Behav Ecol Sociobiol (2001) 49:304–310
DOI 10.1007/s002650000303

ORIGINAL ARTICLE

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Balancing between mutualism and exploitation: the symbiotic interaction between *Lasius* ants and aphids

Received: 3 August 2000 / Revised: 27 October 2000 / Accepted: 5 November 2000 / Published online: 26 January 2001

Abstract Nests of *Lasius niger* (L.) ants were given varied food regimens to test whether their behaviour towards an aphid partner, *Aphis fabae* (Scop.), changed with alternative food supplies. Honeydew collection and predation on aphids were measured by video monitoring the movement of ants between their nest and an aphid aggregation. Data collected from the aphid aggregations enabled comparisons between remaining aphid biomass and between the tending intensities of the ants. I tested how ant behaviour was influenced by their access to alternative prey and sugar. The results showed that ants accepted a honey solution as a substitute for the honeydew produced by aphids. Ants not only attended their aphid partners, but also preyed on them. The average predation rate increased eightfold when ants were offered the alternative of sugar, whereas alternative prey had no significant effect. In contrast, ant-tending intensity decreased with alternative sugar whereas alternative prey elicited no effect.

Keywords Ant-aphid symbiosis · Mutualism · Predation · Ant behaviour · Conditional interaction outcome

Introduction

Symbiotic interactions can be mutualistic, neutral or exploitative and animals make facultative changes between these options (Cushmann and Addicot 1991; Bronstein 1994). Symbiosies involving ant-attended Homoptera and their ant partners are conventionally categorised as mutualisms. In these interactions, homopterans excrete honeydew that serves as an energy resource for ants. Ants, in return, provide a number of beneficial services to their partners. Ants imbibe honeydew directly from the homopterans, thereby reducing their contamination by waste products (Way 1954), remove dead individuals and exuviae (Nixon 1951; Banks 1962; Buckley 1987b), provide protection against natural enemies (Way 1954; Banks 1962; Banks and Macauley 1967), provide transport to feeding sites (Way 1954; Ho and Khoo 1997), provide shelter (Nixon 1951), and brood care (Lubbock 1882; Wood 1982; Bristow 1983; Cushmann and Whitham 1989).

However, ants also prey on their homopteran partners (Pontin 1958, 1978; Edinger 1985; Cherix 1987; Rosengren and Sundström 1991; Sakata 1994, 1996). Way (1954) suggested that predation by weaver ants on attended scale insects was initiated when the ant colony had excess sugar. Rosengren and Sundström (1991) explained predation on attended aphids by *Formica* ants with the same mechanism. Pontin (1958) hypothesised that ants would maintain a balanced protein-carbohydrate intake by initiating predation on attended aphids when other prey were scarce. These ideas have never been tested experimentally, but the general hypothesis is that ants exploit their homopteran partners as a source of sugar, by tending them, and protein. Honeydew is an incomplete diet because prey are also needed (Way 1963; Buckley 1987a). More information on ant-Homoptera interactions can be found in reviews by Nixon (1951), Way (1963) and Buckley (1987b).

Thus, ant-Homoptera interactions are likely to vary and may cover the spectrum from mutualistic ant-tending to exploitative predation by ants (Cushmann and Addicott 1991; Bronstein 1994). Moreover, if abundant sugar results in increased exploitation of homopterans by their ant partners, then sugar-producing extrafloral nectaries may protect plants against harmful homopterans (Becerra and Venable 1989). Experimental studies which examine factors that cause a change in the ant-Homopteran interaction are clearly needed. This study investigates whether *Lasius niger* (L.) ants change their behaviour towards their aphid partner, *Aphis fabae* (Scop.), according to food supply. Predation by ants

Communicated by F. Ratnieks

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and ant-tending behaviour were recorded when ants were offered diets with and without sugar, and with and without prey. When ants were fed sugar their predatory behaviour increased whereas their tending behaviour and honeydew collection decreased. Supplementing the diet with prey induced no significant behavioural changes.

Methods

Study organisms and study site

L. niger, the common garden ant, attends aphids including *A. fabae* (Pontin 1958). The experimental ant colony was collected from a garden in Aarhus, Denmark, in March 1997, and subsequently maintained in the laboratory. The experiment commenced (June 1998) with a colony of one queen, approximately 500 workers and brood. Three closed Plexiglas boxes (14×14×2 cm) filled with garden soil housed the nest. These boxes were connected by plastic tubes (5 mm diameter) together with a foraging arena (a plastic bowl, 35×25×13 cm). Data collection began 3 months after artificial winter hibernation (4 months at 5°C, 24 h darkness). From the end of hibernation to data collection, ants were kept at 16–20°C and in a 16:8 h light:dark photophase.

A. fabae, the black bean aphid, is a facultative myrmecophilous aphid species occasionally attended by *L. niger* (Banks 1959). The aphid culture used for this experiment had been kept in the laboratory for several years. Aphids were reared on broad bean [*Vicia faba* (L.)], a secondary host plant (Banks and Macaulay 1967; Heie 1986). Broad beans were grown in fine vermiculite (Skamol, Denmark) and the culture kept at 20 (±0.5)°C and a 16:8 h light:dark photophase.

Experimental set-up

To ensure that approximately equal numbers of aphids were introduced in each dietary treatment (see below), 20 bean plants were grown (each in a 60-ml glass vial) to a size of 3–4 cm and each plant was infested with four adult apterous aphids. Plants and aphids were then allowed to develop for 21 days. Then, 15 aphid-infested plants were randomly selected and constituted a standardised aphid population.

Ants and aphids were prevented from escaping by being placed on “islands”, the ant nest and foraging arena on one, and a standardised aphid population on the other. Islands were made by placing plastic trays in a larger tray filled with a soap solution. The foraging arena and the aphid island were connected by a stick (4 mm diameter). The central section of the bridge was a cardboard rectangle (2.5×0.5 cm) marked with a scale. Double-sided adhesive tape denied ants access to the underside of the cardboard. A camera (FlexCam, Student Cam Pal Rev 6.0) connected to a video recorder (Philips model VR 475/02) was focused on the upper side of the cardboard to monitor all passing ants and to estimate the size of the aphids they carried. The set-up was kept at 24 (±1)°C and in a 16:8 h light:dark photophase.

Diet treatments

The ant colony was exposed to four different dietary treatments which represent the four combinations of a diet with or without prey (p+ or p–) and with or without honey (h+ or h–). Prey consisted of freshly freeze-killed 100-mg *Drosophila melanogaster*, 50-mg housefly (*Musca domestica* L.) and 50 mg of mealworm (*Tenebrio molitor* L.) per day. Honey was a solution of acacia honey and demineralised water (3.5 g honey in 10 ml solution) given ad libitum. Water (replenished daily), and prey or honey, if given, were changed once a day at 1500 (range ±0.5) hours.

Experimental design

The experiment was designed as a complete randomised-block design. One block represented a period of 16 days. Three consecutive blocks were conducted. In each block, the ant colony was exposed to the four dietary treatments. Each treatment lasted 4 days. During the first 2 days, the colony was given prey and honey (p+h+), to prevent starvation, followed by one of the four diets for the next 2 days. The order of treatments within each block was randomised. On the first day within each treatment, a new standardised aphid population was introduced. During the last 2 days, ant activity on the bridge was recorded on video, six periods of 0.5 h per day with 0.5 h in between. The first period started at 0700 hours, the morning after the diet had been introduced, on the 3rd day of the treatment.

Data collection

Within each 0.5-h period, ant activity was measured from the videotapes. Individual ants crossing the bridge towards the nest were counted and categorised as (1) crossing (total ants), (2) carrying an aphid (predator) or (3) having a distended gaster (honeydew collector). A distended gaster was easily recognised (tergites were forced apart by the filled crop) and assumed to contain honeydew since this was the only liquid food available from the aphid colony. The number of honeydew collectors may have been underestimated if some individuals had only partly filled their crops. However, this seems unlikely, as returning ants fell in two distinct classes – those with and those without a distended gaster. The aphids carried were placed into size categories (<0.72, 0.72–0.88, 0.89–1.20, and >1.20 mm length). To estimate aphid biomass, ten aphids from each category were weighed and the mean weight of each category calculated. On the final day of each treatment, the number of ants on the bean plants was counted, and the plants and associated aphid population were placed in 70% alcohol. Later, aphids and exuviae were counted and aphids were sized as above.

Statistics

The following were calculated for each 0.5-h period: (1) total activity=total ants, (2) honeydew collection ratio=honeydew collectors/total ants, (3) hunting ratio=predators/total ants, (4) predation biomass=$\Sigma n_i w_i$, where n_i is number of aphids carried by ants belonging to the ith size category, and w_i is the estimated mean weight of aphids belonging to the ith size category (w_1=0.016 mg, w_2=0.051 mg, w_3=0.138 mg, w_4=0.238 mg). The two proportional parameters, hunting ratio and honeydew collection ratio, were not arcsine transformed because their untransformed residuals were more normally distributed than their transformed residuals. Differences were tested between treatments (prey and honey) and between blocks, with a multivariate repeated-measure analysis. The six periods within one day were treated as repeated measures, and days (1 and 2) were nested within blocks.

The following were calculated from data collected on the bean plants after each treatment: (1) aphid biomass=$\Sigma m_i w_i$, where m_i is the number of remaining aphids belonging to the ith size category, (2) tending activity=number of ants, (3) tending ratio=number of ants/number of aphids, (4) exuviae per aphid=number of exuviae/number of aphids. These parameters were tested individually for differences among treatments and blocks with a two-way ANOVA, blocked for the treatment blocks. All analysis was done with JMP 3.2.2. (SAS 1995).

Results

Activity of ants

Figure 1 shows the means of the ant activities and the amount of aphid biomass taken as prey in the four differ-

Fig. 1 Effects of dietary treatment on ant total activity (**a**), percent honeydew collectors (**b**), percent predators (**c**) and biomass of aphids eaten (**d**). Treatments: *p* prey, *h* honey solution, + included in ant diet, – absent from ant diet. Values are overall means (+SD) of 0.5-h periods for each treatment (*n*=36 for all treatments)

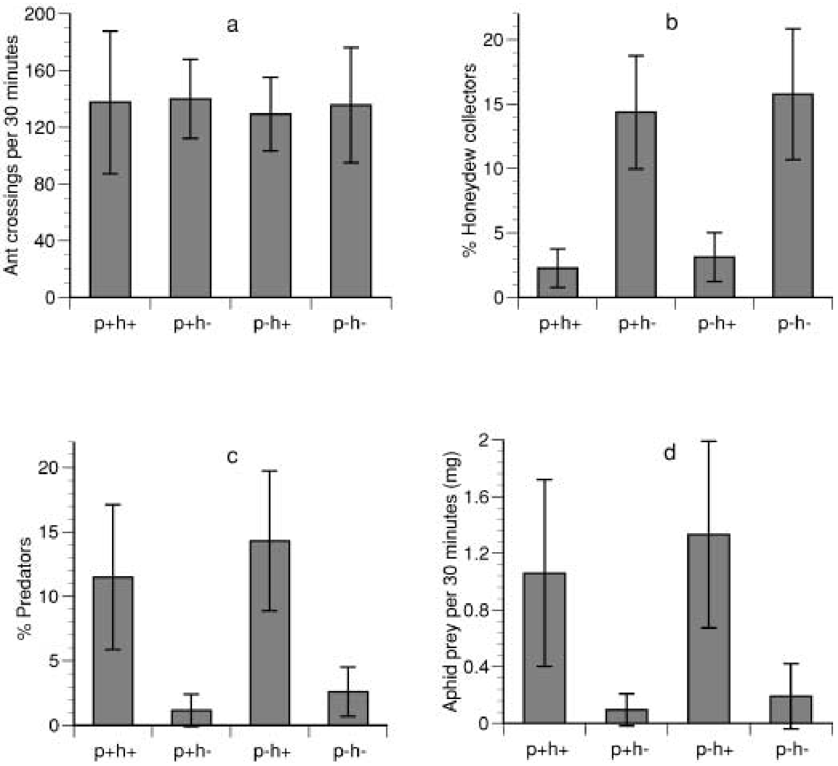

Table 1 Multivariate repeated-measure analysis of ant activity. The six 0.5-h periods within one day were treated as repeated measures and days were nested within blocks (*df* in the denominator were 15 for all combinations of parameters and sources)

Source	*df*	Total activity		Honeydew collection ratio		Hunting ratio		Predation biomass	
		Exact *F*	*P*-value	Exact *F*	*P*-value	Exact *F*	*P*-value	Exact *F*	*P*-value
Block	2	3.559	0.054	2.141	0.152	3.079	0.076	2.971	0.082
Day (block)	3	0.673	0.582	0.495	0.691	3.127	0.057	3.044	0.061
Prey	1	0.249	0.625	1.279	0.276	3.198	0.094	1.893	0.189
Honey	1	0.120	0.734	153.91	<0.0001	85.723	<0.0001	62.106	<0.0001
Prey×honey	1	0.024	0.88	0.072	0.792	0.339	0.569	0.438	0.518

ent dietary treatments. Total ant activity between the aphids and the nest was similar in all treatments (Fig. 1a). However, the proportion of honeydew collectors was highest in treatments without honey (p+h– and p–h–) and lowest in treatments with honey (p+h+ and p–h+) in the diet (Fig. 2b). In treatments without honey, the mean proportion of ants collecting honeydew was 15.1%, whereas only 2.7% of the ants collected honeydew when honey was available. Thus, ants deprived of honey increased the effort spent on honeydew harvest from aphids. This situation was reversed in the case of hunting activity. In the two treatments without honey, the proportion of predators was lowest (Fig. 1c). When ants had no access to honey, the mean proportion of predators was only 1.9%, whereas 12.1% of the returning ants were hunters when honey was available. The implication is that the ant colony depends on live aphids to produce honeydew and will only prey on them when their demand for sugar is fulfilled. In parallel with the hunting ratio, the biomass of aphids, taken as prey, was lowest in treatments without honey and highest when honey was available (Fig. 1d). A more than eightfold increase in predation biomass was observed between treatments without honey (mean=0.144 mg/30 min) and treatments with honey (mean=1.196 mg/30 min).

Table 1 shows the effects of prey and honey (including the effects of blocks and day) on ant activities and predation biomass. Total ant activity was not significantly influenced by either prey or honey (*P*=0.63 and 0.73, respectively). However, the honeydew collection ratio was significantly higher when ants were denied access to honey (*P*<0.0001) and the hunting ratio was higher when access to honey was allowed (*P*<0.0001). Neither the honeydew collection ratio nor the hunting ratio was influenced by prey (*P*=0.28 and 0.09, respectively). As with the hunting ratio, the predation biomass was significantly higher when honey was available (*P*<0.0001) but was not influenced by the availability of prey (*P*=0.19). A similar result was obtained if predation was analysed as the number of aphids brought to the ant nest. Thus,

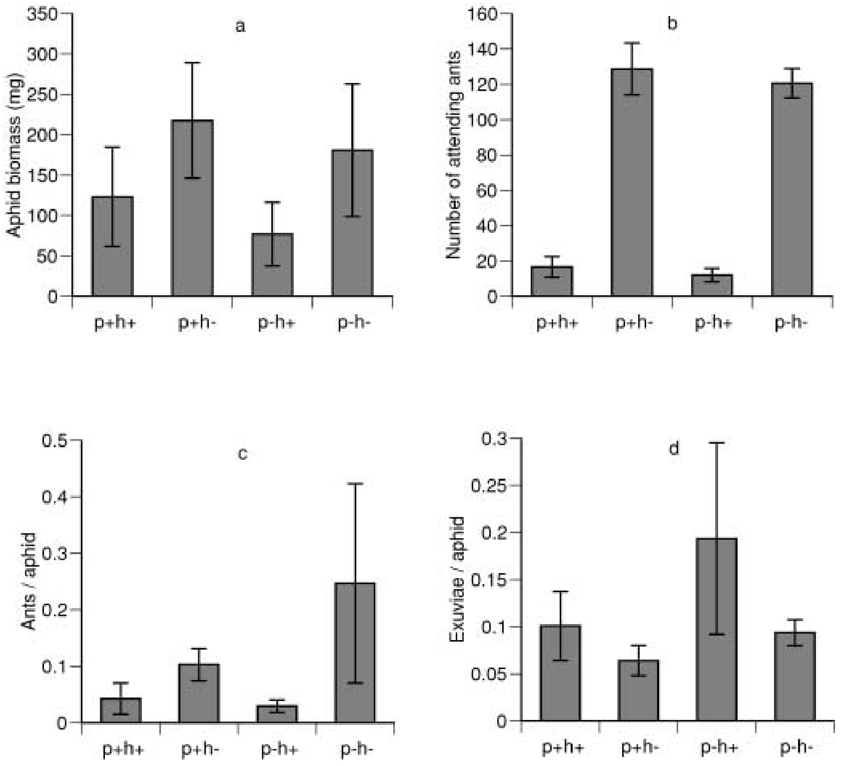

Fig. 2 Effects of dietary treatment on remaining aphid biomass (**a**) and measures of ant tending intensity: tending activity (**b**), tending ratio (**c**) and exuviae per aphid (**d**). Treatments: *p* prey, *h* honey solution, + included in ant diet, – absent from ant diet. Values are means (+SE) of treatments (*n*=3 for all treatments)

Table 2 Univariate analysis of the measurements on aphid populations after each treatment. Within each of the three blocks one measurement was carried out per treatment (**P*<0.05, ***P*<0.01, ****P*<0.0001)

Source	*df*	*F*-ratio			
		Remaining aphid biomass	Tending activity	Tending ratio	Exuviae per aphid
Block	2	15.58**	4.12	1.91	1.89
Prey	1	1.87	0.86	0.64	1.51
Honey	1	10.63*	260.86***	2.87	1.88
Prey×honey	1	0.02	0.06	0.92	0.42
Error	6				

while the overall activity between aphids and nest remained the same between diets, its character changed from honeydew collection to hunting when an additional sugar source became available. The difference observed in honeydew collection showed that honey constituted a substitute for honeydew. Honey was not simply harvested in addition to unchanged honeydew harvesting. Therefore, ants may switch to alternative sugar sources even if honeydew contains ant attractants as suggested by Kiss (1981) and Buckley (1987a).

Effects on aphid populations

Figure 2 shows the means of remaining aphid biomass and three different ant-tending measures in each dietary treatment. Aphid biomass was lowest after treatments where ants had access to honey (mean=100 mg) compared to treatments where ants had no access to honey (mean=199 mg; Fig. 2a). Thus, when ants had access to honey they reduced the aphid populations. The number of tending ants as well as the number of ants per aphid serve as measures of tending intensity. Both measures were lowest in treatments where ants had access to honey (Fig. 2b, c). A more than eightfold decrease in the number of tending ants was observed between treatments without honey (mean=125 ants) and treatments with honey (mean=14 ants). Similarly, the mean ant/aphid ratio decreased from 0.18 in treatments without honey to 0.04 in treatments with honey. The number of exuviae per aphid may serve as an inverse measure of tending intensity as the removal of exuviae may improve the hygiene of the aphid colony. In this case, the exuvia/aphid ratio was highest when ants were offered honey (mean=0.15) and lowest when ants were without honey (mean=0.08; Fig. 2d). Thus, all three measures of tending intensity decreased when ants were offered honey.

Table 2 shows the effects of prey and honey (including the effects of blocks and day) on remaining aphid biomass and ant-tending measures. Aphid biomass was significantly higher after treatments without honey (*P*=0.02) and was not influenced by prey (*P*=0.22). A similar result was obtained if the analysis was performed on the number of aphids remaining after each treatment.

In addition, the number of tending ants was significantly higher when ants were deprived of honey ($P<0.0001$) but was not influenced by prey ($P=0.39$). The ant/aphid ratio was neither influenced by honey ($P=0.14$) nor by prey ($P=0.45$). However, excluding one extremely high value (p–h–) from the analysis results in significantly higher ant/aphid ratios in treatments without honey ($F_{1.5}=14.13$, $P=0.01$). The number of exuviae per aphid was neither influenced by honey ($P=0.22$) nor by prey ($P=0.27$). These results suggest that aphid colonies associated with ant partners with access to alternative sugar may not only experience a cost due to predation but also one due to decreased ant-tending.

Testing a second ant nest

To test the generality of the major findings, a second experiment was performed on another ant nest of similar size. This nest was exposed to the same treatments. However, each dietary treatment lasted for 6 days and was not repeated. Each day the number of aphid prey (taken during 1 h) and the number of attending ants were recorded. A two-way ANOVA was performed on these measures, treating days as independent measures. In treatments with honey, the number of aphids taken as prey was significantly higher than in treatments without honey ($\text{mean}_{+\text{honey}}=50.6$, $\text{mean}_{-\text{honey}}=11.6$; $F_{1.20}=28.2$, $P<0.0001$), and the number of attending ants was lower ($\text{mean}_{+\text{honey}}=10.3$, $\text{mean}_{-\text{honey}}=111.5$; $F_{1.20}=34.1$, $P<0.0001$). Neither predation ($\text{mean}_{+\text{prey}}=28.4$ aphids, $\text{mean}_{-\text{prey}}=33.8$ aphids; $F_{1.20}=0.53$, $P=0.48$) nor ant-tending ($\text{mean}_{+\text{prey}}=58.3$ ants; $\text{mean}_{-\text{prey}}=63.5$ ants; $F_{1.20}=0.09$, $P=0.77$) was influenced by prey. Thus, this second nest confirmed the trend seen in the main experiment.

Discussion

The results show that ants modify their behaviour towards their symbiotic aphid partners according to the availability of alternative food resources. Ants not only attended their aphid partners but also ate them. When offered alternative sugar, the interaction moved from mutualism to exploitation due to decreased ant-tending and increased predation.

Other studies support this observation that ants increase predation on homopteran partners when sugar is in excess supply, but research in this pioneer field is scant. Way (1954) observed that *Oecophylla longinoda*, when fed honey, attacked its coccid partners, but could not confirm that the coccids were eaten. Pontin (1978) provided indirect evidence that *L. flavus* reduces its subterranean aphid population when offered sugar. However, Pontin’s (1958) suggestion that predation should increase when other prey become scarce is not supported by this study. Three further studies provide evidence of increased ant predation on aphids with increased aphid population (Edinger 1985; Sakata 1994, 1996). If aphid population size was positively correlated with honeydew production, one might argue that increased predation was due to increased access to sugar in the form of honeydew.

Honey had a pronounced effect on predation rate, whereas prey did not. The explanation might be that ants rely on sugar as an energy source for all their activities (including foraging for prey) and are therefore deeply dependent on this resource (Carroll and Janzen 1973). In contrast, ants depend less on prey, as only the queen and larvae need significant amounts of protein (Beattie 1985) and because ants are believed to cannibalise their brood when prey are scarce (Carroll and Janzen 1973; Nielsen and Josens 1978; Risch and Carroll 1982; Nonacs 1991; J. Offenberg, unpublished data). Thus, sugar is needed for colony maintenance, whereas prey are needed for colony growth. In this scenario, an ant colony's highest priority should be to secure a constant supply of sugar, while foraging for prey remains secondary. When prey are abundant, the colony should raise additional brood for a potential protein reserve in case of fluctuating prey supply. Ants in this study seemed to secure their sugar source by limiting predation on aphids when aphids were the sole (and limiting) source of sugar. Only when sugar was over-abundant did ants increase predation and prey intake (Fig. 1c, d).

Other studies have shown the benefits for *A. fabae* from interaction with *L. niger*. Ant partners will defend attended aphids from natural enemies (Banks 1962), enabling those aphids to multiply faster than unattended aphids (Banks and Macaulay 1967). These studies demonstrate that ants protect aphids, while the current study offers the additional observation that ants also prey upon aphids under certain conditions. The interaction outcome is therefore variable, and depends on sugar availability as well as factors such as natural enemies. With an abundance of sugar (nectar, fruits, honeydew) and low predation pressure, aphids benefit less from interaction and can experience total costs, although this study only demonstrated a significant reduction in the aphid population in treatments with alternative sugar (Fig. 2a, Table 2). To endorse the suggestion of Cushmann and Addicott (1991), ant-aphid interactions may well alternate between two extreme outcomes – mutualism and predation.

In this study, alternative sugar induced a more than eightfold increase in predation on aphids (Fig. 1d). Furthermore, all three measures of tending intensity – tending activity, tending ratio and exuviae per aphid – decreased when ants had an alternative sugar source (although the difference in exuviae/aphid was not significant; Fig. 2b–d, Table 2). These results support the ant-distraction hypothesis of Becerra and Venable (1989). Their hypothesis argues that extrafloral nectaries defend plants from ant-Homoptera mutualisms by offering a honeydew substitute in the form of extrafloral nectar, thereby distracting the ants from tending herbivorous homopterans. This study suggests further that ants may not only neglect homopterans when offered alternative sugar but also prey more upon them. Extrafloral nectaries may afford better protection against ant-Homoptera mutualisms than previously suspected.

In contrast to this study, Del-Claro and Oliveira (1993) found that *Camponotus* ants did not neglect their membracid partners when offered alternative sugar in the field. That study, however, allowed the ants a maximum of 1 h to respond to the sugar, whereas this study allowed approximately 16 h. Thus, ants might require more than 1 h to adapt their behaviour. A delayed response may be adaptive if ants are thereby able to assess the persistence of a newly discovered sugar source before neglecting (and potentially losing/reducing) their original source. Moreover, Del-Claro and Oliveira's survey did not include ant predation on membracids.

In certain crops, ants impose an indirect cost by tending Homoptera that damage plants (Nixon 1951). This problem may be pronounced where ants have been used for biological control against other herbivorous pests (Way and Khoo 1992). By offering ants artificial sugar, increased predation on attended homopterans, combined with neglect, will reduce the indirect costs. The presence of ants may result in a total benefit to plants if ant-associated Homoptera populations suffer more than their autonomous counterparts. With suitably funded research, the sugar-induced change in ant behaviour could be utilised in biological control.

As suggested by the present study, symbiotic interactions may be more dynamic in nature than previously recognised. Not only may the net benefit received in mutualism vary in magnitude, it may change and become a net cost, moving the symbiosis from mutualism to an exploitative interaction (Cushman and Addicott 1991; Bronstein 1994). Therefore, caution should be taken regarding symbioses as either mutualisms or exploitations, and careful consideration given to the conditions likely to affect the outcome. Furthermore, dynamic outcomes lead to interesting considerations regarding the coevolution between symbiotic partners. True mutualistic interactions will favour the evolution of traits in one species that also benefit the other species. However, in predatory (or parasitic) interactions, the exploited species will tend to evolve defensive traits that have a negative impact on the exploiting species. Then, the exploiting species will try to evolve traits to overcome this acquired defence (coevolutionary arms race). What kind of coevolutionary pathway should we expect in interactions that change between mutualistic and exploitative outcomes? Will species in dynamic interactions be able to evolve plastic traits that facilitate partners under mutualistic conditions but defend them under exploitative conditions? Or does the average outcome determine whether coevolution results in mutualism or an arms race? The dynamics in symbiotic outcomes have demonstrated a need for more research regarding these interactions and their evolution.

Acknowledgements Thanks to Jacob Koella for valuable supervision during the design, analysis and writing of this study, and to David Nash and Simon Frost for constructive comments and linguistic improvements. My appreciation also to Else Bomsholt, Allan Kjaer, David Mayntz, Søren Toft and Fritz Vollrath for helpful ideas and laboratory equipment.

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