and of escaping of adults and larvae of two ladybird species

| | Adults | Larvae | Fisher's exact test |
|--------------------------------------|-------------------------|------------|---------------------|
| (a) Percentage of being attacked (%) | | | |
| <i>C. septempunctata</i> | 88 (14/16) ^a | 47 (8/17) | $p=0.03$ |
| <i>P. japonica</i> | 50 (10/20) | 60 (12/20) | $p=0.75$ |
| Fisher's exact test | $p=0.03$ | $p=0.52$ | |
| (b) Percentage of escaping (%) | | | |
| <i>C. septempunctata</i> | 50 (7/14) ^b | 25 (2/8) | $p=0.38$ |
| <i>P. japonica</i> | 80 (8/10) | 0 (0/12) | $p<0.001$ |
| Fisher's exact test | $p=0.21$ | $p=0.15$ | |

^aNumbers in parenthesis mean the number of individuals being attacked by ants/the total number of individuals used.

^bNumbers in parenthesis mean the number of individuals which left the plant after being attacked by ants/the total number of individuals being attacked by ants.

between the two species (Table 2).

In *C. septempunctata*, the percentage of escaping adults was twice as high as larvae, however, the difference was not significant (Table 2b). In *P. japonica*, the proportion of adults escaping was significantly higher than that of the larvae. There was no significant difference in the percentages in adults and larvae between the two species.

Between the two species there was no significant difference in the percentage of individuals that left the plants after being attacked (adults: *C. septempunctata* 7/16 vs. *P. japonica* 8/20, Fisher's exact test, $p>0.05$; larvae: *C. septempunctata* 2/17 vs. *P. japonica* 0/20, Fisher's exact test, $p>0.05$), although the percentages of adults tend to be higher than those of larvae (*C. septempunctata*: adults 7/16 vs. larvae 2/17, Fisher's exact test, $p=0.057$; *P. japonica*: adults 8/20 vs. larvae 0/20, Fisher's exact test, $p<0.01$).

Effects of ants on residence of the ladybirds

In total, 12.5% of *C. septempunctata* adults in the ant-excluded treatment left the plant within 5 min, after that the percentage remaining on the plant did not change (Fig. 2a). However, a number of adults that were released in the ant-present treatment left the plant, and the percentage remaining in the treatment was significantly lower than that in the ant-excluded treatment after 30 min (Fisher's exact test, $p<0.01$), and 60 min (Fisher's exact test, $p<0.01$). While *P. japonica* adults frequently left the plants in both treatments, there were no significant differences between the treatments at each time period (Fig. 2b, Fisher's exact test, $p>0.05$). In ant-excluded treatments, the percentage of indi-

viduals that left the plants was significantly higher for *P. japonica* adults than for *C. septempunctata* at 30 min (Fisher's exact test, $p<0.05$), and 60 min (Fisher's exact test, $p<0.01$).

Although no *C. septempunctata* larva left the plants in the ant-excluded treatment, 11.8% and 23.5% of larvae left in the ant-present treatment within 5 and 30 min, respectively (Fig. 2c), although the differences were not significant between treatments (Fisher's exact test, $p>0.05$). *Propylea japonica* larvae did not leave the plant in the ant-excluded treatment (Fig. 2d), and this tendency was similar to *C. septempunctata* larvae (Fig. 2c). The percentage of larvae remaining on the plant in the ant-present treatment was 75.0% at 60 min, and this difference was significant between the treatments (Fisher's exact test, $p<0.05$).

DISCUSSION

This study revealed that frequencies of being attacked by the mutualistic ants and escape rates of the ladybirds after attacking varied in the two ladybird species in relation to their developmental stages. We consider firstly these results found here in light of the two hypotheses that we tried to test.

Our results support the hypothesis that the amount of food requirement of ladybirds influences the difference in attack rate by the ants. Large-sized *C. septempunctata* adults preyed on more aphids than another species and developmental stage. This increased predation due to the food requirement would result in increase of the encounter rate with mutualistic ants, consequently the adults were more frequently attacked by the ants. Several

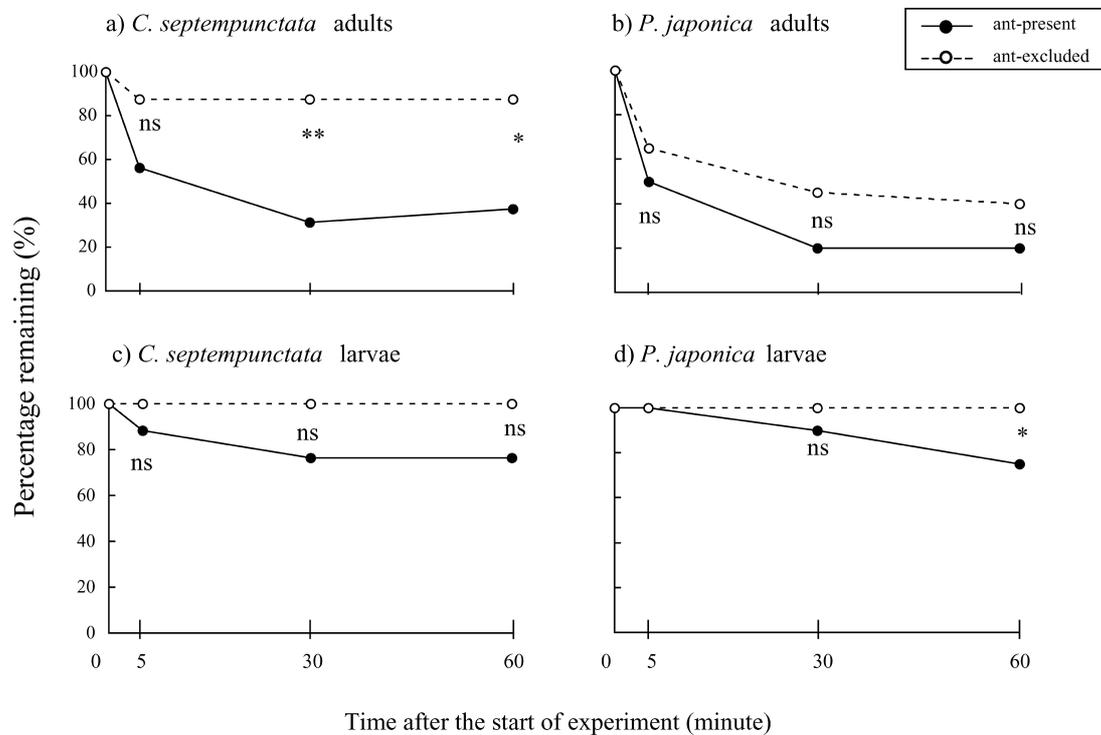


Fig. 2. Percentages of remaining adults and larvae of the two ladybird species on the plants at the beginning of the experiment and at 5, 30 and 60 min after the start of the experiment (ns: non-significant; * $p < 0.05$; ** $p < 0.01$).

studies show that increased food requirement is known to lead to strong interactions between individuals involved in such interactions (Yasuda and Kimura, 2001; Yasuda et al., 2001, 2004; Rosenheim et al., 2004). For instance, in an arthropod predatory community the predatory mite, *Phytoseiulus macropilis* (Banks), whose food requirement is small, has less probability of encountering their higher-order predator than the predatory beetle, *Stethorus siphonulus* Kapur, which has a large food requirement (Rosenheim et al., 2004). Therefore, the food requirement of ladybirds would be one of the important factors in understanding the strength of interactions between ladybirds and mutualistic ants.

In regard to the escape after the mutualistic ants attacked, we hypothesized that adults would escape more often than larvae. For both ladybird species used here, escape rates of adults after being attacked by the ants were higher than those of larvae, although the difference in escape rates of *C. septempunctata* was not significant between adult and larval stages, and these larvae tended to remain on the plant rather than escape. It therefore seems that the escape rate of ladybirds after ant attacks

would be higher in adults than larvae, suggesting that the higher escape rate of adults is likely to relate to their prey searching behavior due to flying activity. Compared to larvae, it is easier for adult ladybirds to locate another aphid colony after leaving a plant by flying, and as a result, they might readily escape from ant attacks knowing that they can locate prey elsewhere. In addition, larvae would have the possibility of being attacked by ants and other predators on the ground before they reach new plants with aphids. The fact that more larvae tended to remain on a plant than adults could be attributed to the predation risk. Although adults have elytra wings, which seem to be an effective defense to ant attack (Völkl, 1995; Hodek and Honek, 1996), and show defensive behavior (Jiggins et al., 1993; Völkl, 1995; Sloggett et al., 1998), the escape rate of adults after ant attacks was higher than that of larvae. This would also relate to the high mobility of adults compared with larvae. Conversely, the low escape rate after ant attacks shown by larvae with soft cuticles, which are a less effective defense, seems to relate to low prey finding ability after emigrating from a plant.

The percentages of remaining *C. septempunctata*

adults on a plant in ant-present treatment were similar to those of *P. japonica* adults, although attacking and escape rates differed between the two species. *Coccinella septempunctata* adults were more frequently attacked by ants than *P. japonica* and the former had a relatively lower escape rate than the latter. The adults of the two species showed apparently similar percentages for remaining on plants; however, the mechanism leading to the similarity was different between the two species. In general, *P. japonica* adults often tended to leave a plant without ants, and this foraging behavior would have an influence on the strength of interactions between ladybirds and ants. So, not only food requirements, but also foraging behaviors seem to be important factors in understanding the relationships.

In addition to food requirement and searching behavior, other factors such as body size, coloration, and chemical substance might also influence ant attacks on ladybirds. In general, ladybirds have morphological differences such as body size and elytra color. Because *C. septempunctata* is larger than *P. japonica*, ants might find *C. septempunctata* more easily than *P. japonica*. As a result, *C. septempunctata* would be more likely to be attacked than *P. japonica*. If this were true, ants would be expected to attack both developmental stages of *C. septempunctata* more frequently than *P. japonica*. However, the attack rate on *C. septempunctata* larvae was not higher than that of *P. japonica* larvae. So, it seems that the size of ladybirds is not a critical factor in terms of the difference in attack rates between the two species shown in this study, although Kaneko (2002, 2003a, b) revealed that the mutualistic ants did not have a negative influence on the number of small-sized ladybirds, while the ants reduced the abundance of the large ladybirds. As the small ladybird shown in his study is less active regarding foraging behavior, the linkage of small body size and less activity would be important for the interaction between mutualistic ants and aphidophagous predators. Adults of the two species used here had different elytra coloration and patterns, but these factors were not assumed to cause the differences in ant attacks since there was no difference in aggressiveness by ants among dummy ladybirds painted individually using different colors (Jiggins et al., 1993).

The intensity of ant attacks is affected by repel-

lent secretion released from the secondary parasitoid of aphids, *Alloxysta brevis* (Thomson) (Völkl et al., 1994) and chemical mimicry of the aphid parasitoid, *Lysiphlebus cardui* (Marshall) (Liepert and Dettner, 1996). In addition, the fact that ladybirds secrete toxic fluid against predators is well known (Hodek and Honek, 1996). The toxic substances in these secretions are species-specific (Marples et al., 1989; de Jong et al., 1991; Holloway et al., 1991), which could possibly affect the incidence of ant attacks on ladybirds. If the toxicity is harmful for ants, it also may affect the aggressiveness of ants. Therefore, it is possible that the influence of these species-specific substances on ant attacks may be revealed in future studies.

Residence times and amount of prey consumed by the larvae of both species did not differ between the ant-present and ant-excluded treatments. On the contrary, Katayama and Suzuki (2003) reported that two ant species, *Tetramorium caespitum* Linnaeus and *Lasius niger* L., gave negative effects on residence time and food consumption of *C. septempunctata* larvae. As it is well known that intensity of ant attacks on ladybirds differs depending on ant species (Kaneko, 2003a, b; Katayama and Suzuki, 2003), the difference between this and previous studies would come from different aggressiveness among ant species in addition to different experimental design. In this study, fourth instar larvae were used, and they are the largest individuals compared with individuals at other developmental stages. This may attribute to less ant effects on residence time and prey consumption between the treatments since the intensity and nature of interspecific relationships of predatory arthropods change with their development (Yasuda and Kimura, 2001; De Clercq et al., 2003). The younger and vulnerable larvae would be more likely to have a negative influence induced by mutualistic ants. The presence of these ants elicited a negative relationship with regard to prey consumption of *C. septempunctata* adults, but not for *P. japonica* adults. The difference in food intake due to ants attacking would result in difference in oviposition behavior and number of eggs laid by female ladybirds. Furthermore, it is well known that ladybird larvae secrete a defensive chemical when they are attacked by predators and it negatively affects larval performance and adult size (Grill and Moore, 1998). Further studies are

needed to understand the effects of mutualistic ants, not only on larval performance throughout their development, but also on adult performance such as oviposition behavior and the number of eggs laid.

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