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ORIGINAL PAPER

Nectar- and pollen-gathering *Cephalotes* ants provide no protection against herbivory: a new manipulative experiment to test ant protective capabilities

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Abstract The question if ant behaviour and biological limitations should be considered before generalisations about the ant's defensive capabilities in ant–plant relationships was explored through a new experimental manipulation. In the Brazilian tropical savanna, we tested the protective action of *Cephalotes pusillus* Klug on the extrafloral nectar-bearing plant *Ouratea spectabilis* Engl. (Ochnaceae). Three treatments were performed: control (free ant access), *Cephalotes*-treatment (access permitted only to *C. pusillus*), and ant free treatment (no ants). No difference was found in the levels of leaf herbivory among experimental stems. Visitation by different ant species to control stems translated into significantly greater fruit and seed production by this stem category than by ant-free and *Cephalotes*-treated stems. Thus, results showed that an investigation of system's natural history, ant's morphological traits, defensive capabilities and behaviour are needed before a protective role is inferred to each associated ant species.

Keywords Ant–plant interaction · Cerrado · Extrafloral nectar · Mutualism

Introduction

Extrafloral nectaries (EFNs) are nectar-producing glands that are usually not involved with pollination but instead attract ants and other arthropods in a wide range of plants from different habitats worldwide (Koptur 2005). Many authors have demonstrated that ant visitation to EFNs can benefit the host because the ants prey upon the herbivores and/or reduce their activity on foliage (Bentley 1977; Koptur 2005; Del-Claro 2004; Rico-Gray and Oliveira 2007). However, the data concerning the effectiveness of this ant–plant mutualism are controversial. Studies in different ecosystems have failed to detect any benefit to EFN-bearing plants (O'Dowd and Catchpole 1983; Mody and Linsenmair 2004). Lack of protection can be explained by (1) difficulties to assess seasonal variation and long-term outcomes in the ant–plant–herbivore interaction (O'Dowd and Catchpole 1983), and (2) differences in ant-foraging behaviour among habitats (Inouye and Taylor 1979), or (3) variable susceptibility of distinct herbivore groups to ant predation (Ito and Higashi 1991), and (4) differences in the deterring skills among species of visiting ants (Dejean et al. 2000).

Many ant species are listed as visitors to EFNs in the neotropics, mainly in the subfamilies Formicinae, Myrmicinae and Dolichoderinae (Davidson et al. 2003). Species in the genus *Cephalotes* (Myrmicinae, Cephalotini) are commonly reported at EFNs in the Brazilian cerrado savanna (Del-Claro et al. 1996; Korndörfer and Del-Claro 2006). However, the protective capabilities of *Cephalotes* ants against insect herbivores are questionable (Sendoya et al. 2009). These ants have small mandibles and feed primarily on plant and insect exudates such as extrafloral nectar and hemipteran honeydew, fallen fruits, faeces of birds, dead animal matter and slow-moving prey (Del-Claro and Oliveira 1996, 1999; Davidson et al. 2003). Although some species such as *Cephalotes atratus* L. can behave aggressively towards other ants (Corn 1980), in general, *Cephalotes* ants appear to be ineffective as herbivore deterrents on EFN-bearing plants (Sendoya et al. 2009). Recent studies have suggested that the

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action of ants only benefits plants when particular ant species are attracted, and positive consequences resulting from these ants are not counterbalanced by their negative effects on other beneficial arthropods (Mody and Linsenmair 2004). However, studies directed to evaluate the influence of specific ant species in trophic interactions are rare. The issue if ant behaviour and biological limitations should be considered before generalisations about ant defensive capabilities was explored here through a new experimental manipulation performed in nature. We tested the hypothesis that one specific ant, *Cephalotes pusillus* Klug, a common visitor of EFNs in cerrado savanna will have a positive effect on visited plants reducing leaf herbivore levels and increasing fruit and seed production. Thus, we tested the direct effects of a specific ant on the outcomes of an ant–plant–herbivore relationship in natural conditions.

Methods

Field work was carried out between August and October 2007 in the cerrado reserve (640 ha) of the Clube de Caça e Pesca Itororó, Uberlândia, State of Minas Gerais, Brazil (18°59′ S, 48°18′ W). The vegetation is a cerrado sensu stricto, consisting of a dense scrub of shrubs and trees with a fair amount of herbaceous plants (see Oliveira and Marquis 2002). A rainy and hot season occurs from September to April and a dry and cold season from May to August (e.g. Réu and Del-Claro 2005).

The extrafloral nectar-bearing plant *Ouratea spectabilis* Engl. (Ochnaceae), an abundant tree (2–5 m tall) in the study area, was used as model in the field study. The plant has EFNs on the stipules that attract many ant species, both day and night (Table 1 and Fig. 1). EFNs are active mainly on young leaves, which are produced all year round, but mostly during the dry/cold season. The leaf expansion phase delay 15–20 days, and the extrafloral nectar in EFNs in this period contains 16.75% of sucrose (mean ± SD=16.75±7.8% of sucrose; n=10 plants; one gland sampled from each of ten plants). The most common herbivores of *O. spectabilis* are two species of Lepidoptera (*Udranomia* sp., Hesperiidae), whose larvae attack young leaves and feed concealed in leaf shelters. Floral buds are attacked by beetles, mainly *Anthonomous ourateae*

Table 1 Ant species observed visiting extrafloral nectar glands on control stems of *Oratea spectabilis* (Ochnaceae) in a cerrado reserve in Uberlândia, Brazil (*D* diurnal species, *N* nocturnal species)

Subfamily	Genera species	Main daily activity
Formicinae	*Brachymyrmex* sp.	D
	Camponotus atriceps Fabricius, 1804	N
	Camponotus aff. blandus Fr. Smith, 1858	D
	Camponotus crassus Mayr, 1887	D
	Camponotus lespesii Forel, 1886	D
	Camponotus leydigi Forel, 1886	D
	Camponotus punctatus Forel, 1886	D
	Camponotus renggeri Emery, 1894	N
	Camponotus rufipes Fabricius, 1775	D/N
	Camponotus sericeiventris Guerin, 1838	D
	Camponotus sp.	D
Ectatomminae	*Ectatomma opaciventre* Roger 1861	D
	Ectatomma permagnum Forel	D
	Ectatomma tuberculatum (Olivier)	D
Ponerinae	*Pachycondyla foedita* (Linnaeus)	N
	Pachycondyla obscuricornis (Emery)	D
	Pachycondyla striata Fr. Smith	D
	Pachycondyla villosa (Fabricius)	D
Dolichoderinae	*Azteca* sp.	D
Pseudomyrmecinae	*Pseudomyrmex gracilis* (Fabricius) 1804	D
Myrmicinae	*Cephalotes atratus* Linnaeus, 1758	D
	Cephalotes clypeatus Fabricius, 1804	N
	Cephalotes pusillus Klug, 1824	D
	Cephalotes simillimus (Kempf)	D
	Crematogaster victima (Smith)	D
	Pheidole sp.	D
	Solenopsis sp.	D

Fig. 1 A worker of *Camponotus crassus* Mayr feeding on an extrafloral nectar of the tree *Oratea specatibilis* Engl. (Ochnaceae) in the Brazilian tropical savanna (Cerrado)

(Coleoptera: Curculionidae). Reproductive structures (stigma and stamens) are attacked by *Frankliniella* sp. (Thysanoptera: Thripidae) and petals by *Anhtonomous* sp.

In the first week of August, we tagged 11 individuals of *O. spectabilis* in the same phenological state (young leaves and inflorescence shoots), level of foliar herbivory (<1%), height (~2.5 m), and number of stems (seven). In each individual plant, we selected three similar-sized stems and randomly assigned them as (1) control, (2) *Cephalotes* treatment, or (3) ant-free treatment. Control stems received no manipulation and had free access by ants and other arthropods that climbed onto the plant. *Cephalotes* treatment stems received a band of a sticky resin (Tanglefoot®) at the base of the stem, to isolate treatment from ant visitation. Then, a glass tube (20 cm long, with 2 cm of water concealed by cotton in its bottom and covered with red cellophane paper) containing a colony of *C. pusillus* (one queen, 30 minor workers, and ten major workers) was attached to the stem with wire about 5 cm beyond the tanglefoot barrier. *C. pusillus* colonies nesting in dead trunks in the same area have similar number of individuals (one queen, 27±5 minor workers and 8±6 major workers; $N=8$). The tube was placed on the stem to protect the ant colony from direct sun or rain. Ant colonies were collected in the study site and maintained in the laboratory for 6 months before this experiment. Ant-free treatment stems also received a band of sticky resin and a glass tube in the same manner as described for the *Cephalotes* treatment stems, but without an ant colony inside.

We monitored ant colonies, stems and buds weekly in the field. For each category of experimental stem, nine young leaves (three near the basis, three in the middle and three in the apex of the stem) were tagged on the first day of the experiment and checked for herbivory levels late in October. Measurements of herbivory rates on leaves were assessed by placing them on a transparent grid (divided into millimetres). An index of herbivory from each leaf was estimated as the proportion of points in the grid falling within damage and undamaged areas of the leaf blade. Thus, a mean herbivory index for each tree was calculated (e.g. Dirzo and Domingues 1995; Körndorfer and Del-Claro 2006). In addition, the number of floral buds produced by each stem was counted in late August. Fruit and seed production by experimental stems were expressed as the proportion of fruits formed per buds produced and as the proportion of seeds per fruits produced, respectively. Comparisons among treatments (mean of nine leaves per treatment per tree to estimate herbivory, and mean of buds, fruits and seeds produced on the 11 stems of each treatment) were performed with non-parametric statistics (Friedman Anova test), using Statistica 7.0.

Results

C. pusillus uses extrafloral nectar of *O. spectabilis* without providing any significant service to the plant. On the other hand, diversity of ant visitors (27 species, Table 1) seems to improve plant fitness. Results showed no differences in floral bud production (ANOVA $\chi^2=0.7272$; $df=2$; $p=0.69$, Fig. 2) between groups. However, visitation by different ant species to control stems translated into significantly greater fruit (ANOVA $\chi^2=5.6364$; $df=2$; $p=0.05$) and seed (ANOVA $\chi^2=6.7273$; $df=2$; $p=0.03$) production by this stem category than by ant-free and *Cephalotes*-treated stems (Fig. 2).

No difference was found in the levels of leaf herbivory (ANOVA $\chi^2=2.3888$; $df=2$; $p=0.30$) among experimental stems. In fact, the level of foliar loss was reduced in all groups (<6%; Fig. 2). However, we never observed *C. pusillus* attacking or removing any herbivore from the plants. On the contrary, workers of *C. pusillus* remained mostly inside their nest tubes, gathering EFNs or feeding on pollen. Ant foragers on flowers of *Cephalotes*-treated stems removed almost all pollen available during the time between floral anthesis (around 0600 hours) and noon. On

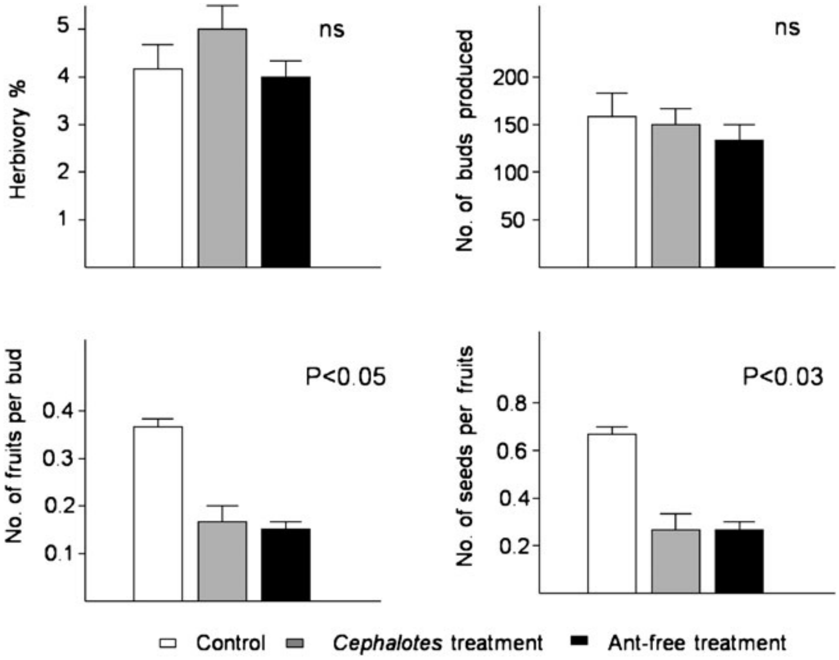

Fig. 2 Manipulative experimental tests on stems (control—stems with free ant access; *Cephalotes* treatment—stems only with *Cephalotes pusillus* ants; ant-free treatment—stems without ants) of the extrafloral nectar bearing plant *Ouratea spectabilis* (Ochnaceae; *N*=11 trees) in the cerrado vegetation. Data are means of leaf herbivory, fruits per bud or seeds produced per fruits, of 11 stems of each treatment±SE. Results showed no differences in foliar herbivory and floral bud production between groups. Control stems produced significant more fruits and seeds that the other ones. Analysis through Friedman ANOVA test

control stems, we observed *Camponotus crassus* (N=10 events), *Camponotus rufipes* (*N*=9), *Camponotus rengeri* (*N*=7), *Ectatomma permagnum* (*N*=3) and *Pseudomyrmex gracilis* (*N*=2) attacking and chasing herbivores on leaves (Coleoptera, Hemiptera, Orthoptera). The ants *P. gracilis, Crematogaster victima* and *Pheidole* sp. were commonly seen visiting flowers and preying on thrips (*Frankliniella* sp.; Thysanoptera: Thripidae). These ant species and *Pachycondyla obscuricornis* (*N*=3) also disturbed *A. ourateae* on buds. The beetle usually flew away or jumped off the leaf when approached or attacked by ants. Although also visiting *O. spectabilis* flowers, these ants did not feed on or remove pollen.

Discussion

Variation in the effects of EFN-gathering ants on plants has been reported for various ant–plant systems (Bronstein 1998; Rico-Gray and Oliveira 2007; Del-Claro and Torezan-Silingardi 2009, and references therein). Differences in capabilities among ant species (Dejean et al. 2000) to inhibit herbivore activity is pointed out as a possible cause for these variable outcomes (Sendoya et al. 2009). Our study corroborates this view by showing that each species of the ant guild needs to be examined before included in a general context as plant defender. The methodology we proposed, the use of artificial nests in natural conditions, seems to be appropriate to test this type of question. Besides providing no benefit to the plants, pollen consumption by *C. pusillus* may reduce flower fertilisation. Although commonly cited in the lists of plant visitors to EFNs and hemipteran honeydew (Del-Claro and Oliveira 2000) in cerrado, *C. pusillus* in fact is not a plant defender as recently showed by Sendoya et al. (2009), but instead seems to act as a parasite of ant–plant–herbivore systems in this savanna.

Foliar herbivory, <6%, may be considered low same to an EFN plant (see examples in Rico-Gray and Oliveira 2007). Oliveira and Del-Claro (2005) showed that in cerrado vegetation, leaf herbivory can surpass 50% in ant excluded plants. Indeed, herbivores like thrips can completely destroy apical meristems in some plant species (e.g. Del-Claro et al. 1997; Oliveira and Del-Claro 2005). We suggest that the reduced herbivory action on leaves of *O. spectabilis* is directly related to the lack of statistical difference observed in leaf herbivory between control and treatments. On the other hand, some authors have already shown differences in ant capabilities against herbivores in cerrado. For example, *C. rufipes*, *Camponotus renggeri* and *C. crassus*, which attack herbivores on *O. spectabilis*, are also effective plant defenders in other ant–plant–herbivore systems (Del-Claro and Oliveira 2000). The outcomes of these ant–plant–herbivore interactions can also vary through time, depending on biotic and abiotic variations in the cerrado (Del-Claro and Oliveira 2000). Diversity represents not only the quantity of species in space and time but also a progressive increase in different modes of life, including strategies used by predators to overcome prey defence mechanisms (Polis et al. 2000). We have also to consider that different herbivores attack different plant parts (Mothershead and Marquis 2000; Mody and Linsenmair 2004; Rosumeck et al. 2009), and different predators, as ant species, can also have a different impact in distinct plant parts. Thus, the diversity of deterring traits exhibited by ant visitors should be considered when evaluating possible ant-derived benefits to plants bearing ant attractants.

Conditionality in the outcomes of mutualistic relationships appears to be a general rule (Bronstein 1998; Rosumeck et al. 2009). The ant–*Ouratea*–herbivore system shows that generalisations about ant-derived benefits to ant-visited plants are not possible without testing species-specific effects of ant visitors. Our findings support recent studies that have begun to place mutualisms in their community context. Mutualisms more often involve guilds of interacting species (Stanton 2003), and alternate partner species are often not equally effective, making partner identity an important source of variation in benefits (Fraser et al. 2001; Mody and Linsenmair 2004; Bronstein et al. 2006; Miller 2007 and references therein). *C. pusillus* are morphologically limited to act as effective predators. They do not present a mouth adapted to grab, bit or cut animal prey efficiently. In the Costa Rican rain forest, due to their liquid diet, some *Cephalotes* species are also suggested to be more parasitic than mutualistic associates in an ant–hemipteran–plant system (Tillberg 2004). In addition, the use of pollen by *C. pusillus* as food can negatively affect pollination. When ants enter flowers in the course of their activities, they can reduce pollen viability and/or deter pollinator visits (Mothershead and Marquis 2000; Ness 2006).

Extrafloral nectar represents key resource for arboreal ant species (Davidson et al. 2003) and is more predictable than prey, with strong bottom–up effects on the ant community structure (Blüthgen et al. 2004). However, most nectar-feeding ants are at least partly carnivorous (Hölldobler and Wilson 1990). Considering that herbivores are not abundant in the cerrado savanna, but enormously diversified (Price et al. 1995), this reveals the importance of diversity in plant defences against herbivory in this system, including diversity of hunt strategies in the associated ant defenders. Stems open to ant visitation potentially received at least 27 different ant species (Table 1), with the predominance of eight species, foraging day and night for nectar and animal prey on leaves, buds and flowers. Some of the common ants had clear beneficial impact in control stems, like *P. obscuricornis* that visits flowers and preys on herbivores without removing pollen or altering floral characteristics. Another example is *C. renggeri*, a very aggressive nocturnal ant. The cerrado is a hot and dry ecosystem during daylight hours; thus, many herbivores display strong nocturnal activity. At this time, *C. pusillus* is resting but *Camponotus renggeri* is active, complementing the services of diurnal ants. Co-occurrence, diversity and specialisation are common processes in ant–plant associations, with great impact in the whole community due its vertical and horizontal effects in the trophic chans (Davidson and McKey 1993; Bluthgen et al. 2004; Miller 2007).

Our utilisation of this new type of manipulation (ant nest addition) demonstrates that each ant visitor species should be investigated in an individual way to elucidate its real potential as plant defender. A close investigation of the natural history of the system, including the ants' morphological traits and defensive capabilities, are needed before a protective role is inferred. Therefore, local ant diversity should be considered as an important parameter suggesting positive effects in a general context of ant–plant–herbivore system. However, some authors have discussed that, for plants that secrete extrafloral nectar (EFN), visitation by multiple ant species that vary in anti-herbivore abilities may result in reduced benefits relative to an exclusive association with a high-quality mutualist (Stanton 2003; Miller 2007).

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