Popul Ecol (2000) 42:171–178

ORIGINAL ARTICLE

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# Should aphids attract or repel ants? Effect of rival aphids and extrafloral nectaries on ant–aphid interactions

Received: January 17, 2000 / Accepted: July 4, 2000

**Abstract** Among plants and herbivores, two types of conflicts occur in relation to mutualism with ants: one is competition for ant mutualism among myrmecophilous herbivores and plants, and the other is the conflict whether to attract or repel ants between myrmecophiles and nonmyrmecophiles that are damaged by ants. We investigated the extent to which two species of aphids (*Megoura crassicauda* and *Aphis craccivora*) and extrafloral nectaries on their host plant (*Vicia faba* var. *minor*) interact with one another for their relationships with ants. We designed an experiment where ants can choose to visit seedlings colonized by (1) *M. crassicauda*, (2) *A. cracivora*, (3) both aphid species, or (4) neither aphid species. Ants preferred *A. craccivora* to extrafloral nectaries and avoided tending *M. crassicauda*. We also analyzed the population growth of each aphid when it coexists with (1) ants, (2) the other aphid species, (3) ants and the other aphid species, or (4) neither of them. Under ant-free conditions, we detected an exploitative competition between the two aphid species. The ants had no significant effect on the population of *A. craccivora*, whereas they had negative effects on the population growth of *M. crassicauda* by attacking some individuals. When both aphids coexisted, *M. crassicauda* suffered ant attack more intensely because *A. craccivora* attracted more ants than extrafloral nectaries despite ant-repelling by *M. crassicauda*. On the other hand, the ants benefited *A. craccivora* by eliminating its competitor. To avoid ant attack, aphids may have been selected either to be more attractive to ants than other sympatric sugar sources or to repel the ants attracted to them. We hypothesize that competition among sympatric sugar sources including rival aphids and extrafloral nectaries is a factor restricting aphids to be myrmecophilous.

**Key words** Interspecific relationships · Indirect interactions · Mutualism · Competition · Honeydew · Extrafloral nectary · Myrmecophily

## Introduction

In the systems consisting of plants, honeydew-producing herbivores, and ants, various types of interactions are involved (i.e., mutualism, predation, competition, etc.), and the inclusive outcomes of the interactions are complicated (Buckley 1987; Huxley and Cutler 1991). Plants with extrafloral nectaries attract ants and induce them to protect the plants from herbivory (Keeler 1989; Koptur 1992; Oliveira 1997). Many herbivores also attract ants by excreting sugar-rich honeydew and derive services from the ants including protection against natural enemies (Way 1963; Boucher 1985). In relation to ant attendance, two types of conflicts are possible among plants and herbivores. One is competition among myrmecophiles for ant mutualists; the other is the conflict between myrmecophiles and nonmyrmecophiles whether to attract or repel ants.

The fact that ants utilize waste sugar of honeydew-producing herbivores suggests that they are potentially favorable partners for mutualism. However, a large proportion of honeydew-producing herbivores are not associated with ants. For example, in the Rocky Mountain region in the United States, only 117 of 479 aphid species are myrmecopilous (Bristow 1991). Even for myrmecophilous aphids, ant attendance imposes a physiological burden (Stadler and Dixon 1998; Yao et al. 2000), and ants do not consistently benefit honeydew-producing herbivores. The effects of ants on myrmecophilous herbivores depend on the species of both taxa and ecological factors such as their densities and the availability of alternative resources (Addicott 1979; O'Dowd 1979; Skinner and Whittaker 1981;

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Bristow 1984; Koptur 1985; Cushman and Addicott 1989, 1991; Cushman and Whitham 1989, 1991; Breton and Addicott 1992; Bronstein 1994; Itioka and Inoue 1996, 1999). For example, effects of the ant *Lasius niger* on aphids depend on the supply–demand balance of sugar foods. When honeydew is in excess, the ants have a negative effect on the aphid populations in that the ants benefit when honeydew is in short (Sakata 1994, 1995, 1999).

As well as honeydew-producing herbivores, plants with extrafloral nectaries cannot consistently derive benefit from the ant (Becerra and Venable 1989; Koptur 1992; Rashbrook et al. 1992). Indirect interactions among plants, herbivores, and ants complicate the inclusive effect of ants on the plants (Bach 1991). In some systems, ants have a negative effect on the plants by making their tended herbivores vigorous (Way 1963; Boucher 1985; Buckley 1987) or by deterring the natural enemies of herbivores (Fritz 1983). In other systems, honeydew-producing herbivores can indirectly benefit their host plants by attracting ants that reduce infestation of other herbivores (Messina 1981; Compton and Robertson 1988, 1991; Ito and Higashi 1991; Rashbrook et al. 1992).

The supply of sugar-rich food by one myrmecophilous organism influences the relationships between the other myrmecophilous organism and ants. When more than one myrmecophilous aphid is coexisting, depending on the supply–demand balance of honeydew, ants select more desirable aphid species and eliminate or prey on less desirable species (Sakata 1994, 1995, 1999). Extrafloral nectaries also could be competitors of myrmecophilous herbivores (Becerra and Venable 1989). If ants discriminate against less desirable aphids distinctively, repelling the ants is an alternative strategy for the aphids.

These interferences among sympatric sugar sources could influence the ant attendance effect and selection pressure for myrmecophily on one another. To test these hypotheses, using a system including ants and two species of aphids (nonmyrmecophilous and myrmecophilous) on a plant species with extrafloral nectaries, we examined how ants respond to different sugar sources and how sympatric sugar sources influence one another. Based on the results, we present a hypothesis to explain why so many aphids do not relay on ants.

## Materials and methods

### Materials

*Aphids*

Two species of aphids, *Megoura crassicauda* Mordvilko and *Aphis craccivora* Koch, were collected from a wild leguminous weed, *Vicia angustifolia*, at Sanda, Hyogo, Japan. Both aphids are common and abundant on wild and cultivated legumes in this area.

The habitats of the two aphids overlap considerably, and they sometimes coexist on a single plant. Ants rarely tend *M. crassicauda* while they sometimes tend *A. craccivora. Megoura crassicauda* and *A. craccivora* belong to Macrosiphini and Aphidini in Aphidinae, respectively. According to the investigation in the Rocky Mountain region in the United States, 11 of 25 genera in Macrosiphini and 19 of 37 genera in Aphidini include myrmecophilous species (Bristow 1991). Before the experiments, we reared both aphid species on the pigeon bean, *Vicia faba* var. *minor*, in an insectary maintained at 20° ± 3°C and in LD 16:8.

*Ants*

Ten colonies of ants, *Lasius niger* (Linnaeus) and *Pristmyrmex pungens* Mayr, were collected in the same area where the aphids were collected. The ants were housed in plaster-floored styrene cases with a lid (nest cases). These ants are two of the most dominant species in this area, foraging on honeydew of many aphid species and extrafloral nectaries.

### Experimental condition and design

To detect competition between two species experimentally, substitutive designs and additive designs are common (Begon et al. 1996). The former strategy is suitable to compare the intensities of interspecific and intraspecific competition, and the latter can detect the existence and direction of interspecific effects. We employed additive designs in this study.

We prepared five replicate colonies per ant species, and housed a fragment of each colony in a nest case that contained approximately 300 workers and 150 larvae at the start of the experiment. Each nest case was connected to four cylinders (cultivation cylinders) by vinyl tubes. In each cylinder, a seedling of *V. faba* 8 ± 1 cm tall was hydroponically cultured. These cultivation cylinders were equidistant from the nest case through an open junction cylinder (Fig. 1).

Four cultivation cylinders connected to each nest case contained (1) a seedling without aphids, (2) a seedling with ten *M. crassicauda*, (3) a seedling with ten *A. craccivora*, and (4) a seedling with ten *M. crassicauda* and ten *A. craccivora*. Each group of ten aphids consisted of four apterous viviparous female adults and six nymphs at the third or fourth instar. As a control, we arranged additional five repetitions of the same experimental devices that were not connected to the nest case of ants.

We observed the foraging activities of the ants and population growth of the aphids at 24-h intervals for 5 days at 20 ± 3°C and in LD 16:8. At the middle of light period in each day, we recorded the numbers of ants at a moment foraging (1) on a seedling in each cultivation cylinder, (2) at the extrafloral nectaries of the seedling, and (3) in the cylinder but not on the seedling (around a seedling). Simultaneously, we also counted the number of aphids of each species as a measure of their population size.

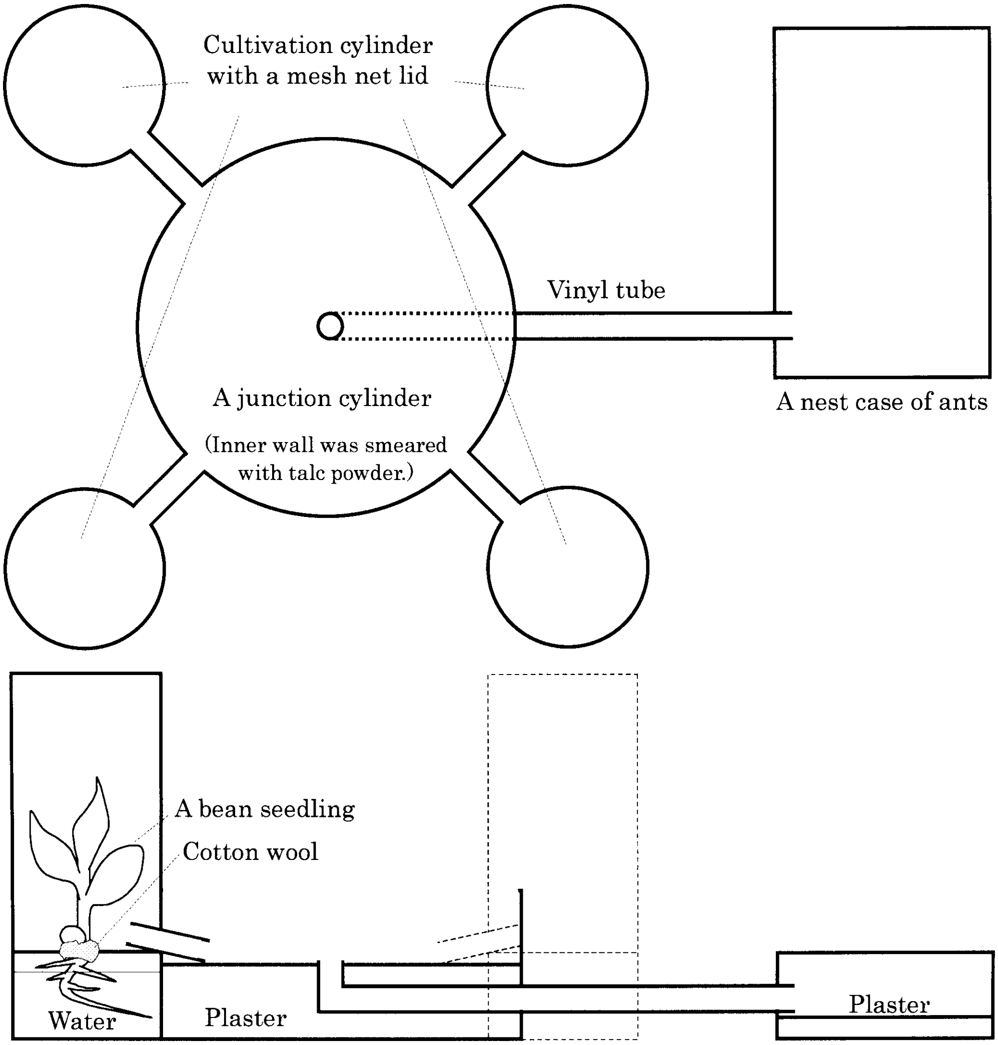

**Fig. 1.** The experimental device. A nest case (10.5 × 7.5 × 3 cm) was connected to four cultivation cylinders (20-cm height, 7.5-cm internal diameter, 0.5-mm mesh net lid) by vinyl tubes (4-mm internal diameter). In each cultivation cylinder, a seedling of *Vinea faba* 8 ± 1 cm in height was hydroponically cultured. These cultivation cylinders were equidistant from the nest case through an open junction cylinder (13.5-cm internal diameter, 5-cm height) with the exit of a vinyl tube from the nest case located at the center

To examine the relationships between the numbers of aphids on a seedling and the foraging activities of ants on the seedling (1), at the extrafloral nectaries (2), and around the seedling (3), we used multiple regression analyses. The treatments of initial introduction of aphids and time progress were closely related to the numbers of aphids, and the numbers of aphids were considered to influence the ant foraging more directly than the initial treatments of aphids and the passage of time. Therefore, to avoid the problem of collinearity between explanatory valuables, we regressed the numbers of foraging ants only on the numbers of two aphid species. In these analyses, all observations on seedlings for different treatments at different days were pooled within each ant species.

The effects of interspecific interaction on the population of each aphid species were examined by repeated-measure ANOVA. As the between-subject factor, we tested the effect of four treatments: rearing focal aphid species (1) alone, (2) with another species of aphid, (3) with ants, and (4) with both ants and another species of aphids. The variation among five observations at different days for each subject was regarded as the within-subject factor. To test the difference between each pair of treatments, we conducted contrast *F-tests*.

If aphid colonies increase successfully, the seedlings wither in 2 weeks and the aphids begin to leave the seedling in a week. In the field, dispersing aphids colonize another host plant and repeat this dispersion–colonization process. Thus, the population growth in the long term depends on the cumulated short-term increase achieved on single host plants. Therefore, population growth of aphids for 5 days in the laboratory is an important factor to determine long-term population growth in the field.

## Results

### Foraging activities of the ants

The foraging activities of the ants *L. niger* and *P. pungens* on bean seedlings depended on the number of aphids (Table 1, Fig. 2). The results of multiple regression analyses showed that the numbers of both ants foraging on a seedling

**Table 1.** Results of multiple regression analyses for the number of foraging ants

| Variable | *Lasius niger* | | | *Pristmyrmex pungens* | | |
|---|---|---|---|---|---|---|
| | Coefficient ± SE | *t* | *P* | Coefficient ± SE | *t* | *P* |
| A. Dependent: no. of ants foraging on a bean seedling | | | | | | |
| No. of *Megoura crassicauda* | −0.030 ± 0.013 | −2.26 | 0.026 | −0.059 ± 0.021 | −2.80 | 0.006 |
| No. of *Aphis craccivora* | 0.059 ± 0.009 | 6.64 | <0.001 | 0.080 ± 0.015 | 5.30 | <0.001 |
| B. Dependent: no. of ants feeding at EFN on a bean seedling | | | | | | |
| No. of *M. crassicauda* | −0.005 ± 0.007 | −0.82 | 0.413 | −0.027 ± 0.009 | −2.95 | 0.004 |
| No. of *A. craccivora* | −0.027 ± 0.005 | −6.06 | <0.001 | −0.029 ± 0.006 | −4.47 | <0.001 |
| C. Dependent: no. of ants foraging around a bean seedling | | | | | | |
| No. of *M. crassicauda* | 0.012 ± 0.003 | 3.57 | <0.001 | −0.019 ± 0.010 | −1.85 | 0.067 |
| No. of *A. craccivora* | −0.001 ± 0.002 | −0.57 | 0.570 | −0.018 ± 0.007 | −2.45 | 0.016 |

EFN, extrafloral nectary

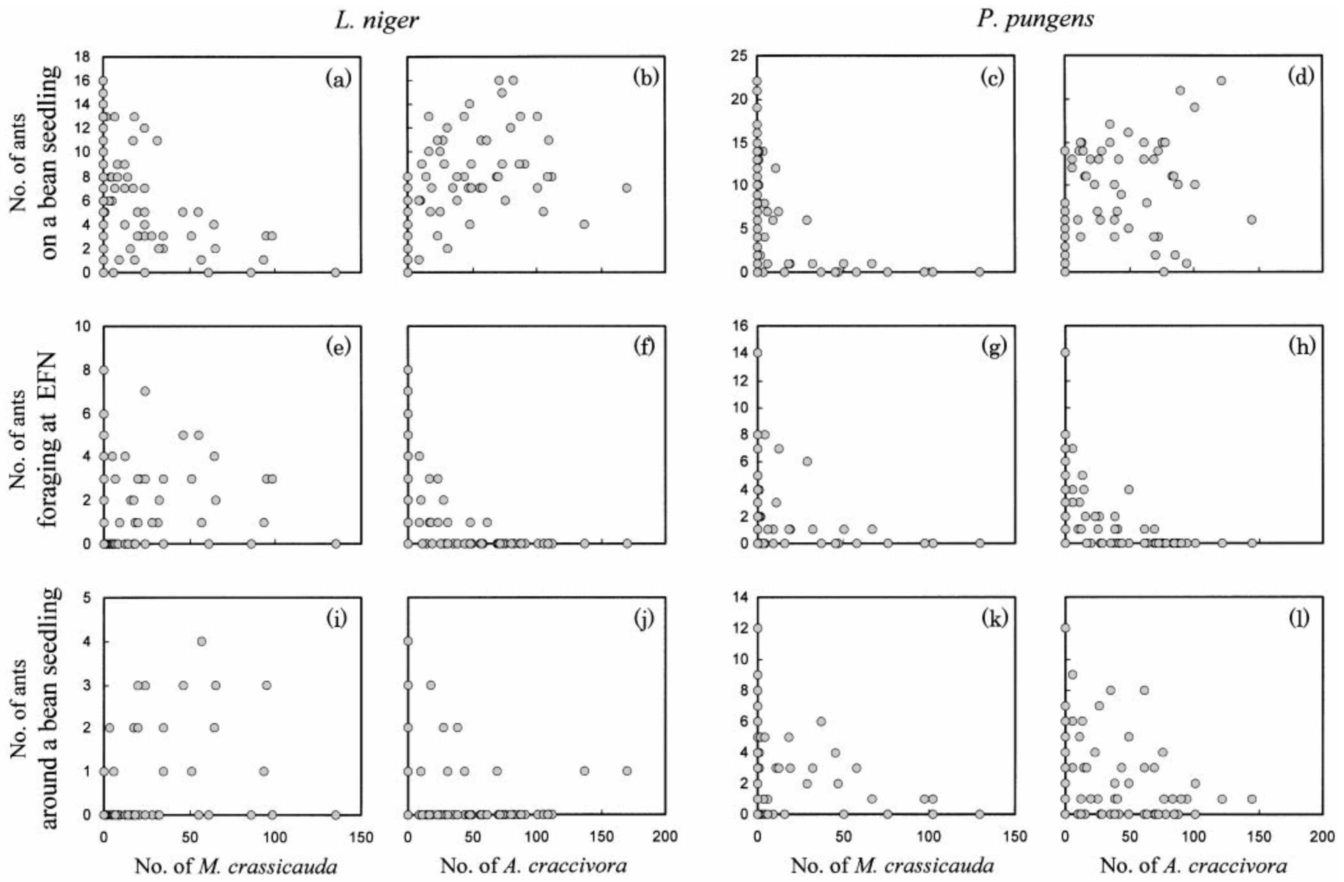

**Fig. 2.** The relationships (**a–l**) between the number of aphids, *Aphis craccivora* and *Megoura crassicauda*, on a seedling and the numbers of foraging ants, *Lasius niger* and *Pristmyrmex pungens*

decreased significantly with the number of *M. crassicauda* (Table 1A; Fig. 2a,c), and increased significantly with the number of *A. craccivora* (Table 1A; Fig. 2b,d).

For both species of ants, the number of individuals feeding at extrafloral nectaries decreased with the number of both aphid species (Fig. 2e–h). These negative correlations were significant excepting the correlation between the number of *A. craccivora* and the number of *L. niger* feeding at extrafloral nectaries (Table 1B).

The number of *L. niger* foraging around the bean seedling (in a cylinVer but not on a seedling) significantly increased with the increasing number of *M. crassicauda* on the seedling (Table 1C; Fig. 2i). Around the seedling, *L. niger* were foraging on dry droplets of honeydew that *M. crassicauda* splashed on the floor and wall of the cylinders. On the other hand, the number of *P. pungens* around the seedling decreased with the increasing numbers of both aphids (Table 1C; Fig. 2k,l).

**Table 2.** Results of repeated-measure ANOVA for the number of aphids.

| Source | | *L. niger* | | *P. pungens* | |
|---|---|---|---|---|---|
| | *df* | *F* | *P* | *F* | *P* |
| A. Dependent: no. of *M. crassicauda* | | | | | |
| Between-subjects effects | | | | | |
| Treatment (*A. craccivora* × ant) | 3, 16 | 8.95 | 0.001 | 10.67 | <0.001 |
| Within-subjects effects | | | | | |
| Time | 4, 64 | 38.88 | <0.001 | 32.28 | <0.001 |
| Time × treatment | 12, 64 | 5.88 | <0.001 | 5.79 | <0.001 |
| B. Dependent: no. of *A. craccivora* | | | | | |
| Between-subjects effects | | | | | |
| Treatment (*M. crassicauda* × ant) | 3, 16 | 1.94 | 0.164 | 3.77 | 0.032 |
| Within-subjects effects | | | | | |
| Time | 4, 64 | 63.00 | <0.001 | 100.41 | <0.001 |
| Time × treatment | 12, 64 | 0.98 | 0.482 | 1.87 | 0.056 |

"Treatment" means the effect of four treatments: rearing (1) focal aphid species alone, (2) with another species of aphid, (3) with ants, and (4) with both ants and another species of aphids

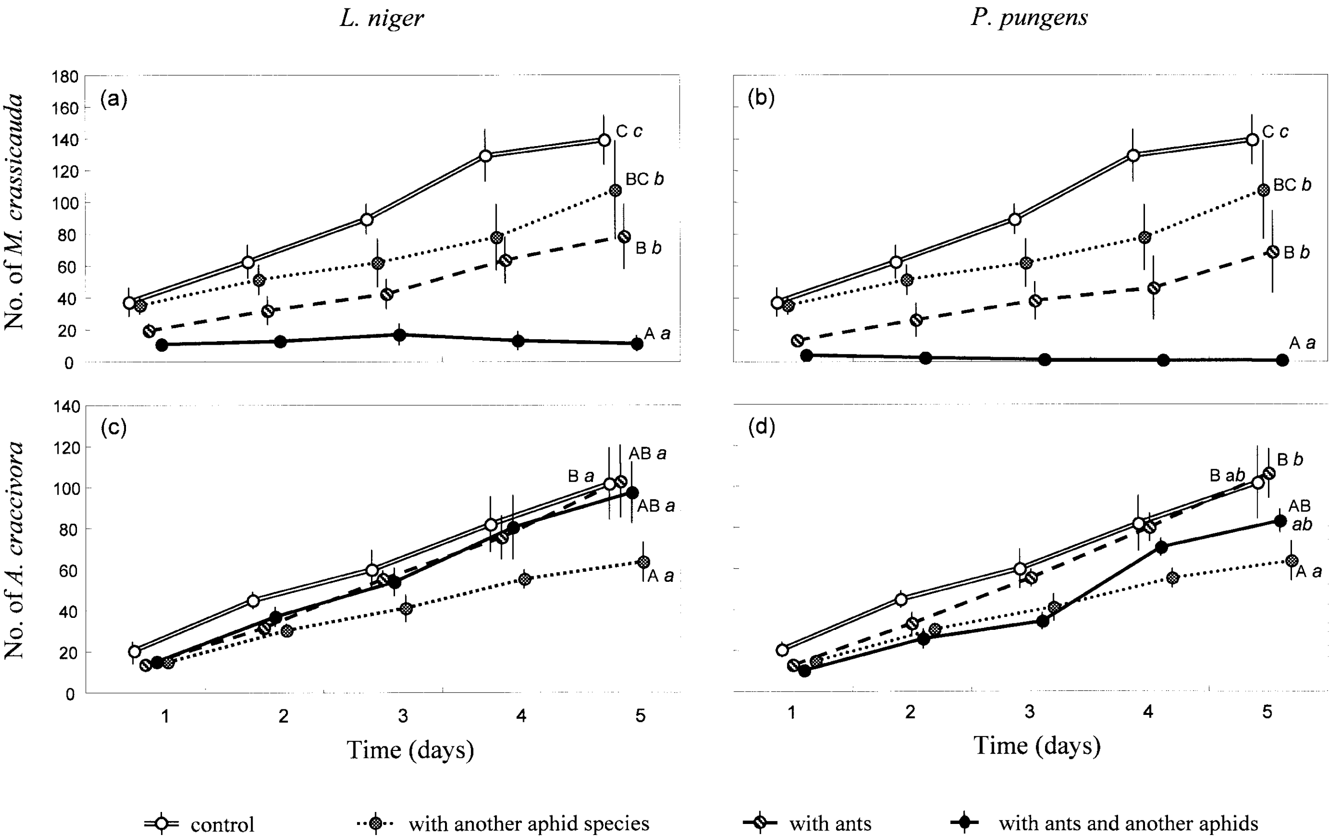

**Fig. 3.** The population growth of aphids, *M. crassicauda* (**a,b**) and *A. craccivora* (**c,d**), on a bean seedling assigned to each treatment with ants or on another aphid species. Each *line* shows the change in the number corresponding to each treatment; each *plot* shows mean ± SE. The lines attached to the same *capital letter* were not significantly different on average (between-subject effect, treatment); the lines attached to the same *italic small letter* were not significantly different in the pattern of temporal change (within-subject effect, treatment × time), by the contrast *F-test* at 5% level of significance

### Population growth of aphids

The population growth of one aphid species depended on the presence of ants and the other aphid species (Table 2, Fig. 3). Each aphid species negatively influenced the population growth of the other species. In the treatment without ant attendance, the growth rate of *M. crassicauda* population was lower on seedlings on which *A. craccivora* coexisted than on the control (Fig. 3a,b), and that of the *A. craccivora* population was significantly lower on a seedling with *M. crassicauda* than on the control (Fig. 3c,d). The effect of *M. crassicauda* on *A. craccivora* was more intense than that of *A. craccivora* on *M. crassicauda*.

The population growth of *M. crassicauda* was negatively influenced by both the ants (*L. niger* and *P. pungens*) (Table 2A; Fig. 3a,b). Both ants attacked and killed *M. crassicauda* and then brought them into their nest or discarded them at the verge of a cylinder. Especially when *M. crassicauda* coexisted with *A. craccivora* under ant attendance, the *M. crassicauda* population did not increase and was often exterminated by the ants (i.e., 2/5 were exterminated by *L. niger* and 5/5 by *P. pungens*). On the seedlings harboring *M. crassicauda* alone, the ants attracted to extrafloral nectaries suppressed the population growth of *M. crassicauda*, although the ant effect on *M. crassicauda* was weaker than on the seedlings harboring both *A. craccivora* and *M. crassicauda* (Fig. 3a,b). The attendance of either species of ants did not, in itself, significantly affect the number of *A. craccivora* when *M. crassicauda* was absent. However, when *M. crassicauda* is present, the negative effect of *M. crassicauda* on the *A. craccivora* population was weakened by either species of ant (Fig. 3c,d).

## Discussion

To address the question why only a quarter of aphids species are myrmecophilous, Bristow (1991) examined many hypotheses involving phylogenetic constraints, incompatibility of myrmecophily with alternative predator defense, and constraints by host plant characters; these could not be definitive explanations. Bristow suggested the importance of several ecological factors including availability of ants and competition for mutualism.

Our study shows that *L. niger* and *P. pungens* exhibited almost the same preference for the sugar sources: they preferred *A. craccivora* to extrafloral nectaries, and avoided *M. crassicauda*. In the absence of natural enemies, the ants had no significant effect on *A. craccivora* population growth, whereas they had negative effects on *M. crassicauda*. In the field, these aphids are subject to predation by ladybeetles and larvae of the drone fly. Under predation pressure, *A. craccivora* can benefit from the protection by ants, while the ants themselves act as another natural enemy to *M. crassicauda*.

*Aphis craccivora* and *M. crassicauda* each negatively influenced the population growth of the other species. They were not observed to interfere directly with each other. The negative effects should result from exploitation competition through debasing the quality of host plant. Our results show that the tending ants benefited *A. craccivora* by eliminating its competitor. As an increase in the population of the preferred aphid species should be desirable for the tending ants, the selective predation on *M. crassicauda* can be considered to be adaptive for the ants.

An analogous result was obtained in another ant–aphid system on chestnut trees (Sakata 1995). In the system consisting of an ant, *L. niger*, and two aphid species, *Lachnus tropicalis* and *Myzocallis kuricola*, the ants preferred *L. tropicalis* to *M. kuricola*, although they utilized both as honeydew sources. The ants benefit both aphids when the aphid density per ant is low. However, as the aphid density becomes higher and honeydew is in excess, the ants more frequently prey on *M. kuricola*. The effects of ants on aphids seem to reflect the preference of the ants: ants bring benefit most to the aphids from which the ants benefit most.

These phenomena can be explained by the collective decision-making system of *L. niger*. It is hypothesized that each worker can perceive some mark on an aphid that her nestmates have left in collecting honeydew and decide not to attack the aphids that they are using (Sakata 1994). Consequently, when the aphids are in excess, the surplus aphids are inevitably not used as a honeydew source and are attacked by the ants. Thus, the ants can control their foraging activities according to balance between the supply and demand of honeydew. Furthermore, if there are differences in attractiveness to the ants among aphids, less attractive aphids should have less chance to be used as a honeydew source. As a result, the ants more often attack less attractive aphids.

The decision-making system of the ants leads to competition among sugar sources. To maintain the association with ants, myrmecophilous aphids must be more attractive to ants than other sugar sources. Otherwise, the ants will use other sugar sources and eliminate the aphids. For the aphid species for which attracting ants is too costly or restricted, repelling ants should be an alternative strategy. If selection through discrimination by ants is to work completely, only the most attractive aphid species could be myrmecophilous on one host plant species. Competition among sugar sources should provide an answer to Bristow' s (1991) question, "Why are so few aphids ant-tended?"

*Megoura crassicauda* repelled the ants from their host plant. The honeydew of *M. crassicauda* is potentially utilizable for ants because the ant *L. niger* was attracted to dry droplets of honeydew that *M. crassicauda* scattered on the floor and inner walls of the cultivation cylinders. The aphids have some means to repel the ants so intensely as to counteract the attractiveness of their own honeydew. The quality and quantity of aphid honeydew are different among species feeding on the same plants, and the extent of myrmecophily of aphids and ant preference for their honeydew depends on the sugar composition of the honeydew (Volkl et al. 1999). To avoid ant attack, nonmyrmecophilous aphids are likely to reduce the attractiveness of their honeydew as well as repelling ants. When myrmecophilous and nonmyrmecophilous aphids coexist on their common host plant, conflict occurs between them whether they can attract or repel ants. Because ant-attraction by *A. craccivora* exceeded ant-repelling by *M. crassicauda*, *M. crassicauda* suffered ant attack.

Because of ant discrimination, extrafloral nectaries should also influence the relationships between ants and aphids. To be tended by ants, herbivores must excrete more attractive honeydew than extrafloral nectaries. Otherwise, they would suffer attack by the ants attracted to extrafloral nectaries (EFN). To avoid ant attack, aphids may have been selected either to be more attractive to ants than EFN or to repel the ants attracted by EFN. Supporting this hypothesis, some studies show that myrmecophilous herbivores are more attractive to ants than extrafloral nectaries as well as *A. craccivora* in this study (Messina 1981; Buckley 1983; Sudd and Sudd 1985; Compton and Robertson 1988).

The ant-distraction hypothesis (Becerra and Venable 1989) regards extrafloral nectaries as an organ that operates to distract the ants from tending herbivores. Honeydew-producing herbivores could also distract ants from extrafloral nectaries. It is likely that both ant-attraction of *A. craccivora* and ant-avoidance of *M. crassicauda* were responsible for the negative correlation between the number of each aphid and the number of ants foraging at extrafloral nectaries. It is also possible that the infestations by aphids reduced the attractiveness of extrafloral nectaries to ants by affecting the quality and quantity of its secretion. Irrespective of the exact reason, distracting the ants from feeding at extrafloral nectaries can be adaptive strategy for both aphid species.

The facts that myrmecophilous herbivores often surpass extrafloral nectaries in attracting ants suggest that myrmecophilous herbivores have been selected to negate a defensive effect of extrafloral nectaries. However, extrafloral nectaries could have a potential function not only to distract ants but also to make ants eliminate honeydew-producing herbivores. From an evolutionary point of view, interference among sugar sources involving extrafloral nectaries should play an important role in the relationships among plants, honeydew-producing herbivores, and ants.

**Acknowledgments** We thank Keisuke Iwao, Diane Wagner, and Takao Itioka for valuable comments on this manuscript. We are indebted to Hajime Takada for instructions on the methods to keep aphids and to Kazunori Ohashi and Kuniko Sakata for their assistance. This study was partly supported by a grant-in-aid for J.S.P.S. research fellowships for young scientists from the Japanese Ministry of Education, Science and Culture (#6390).

## References

Addicott JF (1979) A multispecies aphid–ant association: density dependence and species-specific effects. Can J Zool 57:558–569

Bach CE (1991) Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). Oecologia (Berl) 87:233–239

Begon M, Harper JL, Townsend CR (1996) Ecology: individuals, populations and communities, 3rd edn. Blackwell, Oxford

Becerra JXI, Venable DL (1989) Extrafloral nectaries: a defense against ant–Homoptera mutualism? Oikos 55:276–280

Boucher DH (1985) The biology of mutualism. Oxford University Press, New York

Breton LM, Addicott JF (1992) Density-dependent mutualism in an aphid–ant interaction. Ecology 73:2175–2180

Bristow CM (1984) Differential benefits from ant attendance to 2 species of Homoptera on New York ironweed (*Vernonia noveboracensis*). J Anim Ecol 53:715–726

Bristow CM (1991) Why are so few aphids ant-tended? In: Huxley CR, Cutler DF (eds) Ant–plant Interactions. Oxford University Press, New York, pp 104–119

Bronstein JL (1994) Conditional outcomes in mutualistic interactions. Trends Ecol Evol 9:214–217

Buckley RC (1983) Interactions between ants and menbracid bugs decrease growth and seed set of a hostplant bearing extrafloral nectaries. Oecologia (Berl) 58:132–136

Buckley RC (1987) Interactions involving plants, Homoptera, and ants. Annu Rev Ecol Syst 18:111–135

Compton SG, Robertson HG (1988) Complex interactions between mutualists: ants tending homopterans protect fig seeds and pollinators. Ecology 69:1302–1305

Compton SG, Robertson HG (1991) Effects of ant-homopteran systems on fig–figwasp interactions. In: Huxley CR, Cutler DF (eds) Ant–plant interactions. Oxford University Press, New York, pp 120–130

Cushman JH, Addicott JF (1989) Intraspecific and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. Oecologia (Berl) 79:315–321

Cushman JH, Addicott JF (1991) Conditional interaction in ant–plant-herbivore mutualism. In: Huxley CR, Cutler DF (eds) Ant–plant Interactions. Oxford University Press, New York, pp 104–119

Cushman JH, Whitham TG (1989) Conditional mutualism in a membracid–ant association: temporal, age-specific, and density-dependent effects. Ecology 70:1040–1047

Cushman JH, Whitham TG (1991) Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. Am Nat 138:851–865

Fritz RS (1983) Ant protection of a host plant defoliator: consequence of an ant–membracid mutualism. Ecology 64:789–797

Huxley CR, Cutler DF (1991) Ant–plant interactions. Oxford University Press, New York

Itioka T, Inoue T (1996) Density-dependent ant attendance and its effects on the parasitism of a honeydew-producing scale insect, *Ceroplastes rubens*. Oecologia (Berl) 106:448–454

Itioka T, Inoue T (1999) The alternation of mutualistic ant species affects the population growth of their trophobiont mealybug. Ecography 22:169–177

Ito F, Higashi S (1991) An indirect mutualism between oaks and wood ants via aphids. J Anim Ecol 60:463–470

Keeler KH (1989) Ant–plant interactions. In: Abrahamson WG (ed) Plant–animal interactions. McGraw-Hill, New York, pp 207–242

Koptur S (1985) Alternative defenses against herbivores in *Inga* (Fabaceae: Mimosoideae) over an elevational gradient. Ecology 66:1639–1650

Koptur S (1992) Extrafloral nectary-mediated interactions between insects and plants. In: Bernays E (ed) Insect–plant interactions. CRC Press, Boca Raton, pp 81–129

Messina FJ (1981) Plant protection as a consequence of an ant–membracid mutualism: interactions on goldenrod (*Solidago* sp.). Ecology 62:1433–1440

O'Dowd DJ (1979) Foliar nectar production and ant activity on a Neotropical tree, *Ochroma pyramidale*. Oecologia (Berl) 43:233–248

Oliveira PS (1997) The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). Funct Ecol 11:323–330

Rashbrook VK, Compton SG, Lawton JH (1992) Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. Ecology 73:2167–2174

Sakata H (1994) How an ant decides to prey on or to attend aphids. Res Popul Ecol 36:45–51

Sakata H (1995) Density-dependent predation of the ant *Lasius niger* (Hymenoptera: Formicidae) on two attended aphids *Lachnus tropicalis* and *Myzocallis kuricola* (Homoptera: Aphididae). Res Popul Ecol 37:159–164

Sakata H (1999) Indirect interactions between two aphid species in relation to ant attendance. Ecol Res 14:329–340

Skinner GJ, Whittaker JB (1981) An experimental investigation of interrelationships between the wood ant (*Formica rufa*) and some tree-canopy herbivores. J Anim Ecol 50:313–326

Stadler B, Dixon AFG (1998) Cost of ant attendance for aphids. J Anim Ecol 67:454–459

Sudd JH, Sudd ME (1985) Seasonal changes in the response of wood ants (*Formica lugubris*) to sucrose baits. Ecol Entomol 10:89–97

Volkl W, Woodring J, Fisher M, Lorenz MW, Hoffmann KH (1999) Ant–aphid mutualism: the impact of honeydew production and honeydew sugar composition on ant preferences. Oecologia (Berl) 118:483–491

Way MJ (1963) Mutualism between ants and honeydew-producing Homoptera. Annu Rev Entomol 8:307–344

Yao I, Shibao H, Akimoto S (2000) Costs and benefits of ant attendance to the drepanosiphid aphid *Tuberculatus quercicola*. Oikos 89:3–10