

EXUDATE-GATHERING ANTS (HYMENOPTERA; FORMICIDAE) AT THREE DIFFERENT LIQUID FOOD REWARDS

Liliana M. BUFFA, Pedro JAUREGUIBERRY* & Miguel Angel DELFINO

Cátedra de Entomología, F.C.E.F. y N., Universidad Nacional de Córdoba, Argentina. Av. Vélez Sarsfield 299, X5000JJC, Córdoba, ARGENTINA.

*Correspondencia: Pedro Jaureguiberry, Cátedra de Entomología. F.C.E.F. y N., Av. Vélez Sarsfield 299, CP 5000, Córdoba, Argentina. pedrojaureguiberry@efn.uncor.edu

Buffa, L. M., P. Jaureguiberry, and M. A. Delfino. 2009. Exudate-gathering ants (Hymenoptera:

Formicidae) at three different liquid food rewards. *Acta Zoológica Mexicana (n. s.)*, 25(3): 515-526.

ABSTRACT. Extrafloral nectaries (EFNs) and hemipteran honeydew are liquid food rewards (FRs) that encourage ant visitation in many plant families in a wide variety of habitats. In this study we explored the diversity, distribution and interactions of exudate-gathering ants at three different liquid food rewards: nectar from EFNs on *Croton sarcopetalus* and honeydew from the aphids *Aphis spiraeicola* and *Dysaphis foeniculus* on *Eupatorium hookerianum* (Asteraceae) and *Foeniculum vulgare* (Apiaceae) respectively. For each FR we measured ant diversity and performed quantitative and qualitative comparisons among ants associated with the FRs. In addition, a linear regression was performed to test for possible associations between aphid and ant abundances in the case of honeydew FRs. Eight out of the 23 ant species found fed on both nectar from EFNs and honeydew from aphids, four of which fed at all FRs. Two ant species visited both aphid species and 13 were found exclusively at either one of the FRs. *Brachymyrmex brevicornis* was the most abundant ant species and *Pheidole* sp.2 had the greatest occurrence. Both ant species diversity and richness were higher at EFNs of *C. sarcopetalus*. Regressions showed positive significant association between ants and aphids abundances both on *E. hookerianum* and *F. vulgare*. We can conclude that the three liquid food rewards compared here showed modest similarity in their ant fauna. Furthermore, there was selectiveness of ants towards EFNs of *C. sarcopetalus*, which might be due to food source attributes rather than co-evolutionary factors.

Key words: ant-plant-hemipteran interaction, extrafloral nectaries, hemipteran honeydew, Argentina.

Buffa, L. M., P. Jaureguiberry, and M. A. Delfino. 2009. Hormigas melívoras (Hymenoptera: Formicidae) en tres fuentes de alimento líquido. *Acta Zoológica Mexicana (n. s.)*, 25(3): 515-526.

RESUMEN. Los nectarios extraflorales (NEFs) y el melado excretado por hemípteros son fuentes de alimento (FsA) que favorecen la participación de hormigas en las interacciones mutualistas que establecen con las plantas y/o hemípteros. El objetivo de este trabajo fue estudiar, en una zona serrana del centro de la provincia de Córdoba, Argentina, la diversidad, distribución e interacción de hormigas melívoras en tres FsA diferentes: néctar de NEFs de *Croton sarcopetalus* (Euphorbiaceae) y melado de *Aphis spiraeicola* y *Dysaphis foeniculus* en *Eupatorium hookerianum* (Asteraceae) y en *Foeniculum vulgare* (Apiaceae), respectivamente. En cada FA se contabilizaron e identificaron los áfidos y hormigas

Recibido: 16/01/2009; aceptado: 07/07/2009.

melívoras presentes. Se obtuvo la riqueza y abundancia de hormigas y se calcularon los índices de diversidad de Shannon-Wiener y Sorenson (cualitativo y cuantitativo) para comparar las comunidades de hormigas en las diferentes FsA. Por último se realizó una regresión lineal entre la abundancia de áfidos y la abundancia de hormigas melívoras en las dos últimas FsA mencionadas, para determinar si las variables estaban asociadas. De las 23 especies de hormigas registradas, ocho (34.8%) se alimentaron tanto en NEFs como en las colonias de áfidos, de las cuales 4 spp. (17.4%) fueron encontradas simultáneamente en las tres fuentes. Además, dos especies de hormigas visitaron ambas especies de áfidos y 13 especies visitaron exclusivamente alguna de las FsA. *Brachymyrmex brevicornis* fue la especie más abundante, mientras que *Pheidole* sp.2 registró la mayor ocurrencia. Tanto la diversidad como la riqueza de especies de hormigas fue mayor en NEFs de *C. sarcopetalus*. Se encontró una relación positiva significativa entre la abundancia de áfidos y la abundancia de hormigas melívoras tanto sobre *E. hookerianum* como sobre *F. vulgare*. Podemos concluir que las tres FA estudiadas mostraron una similitud modesta en su fauna de hormigas. Además se observó selectividad por parte de las hormigas hacia los NEFs de *C. sarcopetalus*, que podría deberse a las características de la fuente de alimento más que a factores co-evolutivos.

Palabras clave: interacción hormiga-planta-hemíptero, nectarios extraflorales, melado, Argentina.

INTRODUCTION

Two of the main food sources for exudate-gathering ants are extrafloral nectar and honeydew from sap-sucking hemipterans (e.g. aphids, coccids and membracids) (Koptur 1992; Blüthgen *et al.* 2000). Extrafloral nectaries (EFNs), for example, occur in 93 flowering plant and five fern families (Koptur 1992). Unlike floral nectaries, in many cases EFNs are not related to pollination, but rather to other mutualistic interactions, such as plant protection against herbivores and seed dispersal (Koptur 1992; Pemberton 1998; Rico-Gray & Oliveira 2007). As stressed by Schemske (1983), ant-plant mutualisms mediated by EFNs are facultative and mainly non-specialized, as indicated by the wide variety of associated ant visitors (see also Thompson 1988 and Bronstein 1998). Likewise, ant-hemipteran interactions are often mentioned as facultatively mutualistic (Buckley 1987; Bronstein *et al.* 2006; Rico-Gray & Oliveira 2007) since the hemipterans can do well without their ant associates.

The outcomes of ant-plant-hemipteran interactions are highly variable, ranging from positive effects on plant fitness by decreasing herbivore damage to the plant (see review by Koptur 1992; Freitas & Oliveira 1996; Oliveira & Del-Claro 2004; Rico-Gray & Oliveira 2007), no apparent benefit to plants from ant visitation (Tempel 1983; Whalen & MacKay 1988), or even negative effects such as damage to the host plant by honeydew-producing hemipterans or pollinator deterrence by ants (Rico-Gray *et al.* 2004; Ness 2006). Ant-plant-hemipteran interactions thus provide good models for the study of mutualisms, which might explain why published studies of these interactions have increased markedly in the last few years (Engel *et al.* 2001; Davidson *et al.* 2003; Oliveira & Del-Claro 2004; Stadler & Dixon 2005; Bronstein *et al.* 2006).

The majority of ants appear to have an opportunistic diet that combines plant/insect exudates with animal prey (Blüthgen *et al.* 2000; Davidson *et al.* 2003). Ants within the subfamilies Myrmicinae, Formicinae and Dolichoderinae are known to be the most frequent visitors of plants bearing EFNs and honeydew-producing hemipterans both in temperate and tropical habitats (Sudd 1987; Hölldobler & Wilson 1990; Rico-Gray *et al.* 1998; Davidson *et al.* 2003). For example, *Cephalotes* and *Pseudomyrmex* species reported by Davidson *et al.* (2003) are all leaf foragers that search leaf laminae continuously for dispersed foods (such as EFN, cast-off honeydew, pollen and preys). Whereas myrmicinae species *Wasmannia auropunctata*, dolichoderine *Linepithema humile* and several species of the formicine genus *Camponotus* are mostly sap-sucking hemipteran tenders that complete their diet by preying on other arthropods. In addition to the mentioned above, other genera such as dolichoderine *Azteca* and mirmicines *Crematogaster* and *Pheidole* are very common and abundant in tropical and temperate floras (Davidson 1997; Davidson *et al.* 2003).

Yet, most of the studies on the ant species that visit both EFNs-bearing plants and honeydew-producing hemipterans in neotropical habitats of South America are limited to Brazilian flora (e.g. Oliveira & Brandão 1991; Rico-Gray *et al.* 1998; Del-Claro & Oliveira 1999; Oliveira *et al.* 1999; Blüthgen *et al.* 2000; Ribas *et al.* 2003; Oliveira & Freitas, 2004; Leal *et al.* 2006). Information on these interactions on other floras is lacking. In this sense only a few studies have been made that dealt with particular ant-plant-hemipteran interactions in a similar flora as the one we studied (e.g. Delfino & Buffa 1996; Delfino & Buffa 2000; Perotto *et al.* 2002; Renault *et al.* 2005).

The aim of this study is to contribute knowledge on the diversity and distribution of ants at three liquid food rewards present in three widely distributed plant species in the study area, as well as the interactions between ants and the mentioned FRs. Furthermore, considering that the size of hemipteran aggregations may be an important factor in ant-hemipteran interactions (Breton & Addicott, 1992; Gaume, 1998; Del-Claro & Oliveira 2000), we tested whether the abundance of tending ants was associated with the abundance of the two hemipteran species studied here.

MATERIALS AND METHODS

This research was conducted in a secondary Chaco Serrano woodland near Unquillo, Córdoba Province, Argentina (belonging to the Chaqueño Serrano vegetation district of Luti *et al.* 1979). The vegetation of the sampling area is representative of a Chaco Serrano area that covers approximately 3000 km². It is characterized by an open tree stratum, with native vegetation that includes short trees, thorny shrubs, herbs and epiphytes. The climate is temperate, with cold dry winters and warm wet summers. Total annual precipitation is approximately 730 mm. Mean temperatures of the coldest (July) and warmest (January) months are 18 °C and 8 °C respectively (Capitanelli 1979).

Three native plant species that are widely distributed in this area of Chaco Serrano were selected for the study: *Croton sarcopetalus* Muell. Arg. (Euphorbiaceae), which bears EFNs on petioles, stipules and leaf margins; *Eupatorium hookerianum* Griseb. (Asteraceae), colonized by the aphid *Aphis spiraeicola* Patch; and *Foeniculum vulgare* Miller (Apiaceae), colonized by the aphid *Dysaphis foeniculus* (Theobald). During three consecutive warm seasons (from early November 1995 to early May 1998) we performed biweekly surveys, in which we randomly selected and sampled a total of 180 plants of each of the mentioned species, following two 1 x 50 m transects in each survey. Transects were located at random, while minimizing structural heterogeneity between transects. All sampled plants of each species were sexually mature and had similar age and size (0,40 to 1,00 m for *Foeniculum vulgare* and 0,80 to 1,50 m for the other plant species). In each plant we performed a direct sampling that consisted of a visual search of ant–aphid and ant-EFN associations. For each of these associations, we recorded the associated ant species and the number of tending workers, as well as the aphid species and its abundance. When necessary, insect specimens were collected for taxonomic identification in the laboratory.

Data analysis. To compare ant faunas on the different reward attractants (FRs), ant species richness, abundance and occurrence were measured and used to calculate a Shannon-Wiener diversity index (H') as well as qualitative and quantitative Sorenson indexes (Moreno 2001). In addition, a linear regression analysis was carried out between the mean abundances of ants and aphids on *E. hookerianum* and *F. vulgare* (using the InfoStat software, Profesional version 2007; Grupo Infostat, F.C.A., Universidad Nacional de Córdoba, Argentina).

Finally, to test the completeness of our study we compared the number of ant species found in the three FRs with the expected species number as calculated by the second order Jackknife estimator (Moreno 2001). Taxonomic identifications were carried out by specialists at the Centro de Investigaciones Entomológicas, Universidad Nacional de Córdoba, Argentina.

RESULTS

1.- Ant fauna associated with each liquid food reward

1.1.- EFNs of *Croton sarcopetalus*. A total of 176 ant individuals, belonging to 15 species from nine genera were recorded (Table 1). Myrmicinae was the subfamily with the greatest species richness (six species) distributed in the genera *Pheidole*, *Crematogaster*, *Solenopsis* and *Cephalotes*. Three other subfamilies were found: Formicinae (five species, genera *Camponotus* and *Brachymyrmex*); Dolichoderinae (two species, genera *Dorymyrmex* and *Linepithema*) and Pseudomyrmecinae (two species, genus *Pseudomyrmex*).

Table 1. Abundance and occurrence of exudate-gathering ant species at three different liquid food rewards in the studied Chaco Serrano woodland (Córdoba, Argentina).

		Liquid food rewards					
		Extrafloral Nectaries of <i>Croton sarcopetalus</i>		<i>Aphis spiraeola</i> on <i>Eupatorium hokerianum</i>		<i>Dysaphis foeniculus</i> on <i>Foeniculum vulgare</i>	
Ant subfamily	Ant species	Abundance (%) (N=176)	Ocurrence (%) (N=60)	Abundance (%) (N=105)	Ocurrence (%) (N=24)	Abundance (%) (N=541)	Ocurrence (%) (N=43)
Pseudomyrmecinae							
	<i>Pseudomyrmex</i> cf. <i>flavidulus</i>	4.55	8.33				
	<i>Pseudomyrmex denticollis</i>	1.14	3.33				
Myrmicinae							
	<i>Crematogaster iheringi</i>	3.98	6.67			26.25	9.30
	<i>Crematogaster brevispinosa</i>	12.50	6.67				
	<i>Pheidole</i> sp.1					5.73	11.63
	<i>Pheidole</i> sp.2	34.09	15.00	33.33	20.83	1.48	6.98
	<i>Pheidole</i> sp.3	3.98	6.67			1.85	4.65
	<i>Solenopsis invicta</i>	1.14	1.67			2.77	6.98
	<i>Solenopsis</i> sp.2			0.95	4.17		
	<i>Wasmannia auropunctata</i>					14.79	11.63
	<i>Cephalotes</i> sp.1	3.98	8.33				
Dolichoderinae							
	<i>Dorymyrmex</i> sp.1	0.57	1.67				
	<i>Linepithema grupo humile</i>	6.82	8.33	7.62	8.63	4.62	11.63
Formicinae							
	<i>Brachymyrmex patagonicus</i>	13.64	11.67	0.95	4.17	9.61	9.30
	<i>Brachymyrmex brevicornis</i>			15.24	16.67	28.10	13.95
	<i>Brachymyrmex gaucho</i>					0.37	2.33
	<i>Camponotus blandus</i>	2.27	3.33				
	<i>Camponotus mus</i>	6.82	11.67	2.86	4.17	0.37	2.33
	<i>Camponotus personatus</i>	0.57	1.67				
	<i>Camponotus punctulatus</i>	3.98	5.00	14.29	12.50		
	<i>Camponotus rufipes</i>			0.95	4.17		
	<i>Paratrechina fulva</i>			6.67	8.33	4.07	9.30
	<i>Paratrechina silvestrii</i>			17.14	16.67		

Pheidole sp.2 was the dominant species at this FR, with the highest percentage of both occurrence (15%) and abundance (34.09%). Whereas the genus *Camponotus* showed the highest species richness (four species) and *C. mus* Roger was the most abundant species within this genus.

Ant species diversity at EFNs of *C. sarcopetalus* was $H' = 2.16$ (Table 2).

1.2.- *Aphis spiraecola* on *Eupatorium hookerianum*. *A. spiraecola* was visited by 105 ant individuals, belonging to 10 species within six genera (Table 1). Three ant subfamilies were found at this FR: Formicinae (seven species, genera *Brachymyrmex*, *Camponotus* and *Paratrechina*), Myrmicinae (two species, genera *Pheidole* and *Solenopsis*), and Dolichoderinae (one species, genus *Linepithema*). The ant species *Paratrechina silvestrii*, *Camponotus rufipes* (Fabricius) and *Solenopsis* sp.2 were found exclusively at this FR.

As well as in EFNs of *C. sarcopetalus*, *Pheidole* sp.2 was the most abundant (33.33%) and frequent (20.83%) species and *Camponotus* was the genus with the greatest species richness (three species), and *C. punctulatus* Mayr was the most abundant and frequent species within this genus.

Ant species diversity in this FR was $H' = 1.85$ (Table 2). Linear regression showed a positive association between aphid abundance and abundance of honeydew-gathering ants ($p = 0,0186$; $R^2 = 0,48$; $n = 11$).

1.3.- *Dysaphis foeniculus* on *Foeniculum vulgare*. *D. foeniculus* was visited by 541 ant individuals from 12 species in eight genera (Table 1) and three subfamilies: Myrmicinae (six species, genera *Crematogaster*, *Pheidole*, *Solenopsis* and *Wasmannia*), Formicinae (five species, genera *Brachymyrmex*, *Camponotus* and *Paratrechina*), and finally Dolichoderinae (one species, genus *Linepithema*).

The ant species found exclusively on this FR were *Pheidole* sp.1, *Wasmannia auropunctata* (Roger) and *Brachymyrmex gaucho* Santschi. *Brachymyrmex brevicornis* Emery was found in most samples and showed the greatest abundance (28.10%) and occurrence (13.95%). *Crematogaster iheringi* was also very abundant in this FR (26,25%).

The diversity of ants in this FR was $H' = 1.93$ (Table 2). Linear regression showed a positive association between aphid abundance and abundance of honeydew-gathering ants ($p = 0,0275$; $R^2 = 0,37$; $n = 13$).

2.- Comparison of ant fauna between the three liquid food rewards

A total of 23 ant species (822 individuals) visiting the three FRs were recorded, representing 11 genera in four subfamilies. This represented 83% of the species richness expected for the study area ($Jack\ 2 = 27.74$ species). Formicinae was the richest subfamily (10 species), followed by Myrmicinae (nine species) and Pseudomyrmecinae and Dolichoderinae (two species each). The richest genus was *Camponotus* (Formicinae) with five species. Ant species diversity considering all three liquid food rewards was $H' = 2.44$ (Table 2). Considering all individuals, *Brachymyrmex brevicornis* was the most abundant ant species (20.44%), followed by *Crematogaster iheringi* (18.13%). Furthermore *Pheidole* sp.2 showed the greatest occurrence (13.39%), followed by *Linepithema grupo humile* and *Brachymyrmex*

patagonicus, both with 9.45%. Considering each FR separately, the EFNs of *C. sarcopetalus* showed the highest ant diversity, whereas the other two FRs showed very similar values (Table 2).

While three ant species were exclusive tenders of each aphid species, seven ant species were exclusive visitors of EFNs on *C. sarcopetalus*. On the other hand eight ant species fed on both EFNs and honeydew from aphids. Four of these species were found on the three FRs (Figure 1).

Sorenson indexes showed the ant fauna to be moderately similar, mainly for qualitative data regarding ant species composition between FRs (Table 2). When species composition but not forager abundance was taken into account (qualitative S1), the most similar communities were those associated with the two honeydew FRs (*A. spiraecola* and *D. foeniculus*).

The EFNs ant communities considering not only composition, but abundances of ant foragers (quantitative S2), were more similar to those at *A. spiraecola* on *E. hookerianum* and different to communities related to *D. foeniculus* on *F. vulgare*. There were also differences between the ant communities found on these latter two FRs.

Table 2. Shannon-Wiener diversity index (H') and Sorenson similarity indices (S1=qualitative; S2=quantitative) obtained from exudate-gathering ant fauna visiting three different liquid food rewards (FR) in the studied Chaco Serrano woodland, Córdoba, Argentina. (EFNs = Extrafloral nectaries).

Food reward	EFNs of <i>Croton sarcopetalus</i>	<i>Aphis spiraecola</i> on <i>Eupatorium hookerianum</i>	<i>Dysaphis foeniculus</i> on <i>Foeniculum vulgare</i>
<i>Aphis spiraecola</i> on <i>Eupatorium hookerianum</i>	S1 = 0,40 S2 = 0,38	-	
<i>Dysaphis foeniculus</i> on <i>Foeniculum vulgare</i>	S1 = 0,51 S2 = 0,17	S1 = 0,55 S2 = 0,13	-
H' (for each FR)	2,16	1,93	1,85
H' (total)		2,44	
S1 (total)		0,32	
S2 (total)		0,07	

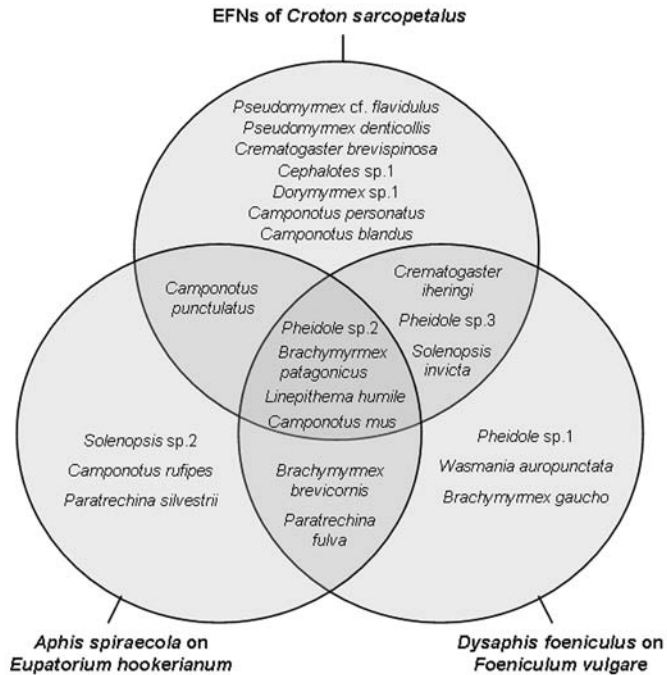


Figure 1. Exudate-gathering ant species found at three liquid food rewards (FRs) (circles) in the studied Chaco Serrano woodland, Córdoba, Argentina. Shared species appear where circles overlap. (EFNs = extrafloral nectaries)

DISCUSSION

The current study confirmed previous findings regarding dominant ant genera in the Neotropical fauna and in the world in general. Firstly we found that *Camponotus* was the richest genus as also reported by other studies in Neotropical habitats (Kusnezov 1951; Oliveira & Brandão 1991; Delfino & Buffa 1996; Davidson *et al.* 2003). In our study, species within this genus were found at the three FRs, especially at EFNs of *C. sarcopetalus*. This agrees with Davidson *et al.* (2003), who reported 21 species of *Camponotus* in lowland Peruvian rainforest canopies, most of which were found to be opportunistic exudate foragers, some others trophobiont tenders and a few species preyed on other arthropods. Furthermore *Pheidole* was the most abundant genus both at EFNs of *C. sarcopetalus* and colonies of *A. spiraeocola* on *E. hookerianum*, whereas *Crematogaster* was the most abundant genus tending *D. foeniculus* on *F.*

vulgare and it was present at the three studied FR, although its abundance was not as large as that of other genera. This genus is reported by Davidson *et al.* (2003) as mostly trophobiont, although some species may be leaf foragers and predators as well. The three ant genera mentioned above are recognized by Wilson (1976) as the most prevalent ant genera in the world, each one occurring with high local abundance and large number of species in most zoogeographical regions.

Ant species richness found on *D. foeniculus*-*F. vulgare* (12 species in eight genera) was very similar to that reported by Delfino & Buffa (2000) for the same ant-plant-aphid association (13 species in eight genera). Moreover, Delfino & Buffa (1996) reported seven ant genera associated with *A. spiraeicola* on different host plants (three on *E. hookerianum*), whereas in this study six ant genera associated with this aphid on the mentioned host plant were recorded.

Qualitative Sorensen index suggest modest similarity in the association of ant species with the different FRs. Nonetheless, when the three FRs are considered simultaneously, selectiveness becomes more evident. Considering that the number of ant species found in our study is close to the expected number, we reasoned that ant-food source associations found here support the existence of some selectiveness between the studied FRs, since EFNs in our study showed a considerable greater ant species richness and diversity. This data is, to some extent, in agreement with the results reported by Rico-Gray (1993), who mentioned that associations between ants and plants with EFNs were not highly specific and were not shaped by close co-evolutionary interactions, but rather were opportunistic and rarely species-specific. Our findings agree with the fact that ant-plant associations are highly dependent on food source and resource attributes (e.g. Blüthgen 2000; Blüthgen & Fiedler 2004; Rudgers & Gardener 2004). In this sense, interference between ant species at the different FRs (i.e. EFNs and hemipteran honeydew) is known to be different. Ant-hemipteran honeydew interactions show less ant diversity and more dominance by aggressive ant species; whereas ant assemblages at EFNs are more diverse and homogeneously distributed, with less dominance and greater coexistence of ant species (Blüthgen & Fiedler 2004; Blüthgen & Stork 2007). Furthermore, Horvitz & Schemske (1984) highlight the importance of spatial variation in the composition of ant communities at the study site, which might also be affecting the incidence of different ant species at each FR.

On the other hand, the differences found with quantitative Sorensen index were mainly due to the great ant abundance associated to *D. foeniculus* on *F. vulgare*. This highlights the importance of this food source for ants where *F. vulgare* grows.

The positive association we found between aphid and ant abundance is consistent with previous reports of honeydew-producing hemipteran acting as ant facilitators (Floate & Whitham 1994; Grover *et al.* 2008). Furthermore, Delfino & Buffa (2000) reported a positive association between ants and their tended aphids *D. foeniculus*

and *Aphis coreopsidis* on their host plants *Foeniculum vulgare* and *Bidens pilosa*, respectively. The ability of either aphids or ants to attract each other will ultimately affect (either interfering or enhancing) the biological control in the plant in which the interaction is occurring (Del-Claro & Oliveira 1996). There is evidence that this ability may depend on the quality and quantity of the sugary secretions of FRs (Engel *et al.* 2001; Katayama & Suzuki 2003)

We can conclude that the three liquid food rewards compared here showed modest similarity in their ant fauna. Furthermore, there was selectiveness of ants towards EFNs of *C. sarcopetalus*, which showed the greatest ant species richness and diversity. As discussed above, our results suggest that these differences in ant richness and diversity might be mediated by ecological rather than evolutionary factors, related to food source attributes. More extensive studies are necessary to determine to what extent are these attributes driving ant distribution at the FRs studied here and to other FRs in the Chaco Serrano woodlands.

ACKNOWLEDGEMENTS. We are very grateful to Fabien Quétier for his helpful comments and suggestions on an early version of the manuscript. We thank two anonymous reviewers for their helpful comments and constructive criticism on the manuscript.

LITERATURE CITED

- Blüthgen, N., M. Verhaagh, W. Goitía, K. Jaffé, W. Morawetz, & W. Barthlott. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia*, 125:229-240.
- Blüthgen, N., & K. Fiedler. 2004. Competition for composition: lessons from nectar-feeding ant communities. *Ecology*, 85(6):1479-1485.
- Blüthgen, N. & N.E. Stork. 2007. Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. *Austral Ecology*, 32:93-104.
- Breton, L.M., & J.F. Addicott. 1992. Density-Dependent Mutualism in an Aphid-Ant Interaction. *Ecology*, 73(6):2175-2180.
- Bronstein, J.L. 1998. The Contribution of Ant-Plant Protection Studies to Our Understanding of Mutualism. *Biotropica*, 30(2):150-161.
- Bronstein, J.L., R. Alarcón & M. Geber. 2006. The evolution of plant-insect mutualisms. *New Phytologist*, 172:412-428.
- Buckley, R.C. 1987. Interactions involving plants, homoptera, and ants. *Annual Review of Ecology and Systematics*, 18:111-135.
- Capitanelli, R.G. 1979. Clima. Pp. 45-138. In: Vázquez, J. B.; Miatello, R. A. & M. E. Roqué (eds.). *Geografía Física de la Provincia de Córdoba*. Boldt., Bs. As., Argentina.
- Davidson, D.W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society*, 61:153-181.
- Davidson, D. W., S. C. Cook, R. R. Snelling & T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, 300:969-972.
- Del-Claro, K., V. Berto & W. Reu. 1996. Effect of herbivore deterrence by ants on the fruit set of an extrafloral nectary plant, *Qualea multiflora* (Vochysiaceae). *Journal of Tropical Ecology*, 12:887-892.

- Del-Claro, K. & P.S. Oliveira.** 1996. Honeydew flicking by treehoppers provides cues to potential tending ants. *Animal Behaviour*, 51:1071-1075
- Del-Claro, K. & P.S. Oliveira.** 1999. Ant-Homoptera Interactions in a Neotropical Savanna: The Honeydew Producing Treehopper, *Guayaquila xiphias* (Membracidae), and its associated ant fauna on *Didymopanax vinosum* (Araliaceae). *Biotropica*, 31(1):135-144.
- Del-Claro, K. & P.S. Oliveira.** 2000. Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity. *Oecologia*, 124:156-165.
- Delfino, M.A. & L.M. Buffa.** 1996. Asociaciones hormigas-áfidos-plantas en La Argentina. *Revista peruana de Entomología*, 39:81-84.
- Delfino, M.A. & L.M. Buffa.** 2000. Algunas asociaciones planta-áfido-hormiga en Córdoba (Argentina). *Zoologica baetica*, 11:3-15.
- Engel, V., M.K. Fischer, F.L. Wäckers & W. Völkl.** 2001. Interactions between extrafloral nectarines, aphids and ants: are there competition effects between plant and homopteran sugar sources?. *Oecologia*, 129:577-584.
- Floate, K.D. & T.G. Whitham.** 1994. Aphid-ant interactions reduces chrysomelid herbivory in a cottonwood hybrid zone. *Oecologia*, 97: 215-221.
- Freitas, A.V.L. & P.S. Oliveira.** 1996. Ants as Selective Agents on Herbivore Biology: Effects on the Behaviour of a Non-Myrmecophilous Butterfly. *Journal of Animal Ecology*, 65(2):205-210.
- Gaume, L., D. McKey & S. Terrin.** 1998. Ant-plant-homopteran mutualism: how the third partner affects the interaction between a plan-specialist ant and its myrmecophyte host. *Proceedings of the Royal Society of London B*, 265:569-575.
- Grover, C.D., K.C. Dayton, S.B. Menke & D.A. Holway.** 2008. Effects of aphids on foliar foraging by Argentine ants and the resulting effects on other arthropods. *Ecological Entomology*, 33:101-106.
- Hölldobler, B. & E.O. Wilson.** 1990. *The Ants*. Harvard University Press, Cambridge.
- Horvitz, C.C. & D.W. Schemske.** 1984. Effects of Ants and Ant-tended Herbivore on Seed Production Of a Neotropical Herb. *Ecology*, 65(5):1369-1378.
- Infostat.** 2007. InfoStat/Profesional version 2007p. Grupo Infostat. Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, Argentina.
- Katayama, N. & N. Suzuki.** 2003. Changes in the use of extrafloral nectaries of *Vicia faba* (Leguminosae) and honeydew of aphids by ants with increasing aphid density. *Annals of the Entomological Society of America*, 96:579-584.
- Koptur, S.** 1992. Extrafloral nectary-mediated interactions between insects and plants. Pp. 81-129 In: E. Bernays (ed). *Insect-plant interactions*. CRC Press, Boca Raton, Florida.
- Kusnezov, N.** 1951. El género *Camponotus* en la Argentina. *Acta Zoologica lilloana* 12:183-251.
- Luti, R., M. Solís, F. Galera, N. Ferreira, M. Berzal, M. Nores, M. Herrera & Barrera, J.** (1979) Vegetación. Pp 297-368. In: J.B. Vázquez; R.A. Miatello & M. E. Roqué (eds.). *Geografía Física de la Provincia de Córdoba*. Boldt., Buenos Aires.
- Moreno, C.E.** (2001) *Métodos para medir la biodiversidad*. M&T-Manuales y Tesis SEA, vol. 1. Zaragoza.
- Ness, J.H.** 2006. A mutualism's indirect cost: the most aggressive plant bodyguards also deter pollinators. *Oikos*, 113:506-514.
- Oliveira, P.S. & C.R.F. Brandão.** 1991. The ant community associated with extrafloral nectaries in the brazilian cerrados. Pp. 182-212. In: C.R. Huxley & D.F. Cutler (eds). *Ant-plant interactions*. Oxford University Press, Oxford.
- Oliveira, P.S., V. Rico-Gray, C. Diaz-Castelazo & C. Castillo-Guevara.** 1999. Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: herbivore dete-

- rence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Functional Ecology*, 13:623-631.
- Oliveira, P.S. & K. Del-Claro.** 2004. Multitrophic interactions in a neotropical savanna: ant-hemipteran systems, associated insect herbivores and a host plant. In: D.F.R.P. Burslem; M.A. Pinar & S.E. Hartley (eds.). *Biotic interactions in the tropics*. Cambridge University Press, Cambridge.
- Oliveira, P.S. & A.V.L. Freitas.** 2004. Ant-plant-herbivore interactions in the neotropical cerrado savanna. *Naturwissenschaften*, 91:557-570.
- Pemberton, R.W.** 1998. The occurrence and abundance of plants with extrafloral nectaries, the basis for antiherbivore defensive mutualisms, along a latitudinal gradient in east Asia. *Journal of Biogeography*, 25:661-668.
- Perotto, M.C., L.M. Buffa & M.A. Delfino.** 2002. Efectos de la atención de *Camponotus rufipes* (Fabricius) (Hymenoptera, Formicidae) sobre agregaciones de *Enchenopa sericea* Walk. (Hemiptera, Membracidae). *Ecología Austral*, 12:91-97.
- Renault, C.K., L.M. Buffa & M.A. Delfino.** 2005. An aphid-ant interaction: effects on different trophic levels. *Ecological Research*, 20:71-74.
- Ribas, C.R., J.H. Schoederer, M. Pic & S. Soares.** 2003. Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species. *Austral Ecology*, 28:305-314.
- Rico-Gray, V.** 1993. Use of plant derived food resources by ants in the tropical lowland of coastal Veracruz, México. *Biotropica*, 25:301-315.
- Rico-Gray, V., M. Palacios-Ríos, C. Díaz-Castelazo, V. Parra-Tabla & J.A. Navarro.** 1998. Geographical and seasonal variation in the richness of ant-plant interactions in México. *Biotropica*, 30(2):190-200.
- Rico-Gray, V., P.S. Oliveira, V. Parra-Tabla, M. Cuautle & C. Díaz-Castelazo.** 2004. Ant-Plant Interactions: Their Seasonal Variation and Effects on Plant Fitness. Pp 221-239. In: Martínez, M.L.; Psuty, N.P. (eds.). *Coastal dunes: ecology and conservation. Ecological Studies: analysis and synthesis 171*. Springer-Verlag, Berlín.
- Rico-Gray, V. & P.S. Oliveira.** 2007. *The Ecology and Evolution of Ant-Plant Interactions*. University of Chicago Press, Chicago.
- Rudgers, J.A. & M.C. Gardener.** 2004. Extrafloral nectar as a resource mediating multispecies interactions. *Ecology*, 85(6):1495-1502.
- Schemske, D.W.** 1983. Limits to specialization and coevolution in plant-animal mutualisms. Pp 67-109. In: M.H. Nitecki (ed.). *Coevolution*. The University of Chicago Press, Chicago.
- Stadler, B. & A.F.G. Dixon.** 2005. Ecology and Evolution of Aphid-Ant Interactions. *Annual Review of Ecology Evolution and Systematics*, 36:345-372.
- Sudd, J.H.** 1987. Ant-Aphid Mutualism. Pp 355-365. In: A.K. Minks & P. Harrewijn (eds.). *Aphids, their biology, natural enemies and control*. Volume A. Elsevier, Amsterdam.
- Tempel, A.S.** 1983. Bracken Fern (*Pteridium aquilinum*) and Nectra-Feeding Ants: A Nonmutualistic Interaction. *Ecology*, 64(6):1411-1422.
- Thompson, J.N.** 1988. Coevolution and alternative hypotheses on insect/plant interactions. *Ecology*, 69(4):893-895.
- Whalen, M.A. & D.A. Mackay.** 1988. Patterns of ant and herbivore activity on five understory euphorbiaceous saplings in submontane Papua New Guinea. *Biotropica*, 20(4):294-300.
- Wilson, E.O.** 1976. Which are the most prevalent ant genera?. *Studia Entomologica*, 19:187-200.