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RELATIONSHIPS BETWEEN ANTS AND APHIDS IN THE PROVINCE OF LEON (SPAIN) (HYM : FORMICIDAE; HOM : APHIDIDAE)

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INTERACTIONS
FORMICIDAE
APHIDIDAE
ESPAGNE

RÉSUMÉ - Un lot de 1.091 échantillons d'Aphidiens de la province du León (Espagne), a permis d'étudier les relations entre Fourmis et Aphidiens. L'analyse de la mirmécophilie des différents genres d'Aphidiens, nous amène à établir deux groupes fondamentaux : l'un mirmécophile, et l'autre, mirmécophobe. En outre, l'affinité des Fourmis pour différents Aphidiens est testée en vue de mettre en évidence les causes possibles pour l'établissement d'une association déterminée entre une espèce de fourmi et une espèce d'Aphidien.

RELATIONSHIPS
FORMICIDAE
APHIDIDAE
SPAIN

SUMMARY - A study of 1.091 samples of aphids collected in the province of León (Spain) analyses the relationships between ants and aphids. Two basic groups of aphids were established : myrmecophiles and myrmecophobes. In addition, the affinity of ants for aphids was examined in an attempt to explain the causes for a particular species of ant to associate with a particular species of aphid.

INTRODUCTION

The relationships of ants with *Homoptera* in general, and with aphids in particular, have been treated in many works since the 1950s (see revisions in Way, 1963 and in Hölldobler & Wilson, 1990), mainly exploring the behaviour and the benefits involved in these relationships. Ants benefit from harvesting aphid honeydew, which adds a form of carbohydrate to the ant diet, while the aphids benefit from ant behaviour such as : cleaning away excretions and thereby reducing pathogens; defense against predators; transport to propitious food environments; and sheltering adults and eggs during the winter. These relationships, possibly of recent origin, have given rise to morphological and behavioural adaptations in aphids, while almost exclusively ethological changes in ants (Wheeler, 1910).

Ants that attend aphids belong largely to the most evolved subfamilies Myrmicinae, Formicinae and Dolichoderinae. Only one species is known from the less evolved subfamily Ponerinae (Evans & Leston, 1971).

While not all aphids accept the care of ants, myrmecophile species of aphids occur in many subfamilies such as Anoeciinae, Thelaxinae, Chai-

tophorinae, Lachninae, Pterocommatinae, and Aphidinae without any apparent evolutionary link. Many species of aphids, including those less evolved, display morphological and/or ethological adaptations which optimize their relationships with ants (Wheeler, 1910). Among the most apparent adaptations are the loss in agility of individuals, the formation of dense colonies, the disappearance or reduced development of cornicles and the reduction of waxy secretions.

Data available on these relationships at the species level are quite scattered. Way (1963) cites various examples of specificity or selectivity among certain species of ants and aphids, although he does not represent this behaviour as being a generality. Evans & Leston (1971) describe a similar situation between *Odontomachus haematodus* (L., 1758) and *Toxoptera aurantii* (Boyer de Fonscolombe, 1841). Other authors such as Stry (1966, 1969), Ebbers & Barrows (1980), Sudd (1983), and Dorow & Maschwitz (1990) have suggested that certain species of ants select certain species of aphids, while, according to Addicott (1978), some aphids may compete to attract ants.

In Spain the few works published on this subject have been limited primarily to those species that could have an impact on agriculture (Garcia Mercet, 1923; Ruiz Castro, 1941). The first work

to investigate this type of relationship from a purely biological standpoint was by Alsina *et al.*, (1988), who studied the diet of *Camponotus cruentatus* (Latreille, 1802) and found that this species depends to a large extent (82 % of its food) upon the deposits of two species of aphids: *Cinara maritimae* (Dufour, 1833) and *Aphis fabae* Scopoli, 1763. Nunez Perez & Nieto Nafria (1991) have studied aphids and their accompanying ant species on cultivated plants in the province of León. The present study, in sharing a larger framework (Tizado, 1990), represents the first work on these types of relationships to be carried out on Iberian fauna which attempts to understand the relationships between the different species of ants and aphids, as well as the role played by the host plants in those relationships.

METHODS

In two representative zones of the province of León, the greatest possible number of aphid species and accompanying ants were collected. A total of 1,091 samples were collected (specimens collected in the same locality, date and plant, it could present several species of aphids and/or species of ants), of which 325 contained ants. The ants collected were all found in aphid colonies, although it is not absolutely certain that all the ants were attending aphids; some may have been gathering honeydew from the plant surface without offering any kind of attention to the aphids.

The field work was carried out between 1987 and 1989 in two areas with marked differences: one, lying in the Euro-siberian phytogeographical zone, is a mountainous area between 950 m. and 2,189 m in altitud, with highly varied vegetation rich in beech (*Fagus sylvatica*) and oak (*Quercus pyrenaica*, and relictic *Q. rotundifolia*). By contrast, the other area, lying in the Mediterranean phytogeographical zone, is a mesa between 750 m and 980 m in altitud, where the vegetation is dominated by dry cultivated grains with patches of oaks (*Quercus rotundifolia*, and *Q. faginea*) and, along the banks of the Esla River, various species of willow (*Salix* spp.), and poplar (*Populus* spp.).

The material used is now kept in the collection of the Department of Animal Biology (University of León), and partially, with respect to the ants, in the Department of Animal Biology at the University of Granada.

The data were analysed by the homogeneity test using the G statistical test, given its characteristics of complete additivity (Sokal & Rohlf, 1980). For the different tables the following questions were answered: 1) Are the proportions of the genera homogeneous and similar to the general proportions

of the sample? For these the G of heterogeneity is calculated (G_H); and 2) Which genera differ from the expected proportions of the sample? For this either the individual G were calculated or the exact binomial probabilities in the case of Table I. In all cases a confidence level of 0.05 was used, if not indicated otherwise.

To test the hypothesis concerning the specificity of the relationships at different levels, such as the affinity between aphidophile ants and the plants where they occurred, the plants were divided into five categories: trees, shrubs, thistles, herbaceous plants, and roots.

RESULTS

Table I lists the most representative aphids found with or without ants, and Table II indicates the relationships of ants with the aphid genera tended as well as types of plants visited.

Table I. – Relationships between aphid genera collected for this work, indicating the number of samples with and without ants.

	with	without	total
<i>Acyrtosiphon</i>	0	38	38
<i>Aphis</i> (<i>Aphis</i>)	171	166	337
<i>Aphis</i> (<i>Protaphis</i>)	17	11	28
<i>Aulacorthum</i>	1	14	15
<i>Brachycaudus</i>	55	55	110
<i>Brevicoryne</i>	1	34	35
<i>Cavariella</i>	2	21	23
<i>Chaitophorus</i>	15	18	33
<i>Cryptomyzus</i>	0	7	7
<i>Dysaphis</i>	13	18	31
<i>Hyadaphis</i>	1	8	9
<i>Hyperomyzus</i>	1	30	31
<i>Lachnus</i>	11	0	11
<i>Macrosiphoniella</i>	3	19	22
<i>Macrosiphum</i>	9	58	67
<i>Metopeuron</i>	4	2	6
<i>Myzus</i>	6	58	67
<i>Nasonovia</i>	1	18	19
<i>Ovatus</i>	0	10	10
<i>Pterocomma</i>	5	0	5
<i>Rhopalosiphum</i>	0	14	14
<i>Semiaphis</i>	6	1	7
<i>Sitobion</i>	2	29	31
<i>Therioaphis</i>	0	9	9
<i>Uroleucon</i>	3	70	73
Total of colonies	327	708	1035

Table II. - Number of aphid colonies from each genera which were considered to be myrmecophile and which were attended by ants, and number of aphid colonies collected from different vegetal types. The G value has been obtained under the hypothesis : proportion of aphid colonies attended by each ant species is 180:18:55:17:12:4:5:6 and proportion of aphid colonies attended in each vegetal types by each ant species is 173:78:18:59:17. (AA: *Aphis* (A); AP: *Aphis* (*Protaphis*); Br: *Brachycaudus*; Ch: *Chaitophorus*; La: *Lachnus*; Me: *Metopeuron*; Pt: *Pterocomma* and Se: *Semiaphis*. He: herbaceous plant; Th: thistle; Sh: shrub; Tr: tree; and Ro: roots). (* = $p < 0.05$; ** = $p < 0.01$).

	AA	AP	Br	Ch	La	Me	Pt	Se	Total	G	He	Th	Sh	Tr	Ro	Total	G
<i>Camponotus aethiops</i>	2	.	.	2	3	.	.	.	7	17.59**	.	2	.	6	.	8	18.14**
<i>Camponotus cruentatus</i>	2	.	.	.	2	12.84**	.	.	.	2	.	2	7.06**
<i>Camponotus piceus</i>	1	.	2	.	1	.	.	.	4	5.85*	.	3	.	1	.	4	7.95**
<i>Camponotus pilicornis</i>	2	.	.	.	2	12.84**	.	.	.	1	.	1	3.53**
<i>Formica cunicularia</i>	3	.	2	5	3.02**	.	4	1	.	.	5	12.80**
<i>Formica decipiens</i>	14	.	2	3	.	1	2	2	24	14.75**	16	.	3	7	.	26	17.67**
<i>Formica dusmeti</i>	1	.	1	.	1	.	.	.	3	4.20*	.	2	.	2	.	4	7.47**
<i>Formica fusca</i>	9	.	1	10	5.89**	11	.	.	.	1	12	14.32**
<i>Formica gerardi</i>	6	1	2	1	10	2.31	4	7	.	1	.	12	8.57**
<i>Formica lemani</i>	15	.	7	3	.	.	.	1	26	9.26**	19	4	3	5	.	31	6.26*
<i>Formica polyctena</i>	3	.	2	5	3.02	4	2	.	2	.	8	1.90
<i>Formica pratensis</i>	5	.	.	.	1	1	1	1	9	12.56**	5	1	2	3	2	13	5.87*
<i>Formica rufibarbis</i>	5	.	2	7	3.38*	5	3	.	1	.	9	2.49
<i>Formica subrufa</i>	3	1	4	6.31*	3	2	.	1	.	6	1.48
<i>Lasius alienus</i>	3	.	2	.	.	.	1	.	6	5.78*	2	5	.	1	.	8	6.76**
<i>Lasius fuliginosus</i>	2	2	2.00	.	1	.	3	.	4	9.07**
<i>Lasius niger</i>	51	.	13	1	65	25.71**	39	17	8	6	.	70	14.90**
<i>Plagiolepis pygmaea</i>	3	.	2	5	3.02	5	2	.	.	.	7	4.47*
<i>Tapinoma nigerrimum</i>	34	12	9	7	2	.	1	1	66	16.50**	27	14	.	17	12	70	24.24**
<i>Crematogaster auberti</i>	5	1	6	5.21*	4	.	1	.	1	6	7.04**
<i>Leptothorax sp.</i>	2	2	2.00	3	3	4.14*
<i>Myrmica ruginodis</i>	5	.	2	.	.	2	.	.	9	11.07**	8	3	.	.	.	11	7.07**
<i>Myrmica scabrinodis</i>	1	1	6.02*
<i>Pheidole pallidula</i>	2	1	1	4	2.67	3	1	.	.	.	4	2.62
<i>Tetramorium caespitum</i>	2	2	4	8	10.07**	11	2	.	.	.	13	9.97**
<i>Tetramorium hispanicum</i>	4	1	1	6	2.58	4	3	.	.	.	7	4.88*
Total of colonies	180	18	55	17	12	4	5	6	297		173	78	18	59	17	345	

Because the ants of this province have not been thoroughly studied, we do not know whether the lack of data about certain species of ants reflects their scarcity in the sample areas or their lack of aphidophilia. In all, we collected 26 species of ants belonging to 10 genera of the three subfamilies, Myrmicinae, Formicinae and Dolichoderinae. These were found in colonies of 87 species of aphids belonging to 25 genera of the subfamilies Anoeciinae, Aphidinae, Chaitophorinae, Lachninae, Pterocommatinae and Thelaxinae.

Aphid-Ant relationships

Aphid colonies were divided into those with and those without ants (Table I) to test the hypothesis that all genera of aphids homogeneously accept the attention of ants (theoretical proportion of samples with ants $p = 325/1091 = 0.298$). A general analysis of the table with 24 freedom degrees leads us to reject the hypothesis ($G_H = 330.03$; $p < 0.001$), and a individual analysis of each genus by means of binomial probabilities reveals three types of aphid genera in relation to ants: myrmecophobic, myrmecophile, and uncertain genera.

Myrmecophobic genera

Those which are less frequented by ants than expected for the proportions in the study (proportion of samples with ants $p_1 = 0.298$), and which generally refuse the attention of ants. Myrmecophobia is not meant to imply that these genera never accept the attention of ants under any circumstances, or that ants collect the honeydew without ever offering any kind of attention to the aphids. In this category are included: *Acyrtosiphon*, *Aulacorthum*, *Brevicoryne*, *Cavariella*, *Cryptomizus* ($p = 0.084$), *Hyperomyzus*, *Macrosiphoniella* ($p = 0.071$), *Macrosiphum*, *Myzus*, *Nasonovia*, *Ovatus*, *Rhopalosiphum*, *Sitobion*, *Therioaphis* and *Uroleucon*.

All these genera except *Therioaphis* belong to the subfamily Aphidinae; they are highly evolved and are found on herbaceous plants, at least as secondary hosts. *Macrosiphoniella* is a genus with myrmecophobic tendencies, although 2 of the 11 species collected, *M. absinthii* and *tanacetaria*, apparently are myrmecophile.

In the majority of myrmecophobic species, as opposed to myrmecophile ones, we found characteristics indicated by Wheeler (1910), such as not forming dense colonies, being agile and having large cornicles or producing wax. Some myrme-

cophobic genera are typical of grasses, where it is rare to find ants attending non-radicolous aphids.

Myrmecophile genera

Those which are more frequented by ants than expected for the proportion in the study (proportion of samples with ants $p_2 > p = 0.298$), and which show a preference for the company of ants. In this category are included: *Aphis* (subgenera *Aphis* and *Protaphis*), *Brachydacaudus*, *Chaitophorus*, *Lachnus*, *Metopeuron* ($p = 0.069$), *Pterocomma* and *Semiaphis*.

Of all of these, the most striking is *Aphis* (*A.*) spp, in which 34 of the 49 species collected were attended by all species of ants (except *Camponotus cruentatus*, *C. pilicornis* Roger, 1859 and *Myrmica scabrinodis* Nylander, 1846, possibly due to the low number of samples). In *Brachydacaudus* spp., 7 of the 8 species collected were associated with ants. These two genera, belonging to the subfamily Aphidinae, display the most adaptations and modifications that favor association with ants. Apart from those already mentioned, one adaptation is the exploitation of a great number of different plants of varying size. The genera *Chaitophorus*, *Lachnus* and *Pterocomma*, basically arboreal and almost strictly monophagous, belong to subfamilies older than Aphidinae and have been found exclusively with Dolichoderinae and Formicinae.

Uncertain genera

Those which show no significant differences in the proportion between the colonies being attended and not being attended by ants and the proportion expected in the study. Two genera occupy this category: *Dysaphis* and *Hyadaphis*.

The genus *Hyadaphis* was found attended by ants on only one occasion and on the same plant with *Aphis* (*A.*) *craccivora* Koch, 1854 and *Semiaphis daucis* (F., 1775), two myrmecophile genera which were probably the true objects of the ants' attention. If we eliminate this datum from Table I a probability of 0.054 is obtained, which could be considered an indication of myrmecophobia.

The genus *Dysaphis* contains dioecious species, with alternation of host plants within their annual cycle. We are therefore uncertain whether species belonging to this genus are myrmecophobic in one host but not in another, or whether some species are myrmecophile and others are myrmecophobic. Neither possibility allows us to describe any of the species as myrmecophile in either of the two host plants. Consequently, for this genus we cannot determine the myrmecophilia or even under what conditions it occurs, possibly because of its being often radicolous in the secondary host

plant. For these reasons, a special study should be made of this genus in the future.

Ant-Aphid relationships

The number of aphid species attended by one ant species can vary greatly, although we have obtained a mean value of 8.38 aphid species per ant species. Three ant species attended a very wide variety of aphids: *Lasius niger* (L., 1758) attending 33 species of aphids; *Tapinoma nigerrimum* (Nylander, 1886), attending 29 species of aphids; and *Formica lemani* Bondroit, 1917 attending 20 species of aphids.

The subfamily Formicinae contains the greatest number of species that attend aphids (18 species belonging to 5 genera), and is the most aphidophile, being present in 199 samples. The subfamily Myrmicinae, though interacting with 7 aphid species belonging to 5 genera, is the least aphidophile, being present in only 40 samples. The average number of species of aphids frequented by a species of ant is greater in Formicinae than in Myrmicinae (8.2 as opposed to 6.4). Some genera of ants, in exceeding this mean value, can be considered to be more aphidophile, such as *Tapinoma*, *Lasius*, *Formica* and *Tetramorium*, with each have a mean value greater than 8 species of aphid per species of ant.

We observed no constant relationship between any ant species and any aphid species. Although we found the ant *Camponotus cruentatus* exclusively with the aphid *Lachnus roboris* (L. 1758), we cannot consider this a specific relationship because (aside from the low number of specimens collected) it has been cited by Alsina *et al.*, (1988) with two other species of aphids: *Cinara maritima* and *Aphis fabae*.

Even for the same location and date, the same ant species can be found with different aphid species. *Lasius niger* was found with seven different species of aphids; *Formica subrufa* Roger, 1859 was collected with five of the six aphid species cited, in the same location and on the same date, including three of these on the same species of plant; and finally *Formica dusmeti* Emery, 1909 was found with four different aphid species in two different locations, but perhaps important to selectivity on only one species of plant in each location.

Having found a low species-to-species affinity, we investigated the affinity of ant species for myrmecophile aphid genera. For each ant species Table II shows the number of aphid colonies collected in each myrmecophile genus. To test the hypothesis that different species of ants homogeneously attend all genera of aphids, we obtained a value of $G_H = 2069.9$ with 168 degrees of freedom ($p < 0.001$). This lead us to conclude

that a particular ant species tends to frequent particular aphid genera.

The analysis of individual G values show the existence of certain preferences such as :

Camponotus aethiops (Latreille, 1798) ($G = 17.59$; $p < 0.01$) appears to be particularly associated with arboreal aphids in the genus *Chaitophorus* on *Populus* and *Lachnus* on *Quercus*. This seems characteristic of all the other species of this genus which frequent *Lachnus* on *Quercus*.

Formica decipiens Bondroit, 1918 ($G = 14.75$; $p < 0.01$) seems to prefer *Chaitophorus* and *Pterocomma* in trees, attending the species of *Brachycaudus* less than expected.

Lasius niger ($G = 25.71$; $p < 0.01$) has shown a preference for *Aphis* (A.) spp., mainly in herbaceous plants and thistles; it has not been found attending radicicolous aphids and has seldom been found attending arboreal aphids.

Tapinoma nigerrimum ($G = 16.5$; $p < 0.01$) more often than expected attends the arboreal aphids of the genus *Chaitophorus* on *Salix* and *Populus* and radicicolous aphids from the subgenus *Protaphis*.

Consequently we can discard the idea of constant species-to-species relationships but not the affinity of certain species of ants for certain genera of aphids. This affinity may, however, derive not from the characteristics of the aphids but instead from the type of habitat. In an effort to clarify this point, we tested the hypothesis that different species of ants attend homogeneously aphids in any type of plant defined under Methods, using the host plant to indicate habitat.

Ant-Plant relationships

An overall analysis of Table II leads us to conclude that ants select the types of plants where they will search for aphids ($G_H = 216.7$, d.f. = 100; $p < 0.001$). Each type of ant showed particular affinities, apart from those mentioned above, such as : *Tetramorium caespitum* (L., 1758) ($G = 9.97$; $p < 0.01$) and *Formica fusca* (L., 1758) ($G = 14.32$; $p < 0.01$) preferred small plants; *Tapinoma nigerrimum* ($G = 24.24$; p) occurred more often than expected in trees and roots, but was not found in shrubs; *Camponotus aethiops* ($G = 18.14$; $p < 0.01$) was found mainly in trees; and *Formica decipiens* ($G = 17.67$; $p < 0.01$) was not found on thistles.

Ant species found attending aphids in trees were also found on thistles but not on shrubs or herbaceous plants. Apparently, the single axis and relative simple branching of both trees and thistles constitute a favorable structure for ants to carry out their searches, as opposed to the complicated structures of shrubs and small herbaceous plants.

CONCLUSIONS

The apparent specificity in ant and aphid relationships may be due to the combination of two characteristics in ants : the territoriality displayed by many species, and the fact pointed out by Ebers & Barrows (1980) that ants from the same colony tend to visit only one aphid colony, or very few. These characteristics can be confused, in our opinion, with specificity in ant-aphid relationships.

After analysing our data we conclude that ants, rather than developing species-to-species relationships with aphids, show affinities for aphid genera. This association depends upon a common geographical range and plant preference. Therefore, in general terms these relationships seem to be the result of coexistence rather than interdependence.

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found attending arboreal aphids. Attending tetraneurid aphids and has seldom been found on other plants and thistles; it has not been found in her-
 C. *Formica ruginosa* (G = 25.71; p < 0.01) has shown
 towards in trees, attending the species of *Formica*
 towards less than expected.

Formica ruginosa (G = 16.2; p < 0.01) more often than expected attends the arboreal aphids of the genus *Chaitophorus* on *Salix* and *Populus* and tetraneurid aphids from the subgenus *Pteropachys*.

Consequently we can discard the idea of constant species-to-species relationships but not the affinity of certain species of ants for certain genera of aphids. This affinity may, however, derive not from the characteristics of the aphids but instead from the type of habitat. In an effort to clarify this point, we tested the hypothesis that different species of ants attend homogeneously aphids in any type of plant defined under Methods, using the host plant to indicate habitat.

Ant-Plant Relationships

An overall analysis of Table II leads us to conclude that ants select the types of plants where they will search for aphids (G = 216.7, d.f. = 160; p < 0.001). Each type of ant showed particular affinities apart from those mentioned above, such as: *Formica ruginosa* (L., 1758) (G = 9.07, p < 0.01) and *Formica fusca* (L., 1758) (G = 14.51, p < 0.01) preferred small plants; *Formica ruginosa* (G = 24.24; p) occurred more often than expected in trees and roots, but was not found in shrubs; *Camponotus ruginosus* (G = 18.14; p < 0.01) was found mainly in trees; and *Formica ruginosa* (G = 17.67; p < 0.01) was not found on thistles.

Ant species found attending aphids in trees were also found on thistles but not on shrubs or herbaceous plants. Apparently, the single size and relative simple branching of both trees and thistles constitute a favorable structure for ants to carry out their searches, as opposed to the complicated structures of shrubs and small herbaceous plants.