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Do extrafloral nectaries distract ants from visiting flowers? An experimental test of an overlooked hypothesis

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ABSTRACT

When ants visit flowers, they can interfere with plant reproduction. Some plant species possess adaptations, such as specialized floral morphologies, that reduce visitation by unproductive or injurious insects. Kerner (1878) hypothesized that extrafloral nectaries, by distracting ants from foraging at floral nectaries, might also serve as an adaptation to reduce ant visitation to flowers. The viability of this hypothesis rests, in part, on ant foraging behaviour. When presented with extra nectar sources, do fewer ants visit each nectary or does recruitment keep visitation constant? Using artificial plants placed near free-living colonies of two ant species, we varied the presence, absence and quality of extra nectar sources and monitored visitation to primary, invariable nectar sources, representing floral nectaries. Significantly fewer ants of both species visited primary nectaries when extra nectar sources were present. Variation in the quality of the extra nectar sources had no significant effect on the number of ants visiting primary nectaries, but did affect visitation to extra nectar sources by one of the two species. Workers of *Forelius* sp. 1 strongly preferred sugar solutions with amino acids over sugar solutions alone and significantly greater numbers of *Forelius* workers visited artificial plants that provided amino acids than plants in other treatments. In contrast, workers of *Formica perpilosa* showed no significant preference among nectar types and neither the presence nor the quality of extrafloral nectar significantly affected numbers of ants on artificial plants. The results suggest that extrafloral nectaries could benefit plants by reducing the number of ants visiting flowers.

Keywords: amino acids, ants, behaviour, extrafloral nectaries, *Forelius*, *Formica perpilosa*, Formicidae, mutualism, sugars.

INTRODUCTION

Many plant species bear nectar-secreting organs on leaves, stems or bracts, known collectively as extrafloral nectaries (Elias, 1983). The most widely accepted hypothesis to explain the evolution and maintenance of extrafloral nectaries is that the nectaries provide

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food for parasitic and predacious arthropods, especially ants, which kill or dislodge herbivores (Bentley, 1977a). Support for the protection hypothesis comes from many experimental studies showing increased herbivory and/or lower seed production when ants are denied access to plants (e.g. Janzen, 1967; Tilman, 1978; Schemske, 1980; Koptur, 1984; Oliveira, 1997; Oliveira *et al.*, 1999). Other studies, however, have found no evidence of protection by ants (for a review, see Becerra and Venable, 1989; see also Rashbrook *et al.*, 1992; Wagner, 1997; Mackay and Whalen, 1998; Zacharides and Midgley, 1999). In some systems, a lack of protection may be due to spatial and temporal variation in the density of ants and herbivores (Tilman, 1978; Horvitz and Schemske, 1984; Barton, 1986; Cushman and Whitham, 1989; Rico-Gray and Thien, 1989; Young *et al.*, 1997).

But extrafloral nectaries can confer benefits other than, or in addition to, plant protection. For example, production of extrafloral nectar may encourage ants to nest in or near plants, where ant waste products can provide valuable mineral nutrients to plants (Rickson, 1979; Treseder *et al.*, 1995; Wagner, 1997; Sagers *et al.*, 2000). Becerra and Venable (1989) suggested that extrafloral nectaries might sometimes serve to distract ants from tending homopterans; however, direct experimental support for this hypothesis is lacking (Fiala, 1990; Del-Claro and Oliviera, 1993). Here we investigate a hypothesis introduced in the nineteenth century but never tested: for plants that produce floral nectar, extrafloral nectaries serve to distract foraging ants from visiting flowers (Kerner, 1878).

Although there are well-documented cases of pollination by ants (e.g. Peakall *et al.*, 1990; Ramsey, 1995; Gomez *et al.*, 1996; Gomez, 2000), ant pollination appears to be relatively rare (Peakall *et al.*, 1991). Ants are nonetheless common visitors to nectar-producing flowers (Rico-Gray, 1989, 1993; Koptur and Truong, 1998; Rico-Gray *et al.*, 1998), where they can decrease plant reproductive output by robbing nectar, chasing off pollinators or destroying floral tissue (McDade and Kinsman, 1980; Herrera *et al.*, 1984; Norment, 1988; Buys, 1990; Yu and Pierce, 1998; Galen, 1999). In addition, ants can reduce pollen viability if they contact pollen while visiting flowers (Wagner, 2000). Many ant species secrete, onto the cuticle, antimicrobial substances that render pollen inviable upon contact (Beattie *et al.*, 1984, 1985; Hull and Beattie, 1988; Peakall *et al.*, 1990).

In this study, we test the most basic assumption of the distraction hypothesis: the presence of extra nectar sources decreases the number of ants at any one nectary. If, instead, extra nectaries simply draw more ants onto plants so that visitation to flowers remains constant, then distraction cannot help to explain the evolution of extrafloral nectaries.

Distraction of ants from flowers by extrafloral nectar could arise through several non-exclusive means. First, extra nectar sources might spread the pool of foraging ants among a greater number of locations, thereby reducing the number of ants at any one nectary. Second, plants might distract ants from flowers by producing extrafloral nectar of higher quality than floral nectar. Foraging theory predicts that consumers will sometimes ignore low-quality foods when higher-quality items are readily available (Charnov, 1976). Consistent with this prediction, studies have shown that ants reject dilute sugar solutions after their colony has been supplied with higher concentration solutions (Sudd and Sudd, 1985; A. Kay, in prep.), and colonies prefer solutions with sugar plus amino acids over sugar solutions alone (Lanza, 1988, 1991).

Compared with floral nectar, extrafloral nectar tends to contain higher concentrations of sugars (Wunnachit *et al.*, 1992; Koptur, 1994) and a greater variety of amino acids (Baker *et al.*, 1978). But there are few direct intraspecific comparisons of floral and extrafloral amino acid concentrations. Those that exist reach conflicting conclusions about which nectar type is more concentrated (Deuth, 1977; Wunnachit *et al.*, 1992). In interspecific comparisons, amino acid concentrations of extrafloral nectar tend to be high relative to floral concentrations, but also more variable [extrafloral nectar 0.6–279 $\text{mmol}\cdot\text{l}^{-1}$ (Inouye and Inouye, 1980; Durkee, 1982; Smith *et al.*, 1990; Lanza, 1991; Wunnachit *et al.*, 1992); floral nectar 0.08–25 $\text{mmol}\cdot\text{l}^{-1}$ (Guerrant and Fiedler, 1981; Baker and Baker, 1983)].

Using artificial plants bearing two types of nectaries, we address three questions regarding the effect of extrafloral nectar on ant foraging: (1) Do extra nectar sources reduce ant visitation to floral nectaries? (2) Do ants prefer to visit nectaries containing amino acids or higher concentrations of sugars compared to those with sugar only? (3) Is distraction more effective when extra nectar sources are of higher quality than floral nectar?

MATERIALS AND METHODS

We conducted fieldwork near Portal, Arizona during August of 1998. The study site was located in desert thornscrub habitat, dominated by *Acacia constricta* and *Prosopis juliflora*. To manipulate nectar presence and quality in a standardized way, we used artificial nectary-bearing plants constructed from dowels (Fig. 1). A dowel-plant consisted of a major trunk (40 mm in diameter, 1 m high) with four branches, each subdivided into six twigs constructed of fine dowels (5 mm in diameter). We used inverted caps of 0.65 ml microcentrifuge tubes as nectar cups. Unnaturally large numbers of nectar sources offered at a single point in time could temporarily saturate the forager population, producing unrealistic results. For this reason, we chose to use a small number of nectaries per dowel-plant. One cup was attached with glue to the end of each branchlet and at the tip of each branch, for

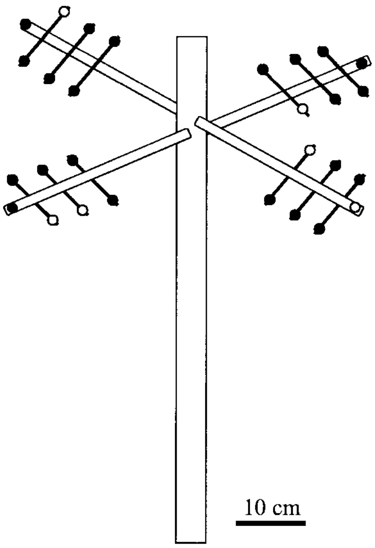

Fig. 1. Schematic drawing of an artificial plant. Grey circles are primary nectaries (representing floral nectaries); black circles represent extra nectar sources. The relative positions of primary and extra nectar sources were determined at random for each artificial plant. Nectary size is exaggerated in the drawing. See text for a detailed description.

a total of 28 nectaries per plant. Each cup was uniquely labelled. On each dowel-plant, we designated six nectar cups, chosen at random, to serve as primary nectaries. These represented floral nectaries. The other 22 nectar cups were designated the extra nectaries.

We studied free-living colonies of two sympatric ant species, *Formica perpilosa* (Formicinae) and *Forelius* sp. 1 (Dolichoderinae). Both species are diurnal and commonly forage on extrafloral nectary-bearing shrubs for plant and insect exudates and insect prey. *Formica perpilosa* workers are 5.0–8.5 mm long and tend to forage singly. *Forelius* sp. 1, apparently an undescribed species (S. Cover, personal communication with A. Kay), is a small ant (1.8–2.5 mm long) that forms trails and recruits strongly to food sources (Hölldobler, 1982). Both ant species have many thousands of workers in each colony (Schumacher and Whitford, 1974; personal observations).

Preliminary trials revealed that exposure to artificial nectars reduced the foraging responses of colonies on subsequent days. Therefore, we located a large number of naive colonies (24 per species) and tested the responses of all colonies of a species simultaneously. We tested each species on a separate day, at the time of day that it was most active on the study site (*F. perpilosa* in the morning and *Forelius* sp. 1 in the late afternoon). Several days before the experiment, we hammered a dowel-plant into the ground about 1 m from the entrance to each colony. Nectar cups remained empty until the day of the experiment.

On the day of the experiment, we filled the primary and extra nectar cups on each dowel-plant with one of four combinations of sucrose and amino acids (Table 1). Casein hydrolysate (ICN Biomedicals, Aurora, OH) served as a source of amino acids. Nectaries were filled with about 0.2 ml of solution and refilled whenever the level of fluid in a nectary dropped below half. We made solutions with distilled water the day before the experiment and refrigerated them until use.

For a given dowel-plant, data collection began when 10 ants were present. At that point, and then every 5 min for 45 min, an observer recorded the number of ants in contact with the fluid in each nectary. In all cases, dowel-plants were visited by the focal ant species only.

We analysed the effect of treatment on the mean number of ants in each colony visiting primary nectaries using multivariate repeated-measures analysis of variance (ANOVA). Data for each ant species were tested separately. We performed statistical analyses in SPSS (SPSS, Inc.) and JMP (SAS Institute, Inc.). If treatment explained a significant amount of variation in the ANOVA model, we performed three planned, orthogonal contrasts on the

Table 1. Composition of solutions added to primary and extra nectaries on artificial plants

	Primary nectaries		Extra nectaries	
Treatment	Sucrose	Amino acids	Sucrose	Amino acids
1	20	0	—	—
2	20	0	20	0
3	20	0	23	0
4	20	0	20	3

Note: Sucrose and amino acid concentrations are expressed as percent (weight/weight). Artificial plants in treatment 1 received no extra nectar.

ant visitation data (Sokal and Rohlf, 1995): (a) artificial plants with extra nectar sources versus those with primary nectaries only (all levels of extrafloral nectar quality combined); (b) artificial plants with extra nectar identical to primary nectar (20% sucrose) versus plants with extra nectar of higher quality than primary nectar (23% sucrose and 20% sucrose plus 3% amino acids); and (c) artificial plants with extra nectar consisting of 23% sucrose versus plants with extra nectar consisting of 20% sucrose plus 3% amino acids.

Ant visitation to the three qualities of extra nectar was also analysed using multivariate repeated-measures ANOVA. Following a significant effect of treatment, we applied contrasts (b) and (c) above.

We also examined the effect of extra nectar on the total number of ants on artificial plants. The number of ants on plants is sometimes correlated with the degree of protection (e.g. Rashbrook *et al.*, 1992); therefore, determining the response of colonies to variation in nectar quality may elucidate how ants affect the evolution of extrafloral nectar composition through protection (Baker *et al.*, 1978). We examined the effect of treatment on the total number of ants, estimated as the sum of all ants at primary and extra nectaries during the final observation period, using a one-way ANOVA followed by unplanned comparisons of means using Tukey-Kramer HSD.

RESULTS

Visitation to artificial floral nectaries

The presence of extra nectar sources substantially reduced ant visitation to the primary nectaries (Fig. 2). Ant visitation to primary nectaries differed significantly among the four treatments (Table 2). As a group, artificial plants with extra nectar sources had fewer ants visiting primary nectaries than plants lacking extra nectar sources (*Forelius* sp. 1: $F_{1,20} = 12.4$, $P = 0.002$; *F. perpilosa*: $F_{1,20} = 30.2$, $P < 0.0001$). The composition of the extra nectar had no significant effect on visitation to primary nectaries (Fig. 2; $F_{1,20} < 1.5$, $P > 0.2$, for both species and all contrasts among qualities of extrafloral nectar). Inspection of Fig. 2a suggests higher visitation to primary nectaries when extra nectaries contained amino acids than when extra nectaries contained only sugar, but the difference was not significant. The numbers of *Forelius* sp. 1 visiting floral nectaries increased significantly over the 45 min of observation, whereas the numbers of *F. perpilosa* increased slightly but not significantly (Fig. 2, Table 2). There were no significant interactions between treatment and time (Table 2).

Visitation to nectar sources of varying composition

The effect of nectar composition on the number of ants visiting extra nectaries was species-specific (Fig. 3). Workers of *Forelius* sp. 1 strongly preferred solutions containing amino acids over sugar-only solutions (Fig. 2a; 23% sucrose *vs* 20% sucrose plus 3% amino acids: $F_{1,15} = 12.3$, $P = 0.003$), but visitation to nectar cups containing 20% and 23% sucrose was almost identical (Fig. 3a). Nectar composition had no significant effect on the number of *F. perpilosa* workers visiting extra nectaries (Fig. 3b, Table 3). Numbers of both species at extra nectar sources increased during the 45 min observation period (Table 3). There were no significant interactions between treatment and time (Table 3).

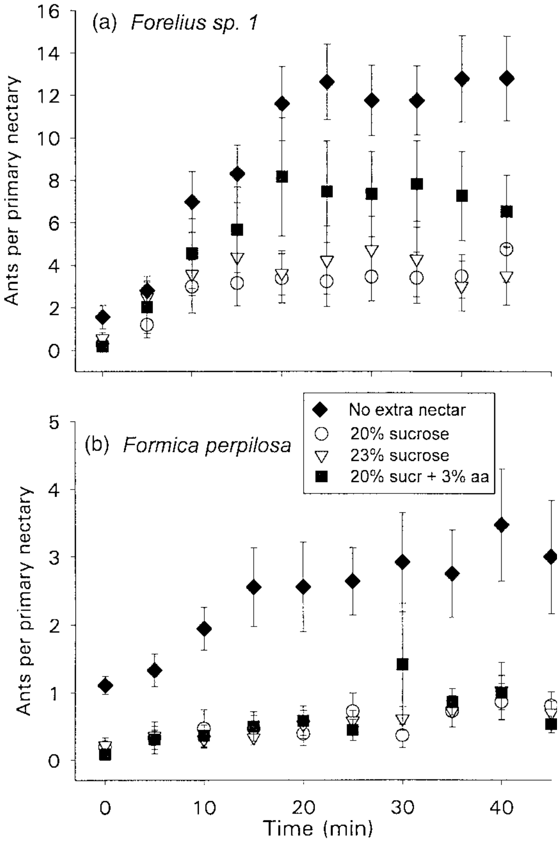

Fig. 2. Visitation by two ant species to primary nectaries on artificial plants. Primary nectaries always contained 20% sucrose. Treatments varied the presence and quality of extra nectar sources available. See text and Table 1 for detailed description of treatments. Each symbol is the mean of six ant colonies. Error bars represent two standard errors of the mean. (A) *Forelius* sp. 1, (B) *Formica perpilosa*.

Total visitation to artificial plants

The presence of extra nectar sources did not in itself lead to higher numbers of ants visiting artificial plants; rather, total visitation depended on nectar quality and on which ant species was involved (Fig. 4). Significantly greater numbers of *Forelius* sp. 1 visited plants when, and only when, nectar contained amino acids (Fig. 4a; $F_{3,20} = 6.5$, $P = 0.003$). For *F. perpilosa*, neither the presence of extrafloral nectar nor its composition significantly affected total visitation (Fig. 4b; $F_{3,20} = 1.1$, $P = 0.4$).

DISCUSSION

When ants visit flowers, they can hinder plant reproduction through both male and female function (Buys, 1990; Galen, 1999; Wagner, 2000). Reductions in plant fitness as a result of ant visitation to flowers can select for floral morphologies that exclude ants, such as narrow

Table 2. Multivariate ANOVA for the effects of extrafloral nectar treatment (none, 20% sucrose, 23% sucrose, or 20% sucrose plus 3% amino acids) on repeated measures of ant visitation to *primary* nectaries (simulated floral nectaries) on artificial plants: visitation by *Forelius* sp. 1 and *Formica perpilosa*

***Forelius* sp. 1** Between-subjects	d.f.	MS	*F*	*P*
Treatment	3	503.6	5.0	0.01
Error	20	101.0		
Within-subjects	d.f.	Wilks' λ	*F*	*P*
Time	9,12	0.2	5.2	0.005
Treatment × time	27,36	0.2	1.2	0.3
Formica perpilosa Between-subjects	d.f.	MS	*F*	*P*
Treatment	3	52.4	10.1	<0.001
Error	20	5.2		
Within-subjects	d.f.	Wilks' λ	*F*	*P*
Time	9,12	0.4	2.4	0.08
Treatment × time	27,36	0.3	0.8	0.8

corolla tubes (Galen, 1999). In addition, some ant-associated plant species deter visitation to flowers by producing ant-repellent substances on floral tissues (van der Pijl, 1955; Guerrant and Fiedler, 1981; Willmer and Stone, 1997). In this study, we found that extra nectar sources reduced ant visitation to primary nectaries on artificial plants. Our results suggest that selection to reduce ant visitation to flowers could also favour plants with large numbers of nectaries, such as those with extrafloral nectaries, relative to other plants in the population.

Extra nectaries functioned to distract ants from primary nectaries because, except in the case of *Forelius* reacting to amino acids, ant colonies did not recruit more workers onto plants with extra nectar sources available. As a result, extra nectaries served to subdivide the set of foragers among more locations, thereby reducing the number of ants at any one nectary. The maximum total number of workers of both species that we observed visiting artificial plants was similar to the number that visit shrubs of about the same height as at the study site (Wagner and Kurina, 1997; D. Wagner, unpublished data), suggesting that the resources we provided did not attract unusually high numbers of foragers.

Extra nectars of higher quality than primary nectar did not enhance distraction. Rather, the presence of amino acids in extra nectar slightly increased, although not significantly so, the number of *Forelius* sp. 1 at primary nectaries relative to artificial plants with sugar-only extra nectar, probably because amino acids attracted more *Forelius* workers onto artificial

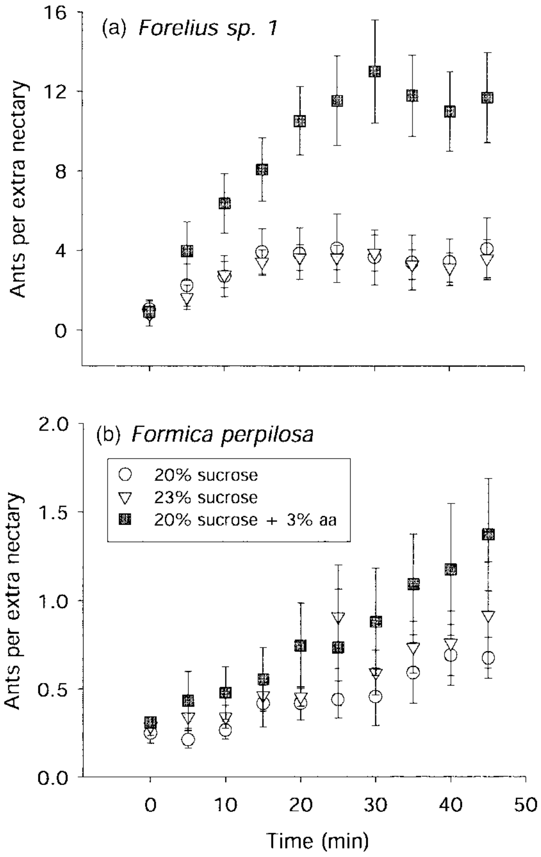

Fig. 3. Visitation by two ant species to extra nectaries bearing nectar of varying quality. The response of ant visitation to extra nectar cups supplying different nutrient qualities was species-specific. Each symbol is the mean of six ant colonies. (A) *Forelius* sp. 1, (B) *Formica perpilosa*.

plants. This suggests that, although negative effects of ants at flowers might select for the presence of extrafloral nectaries, the benefits of distraction alone are unlikely to select for high concentrations of amino acids in extrafloral nectar.

In our experiment, primary and extra nectaries were morphologically identical, whereas floral and extrafloral nectaries are morphologically distinct. We would expect distraction to favour the evolution of distinct extrafloral nectaries, rather than simply an increase in flower number, if extrafloral nectaries could be produced or maintained less expensively than flowers. Since extrafloral nectaries typically lack bright pigments, odours and elaborate support structures, they are indeed likely to cost less than flowers. However, we know of no work that has estimated the absolute or relative cost of producing extrafloral nectaries.

The two ant species differed in their preference for sugars and amino acids. In contrast to *Forelius* sp. 1, *F. perpilosa* did not visit extra nectaries containing amino acids in greater numbers than sugar-only nectaries, and did not recruit more heavily onto artificial plants

Table 3. Multivariate ANOVA for the effects of extrafloral nectar composition (20% sucrose, 23% sucrose, or 20% sucrose plus 3% amino acids) on repeated measures of ant visitation to *extra* nectaries on artificial plants: visitation by *Forelius* sp. 1 and *Formica perpilosa*

***Forelius* sp. 1**				
Between-subjects	d.f.	MS	*F*	*P*
Treatment	2	6643.7	7.9	0.005
Error	15	843.5		
Within-subjects	d.f.	Wilks' λ	*F*	*P*
Time	9,7	0.12	5.4	0.02
Treatment × time	18,14	0.10	1.6	0.2
Formica perpilosa				
Between-subjects	d.f.	MS	*F*	*P*
Treatment	2	17.1	1.3	0.3
Error	15	13.4		
Within-subjects	d.f.	Wilks' λ	*F*	*P*
Time	9,7	0.14	4.8	0.02
Treatment × time	18,14	0.18	1.1	0.4

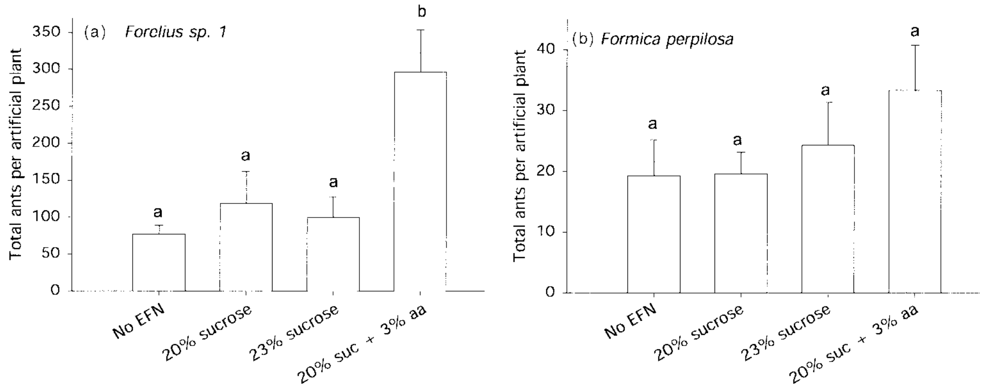

Fig. 4. Total numbers of ants on artificial plants with and without extrafloral nectar and with extrafloral nectar of varying quality. All artificial plants had floral nectar. Each symbol is the mean of six colonies; error bars are one standard error of the mean. Different lower-case letters denote significantly different means.

offering extra nectar sources, even if they contained amino acids. Ant preferences for amino acids and sugars vary over time (Sudd and Sudd, 1985; Bristow and Yanity, 1999), so generalizations based on a single test should be interpreted with caution. However, this result implies two points worthy of further investigation. First, for species with floral nectar to which ants have access, plants with extrafloral nectaries may not draw more ants onto their tissues than plants lacking extrafloral nectaries, unless perhaps extrafloral nectar provides amino acids. In cases where ant density correlates with degree of protection, selection may favour plants that produce extrafloral nectar with high concentrations of amino acids. Second, since not all ant species appear to recruit more heavily when extra nectar sources of high quality are available, the benefits of this strategy depend on the composition of the ant community. Previous work has shown that spatial variation in the benefits of extrafloral nectaries may occur because the ant species present at different sites are not equally effective at deterring herbivory (Barton, 1986; Rico-Gray and Thien, 1989). Our results indicate that variation in the quality of protection may also occur because nectar contents are not equally attractive to all ant species.

Other evidence suggests that ant distraction may have contributed to the evolution of extrafloral nectaries. First, in several species for which the timing of nectar production has been reported, extrafloral nectar is actively secreted primarily when floral nectar and/or pollen are present (Bentley, 1977b; Tilman, 1978; Schemske, 1982; Tanowitz and Koehler, 1986; but see Wunnachit *et al.*, 1992). Thus, extrafloral nectaries are most likely to capture the attention of ants when flowers are most susceptible to exploitation and damage by ants. Second, extrafloral nectaries are sometimes physically associated with flowers and inflorescences (at the base or pedicels of flowers, along the inflorescent rachis, or on floral bracts and involucres; Elias, 1983). Extrafloral nectaries near reproductive structures may divert the attention of ants foraging in the vicinity of flowers. Extrafloral nectaries that are located on reproductive structures are necessarily present and functional only around the time of reproduction. Another interpretation of these patterns is that both the secretion of extrafloral nectar at the time of reproduction and the location of nectaries near reproductive structures may have evolved because they focus protection on flowers and developing fruits and seeds (Bentley, 1977a). These hypotheses are not mutually exclusive.

Just as spines can confer benefits in addition to protection against herbivores (such as decreasing short-wave radiation incident on stems and enhancing a boundary layer; Nobel, 1988), extrafloral nectaries may serve several positive functions. And just as the relative importance of the benefits provided by spines differs among species and populations (Nobel, 1988), we expect the type of benefits provided by extrafloral nectaries, and their relative contribution to fitness, to vary among species and populations, over space and time. In some cases, ants provide protection against herbivores (Bentley, 1977a). In addition, the production of food rewards may encourage ants to nest in plant tissues or in soil near the root system, where ants provide plants with nutrients (Rickson, 1979; Rico-Gray *et al.*, 1989; Treseder *et al.*, 1995; Wagner, 1997; Sagers *et al.*, 2000). For plant species with floral nectar accessible to ants, extrafloral nectaries may also serve to reduce the number of ants that visit flowers and inflorescences.

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