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Coexistence Patterns Between Ants And Spiders In Grassland Habitats

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Abstract

The ecological importance of both ants and spiders is well known, as well as the relationship between certain spiders and ants. The two main strategies - myrmecomorphy (ant-mimicking) and myrmecophagy (ant-eating) - that connect spiders to ants have been mostly studied at the behavioural level. However, less is known about how these relationships manifest at the ecological level by shaping the distribution of populations and assemblages. Our question was how ant-mimicking and ant-eating spiders associate with ant genera as revealed by field co-occurrence patterns. For both spider groups we examined strength and specificity of the association, and how it is affected by ant size and defence strategy. To study spider-ant association patterns we carried out pitfall sampling on the dolomitic Sas Hill located in Budapest, Hungary. Spiders and ants were collected at eight grassland locations by operating five pitfalls/location continuously for two years. To find co-occurrence patterns, two approaches were used: correlation analyses to uncover possible spider-ant pairs, and null-model analyses (C-score) to show negative associations. These alternative statistical methods revealed consistent co-occurrence patterns. Associations were generally broad, not specific to exact ant genera. Ant-eating spiders showed a stronger association with ants. Both ant-mimicking and ant-eating spiders associated more strongly with Formicine ants - species with formic acid or anal gland secretions, and had neutral association with Myrmicine ants - species with stings and cuticle defences.

Introduction

Ants have immense and complex effects on ecosystems because of their sheer abundance, biomass and the complex interactions in which they are involved (Hölldobler & Wilson, 1990). Ants possess various forceful defence mechanisms such as formic-acid, aggressive attack, stings, and social defence (Wilson, 1976; Yanoviak & Kaspari, 2000). Defence makes ants best avoided by most predators, which presents them as ideal models for mimics among arthropods (Schowalter, 2006), or makes them a food best suited for specialist predators. Ant associations that have developed in many arthropod taxa fall into three categories: myrmecomorphy, myrmecophagy and myrmecophily. Myrmecomorphs are ant-mimicking species which have acquired morphological and/or behavioural similarity to ants, myrmecophagous species are ant-eaters that specialise in subduing ant prey. Here - since only those association types occurred in our study area - we only consider the ant-eating and ant-mimicking species and do not deal with the third type of ant associated spiders, the myrmecophils, which are highly integrated into host colonies (Cushing, 2012; Pekar et al., 2012).

Spiders can use one or more of these strategies, making spider-ant relationship a complex system to observe (McIver & Stonedahl, 1993; Cushing, 1997). Ant associates can be found in various spider families (Salticidae, Gnaphosidae, Theridiide, Zodariidae, Liocraniidae, Linyphiidae) (Cushing, 1997; Pekar, 2004b). Ant associated spiders have many morphological and behavioural adaptations. In ant-mimicking species body shape often resembles three body regions, legs are long and slender and there may be cuticle modifications present that resemble mandibles, compound eyes or sting. The movement of ant-mimics frequently becomes ant-like, including holding forelegs like antennae (Reiskind, 1977; Ceccarelli, 2008). Ant association may also manifest in special foraging and predatory strategies, most tangible in specialist ant-eaters, like *Zodarion* spp. (Pekar, 2004).

Spider-ant relationship is also shaped by ants, which are the models of mimicry and/or potential prey. Such a relationship is logically influenced by ant size and also by defence

type ants possess (Holway, 1999; Feener, 2000). Ants concerned in the present study fall into two main categories: ants that rely on cuticular structures, sting and ants that mostly rely on the use of formic acid or gland secretions. These coincide with two broader taxonomic groups, being either "myrmicine" (Myrmicinae subfamily) or "formicine" (Formicinae and Dolichoderinae subfamilies) ants (Edwards et al., 1974; Shattuck, 1992; Bolton, 2003). Myrmicine ants have thick cuticle and cuticle structures, such as spines (also present in some Formicinae, but not present in the genera included in the present study); they possess a distinct postpetiole and a functional sting is always present, while in the formicine group, species armour is different, lack both postpetiole and sting; their defence is based on the use of their mandibles and on toxin exuded from the tips of their abdomens (Hermann, 1969; Edwards et al., 1974). We treated these taxonomic groups as representing two different defence types, because such modifications are important selective factors for both predators and mimics.

Although ant associations have been mostly studied through the resulting morphological and behavioural modifications, it also has an ecological context, because ant models should be present in the same microhabitat, and have direct or indirect ecological interactions that are related to co-occurrence (Edmunds, 1978). Direct trophic connection may exist between ants and spiders, but ants may also influence spiders indirectly through their ecological impact, e.g. aphid tending (Renault et al., 2005; Sanders & van Veen, 2012).

In recent years connection between spiders and ants has gained more and more attention in behavioural, morphological and evolutionary studies (Cushing, 1997; Pekar, 2004b; Pekar, 2004a; Nelson & Jackson, 2009; Cushing, 2012; Nelson & Jackson, 2012), but the ecological patterns observable in the field has to be examined for a complex view on ant-spider relationship. Analysing seasonally divided datasets from 40 pitfalls in a grassland ecosystem we tried to answer the following questions: (i) Is there any non-neutral co-occurrence pattern between ant associated spiders and ants? (ii) How specific is the association between ant associated spiders and ants? (iii) Is the strength of the relationship different between spider strategies and is it influenced by spider and ant size and ant defence type?

Material and Methods

Study area

Our field study took place on the top area of Sas Hill Nature Reserve, Budapest (47°28'48.68"N, 19° 1'1.22"E), between 2010 and 2012. This is a grassland covered dolomitic hill, a refuge for many rare spider species (Szinetár et al., 2012), and has been a nature reserve since 1958. Arachnological research at Sas Hill has an especially rich tradition (Balogh, 1935; Samu & Szinetár, 2000; Rákóczi & Samu, 2012; Szinetár et al., 2012). These studies made us notice the especially high number of ant associated spider species, which reaches 14 species with the present study (Szinetár et al., 2012). Contrary to spiders the ant fauna of the hill have not been previously studied and published neither on generic or specific

level. From Hungary 126 species of ants in 34 genera are known (Csősz et al., 2011). Collection of ants and spiders was made in eight dry dolomitic grassland patches scattered on the 35 ha area of the hill. Botanically they belonged to open and closed dolomitic dry grasslands, with *Festuca pallens* Host as a characteristic grass species. Detailed habitat description and co-ordinates are given in Szinetár et al. (2012).

Sampling

We collected spiders and ants by pitfall trapping. Pitfall traps containing 40% ethylene-glycol with a small drop of liquid soap, had 7.5 cm diameter openings and a laminated plate was applied c. 3 cm higher than the surface as a cover (Kádár & Samu, 2006). Pitfall trap sampling lasted from 29 April 2010 to 24 May 2012. Traps were emptied fortnightly, except in winter when, depending on the weather, the traps were emptied c. every four weeks. Each location was sampled with five traps in a linear transect with 2 m between traps.

Collected samples were placed in 70% alcohol; both spiders and ants were sorted and identified under a stereomicroscope. Adult spiders were determined to species, while ants were determined to genera. Voucher specimens were placed in the collection of the Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences. We used several determination keys for spiders (Loksa, 1969; Loksa, 1972; Roberts, 1995; Nentwig et al., 2013), and for ants (Somfai, 1959; Czechowski et al., 2012). The nomenclature of spiders followed the World Spider Catalogue (Platnick, 2013).

Data classification and analysis

The co-occurrence of spiders and ants was examined at two different levels, for which two datasets were derived from raw data: 'trap' level dataset contained summarized data of a given pitfall trap over all emptying occasions (n = 40 datasets); 'trap-season' level datasets contained summarized data of a given pitfall trap for a season of a year. In the latter datasets we placed winter catches (that represented fewer animals) into autumn or spring, with the division date 1 January, resulting in 7 seasons: 2010 spring, 2010 summer, 2010 autumn, 2011spring, 2011summer, 2011autumn and 2012 spring (n = 280 datasets). In each approach spider species data and ant generic data were used.

We assessed the relationship between spiders and ants based on various, biologically meaningful classifications. Ants were classified by average size in a genera; and by their taxonomic type also related to defence type: myrmicine (cuticular defence, sting) or formicine (formic acid or gland secretions) (Bettini et al., 1978; Bolton, 2003). We considered only workers. Mean worker size was taken from the literature (Somfai, 1959). Size difference between dimorphic worker classes was not small in all cases. Dimorphism was taken into consideration by calculating mean size from the worker classes. List of ant genera, their classification and mean size are given in Table 1. Spiders were divided into two groups based on their association type to ants: ant-eating "myrmecophages" and ant-mimicking "myrmecomorphs", derived from data in

the literature (Cushing, 1997; Pekar, 2004; Platnick, 2010; Pekar & Jarab, 2011; Cushing, 2012; Nentwig et al., 2013), and the average size in each species was also considered; spider classification and size are given in Table 2.

In the statistical analyses we have included only species/genera where more than five individuals were found during the study. We used Spearman correlation to reveal positive or negative correlation between counts of individuals of ant genera and spider species. A non-parametric approach was used because of the skewed distribution of counts (many 0 values and some high counts). Ant and spider related factors that influence the strength of correlation were analysed by linear mixed model. The model included Spearman correlation coefficient values as response variable, spider strategy, ant defence type, average ant and spider size in given genus/species as explanatory variables, and to control for the non-independence of values within genus or species, spider species and ant genera were added to the model as random factors (Faraway, 2005). Specificity of the relationship (measured as the number of significant correlations) was analysed by nominal logistic analysis.

Table 1. List of ant genera in the present study. Subfamily and grouping according to morphs are given, together with mean worker size and number of specimens caught in the study.

Genus	Abbrev. (5 character)	Subfamily	Morph	Mean size (mm)	No. of indiv.
Bothriomyrmex	*Bothr.*	Dolichoderinae	formicine	2.5	13
Tapinoma	*Tapin.*	Dolichoderinae	formicine	3.0	5550
Camponotus	*Campo.*	Formicinae	formicine	10.0	1596
Formica	*Formi.*	Formicinae	formicine	7.0	1074
Lasius	*Lasiu.*	Formicinae	formicine	3.0	1179
Plagiolepis	*Plagi.*	Formicinae	formicine	1.5	210
Leptothorax	*Lepto.*	Mirmicinae	myrmicine	2.5	12
Messor	*Messo*	Mirmicinae	myrmicine	8.5	112
Myrmecina	*Myrme.*	Mirmicinae	myrmicine	5.5	3
Myrmica	*Myrmi.*	Mirmicinae	myrmicine	5.5	185
Solenopsis	*Solen.*	Mirmicinae	myrmicine	1.5	20
Temnothorax	*Temno.*	Mirmicinae	myrmicine	2.5	33
Tetramorium	*Tetra.*	Mirmicinae	myrmicine	2.5	243

Analyses were carried out by R 2.15.2 (R Core Team, 2013).

We used co-occurrence analysis to detect possible non-random patterns in presence absence matrices, comparing them to matrices generated by randomization. Analysis was carried out by EcoSim's (build 021605) co-occurrence module (Gotelli & Entsminger, 2010). We used location by taxon presence-absence matrices, where location datasets were either trap or trap-season, and taxon was (i) only ant genera; (ii) only ant associated spider species; (iii) both ants and ant associated spiders. The co-occurrence analysis searches for checkerboard units (CU), which are 2x2 sub matrices in the original presence-absence matrix. The number of CUs for a species pair is the number of localities where only one of the species occurs, i.e. their occurrence is mutually exclusive (Stone & Roberts, 1990). For a given species-pair the negative association is represented by a large number of CUs in every possible habitat combination. The average number of CUs for all the possible species combination is the Checkerboard score (C-score), which is a measure of negative association in the community (Stone & Roberts, 1990; Gotelli, 2000; Gotelli & Entsminger, 2010). The null-model matrices are Monte-Carlo randomizations of the original matrix. The average of such randomized C-score values represent the case without biological interactions, higher observed C-score values than that indicate negative, while lower observed values indicate positive associations between the species.

Results

Quantitative results

During the whole sampling period we emptied the 40 traps 40 times. In total 10,230 ant specimens and 751 ant associated spiders were found. The total number of ant genera was 13 (Table 1), the ant associated spiders were represented by 11 species (Table 2). Most ant associated spiders were relatively rare, the majority representing the ant-eating strategy. A single ant-eating species, *Z. rubidum*, made up nearly 90% of all ant associated spiders, and it meant a very high, 16% dominance among all spiders.

Table 2. List of ant associated (AA) spider species on Sas Hill. Number of individuals refers to total catch during the period. Catches of AA species also expressed as % of all AA (ΣAA). As a reference total number of spider individuals (including non AA) and total number of AA spiders caught are given. The mean size of each species is also given.

Species name	Family	Association type	No. of indiv.	% of ΣAA	Mean size (mm)
Callilepis schuszteri Simon	Gnaphosidae	ant-eater	15	2.0	5.2
Euryopis quingueguttata Koch	Theridiidae	ant-eater	2	0.3	2.3
Harpactea hombergi (Scopoli)	Dysderidae	ant-mimic	1	0.1	4.8
Micaria dives (Lucas)	Gnaphosidae	ant-mimic	6	0.8	3.1
Micaria formicaria (Sundevall)	Gnaphosidae	ant-mimic	2	0.3	6.6
Micaria pulicaria (Sundevall)	Gnaphosidae	ant-mimic	1	0.1	4.3
Micaria silesiaca Koch	Gnaphosidae	ant-mimic	1	0.1	4.3
Phrurolithus festivus (Koch)	Corinnidae	ant-mimic	8	1.1	2.7
Phrurolithus szilyi Herman	Corinnidae	ant-mimic	42	5.6	2.3
Synageles hilarulus (Koch)	Salticidae	ant-mimic	2	0.3	3.0
Zodarion rubidum Simon	Zodariidae	ant-eater	671	89.3	3.5
All spiders			4,051		
All ant associated spiders (ΣAA)			751		
ΣAA as % of all spiders			18.5		

Correlation analysis

Spearman correlation analyses were performed on the trap-season dataset. There was a strong correlation between the overall number of ants and ant associated spiders ($\rho = 0.65$, $P < 0.0001$). Correlation was also calculated at the functional grouping levels. Spider ant association types showed no correlation with myrmicine ants (ant-eating spiders: $\rho = 0.025$, $P = 0.68$; ant-mimicking spiders: $\rho = 0.024$, $P = 0.69$), but correlation with formicine ants was significant and of similar strength for both spider groups (ant-eating spiders: $\rho = 0.55$, $P < 0.0001$, ant-mimicking spiders: $\rho = 0.54$, $P < 0.0001$).

Correlation analysis between individual spider species and ant genera was also performed (Table 3). Analysing the pattern of significant correlations, it is clear that the association of spiders is broader than ant genera, because all spider species were significantly positively associated with more than one ant genus (Table 3).

Analysing the number of significant correlations of the spider species in a nominal logistic model including spider strategy, ant type, average ant and spider size as explanatory variables, ant size proved to be marginally significant (Wald test: $\chi^2 = 4.052$, df = 1, $P < 0.04$), the spider association became more frequent with increasing ant size. Ant type proved to be highly significant (Wald test: $\chi^2 = 13.70$ df = 1, $P < 0.0002$), with much more significant associations of spiders with formicine ants.

We also wanted to know how the strength of associations was dependent on spider and ant strategies and average spider and ant size. We tested a linear mixed model on Spearman correlation coefficients, which had normal distribution (Kolmogorov-Smirnov test, d = 0.131, NS). The model included spider strategy, ant defence type and ant and spider size as explanatory variables, and spider species and ant genus as random factors. Spider size was marginally significant, with smaller spiders correlating more with ants (F = 21.51, df = 1, $P = 0.044$); spider strategy was also marginally significant, with ant-eaters more strongly associated with ants (F = 22.83, df = 1, $P = 0.041$). The most important factor proved to be ant defence type showing a much higher correlation of spiders to the formicine group than to myrmicine (F = 12.92, df = 1, $P = 0.005$).

Co-occurrence analysis

The co-occurrence analysis revealed positive association in the ant-spider assemblage. We made simulations on data of "just spider", "just ant" and "ant+spider" assemblages. Observed C-scores were consistently lower than simulated ones, as measured by standard effect size (S.E.S.) in the spider-ant assemblage, meaning that on average the mixed assemblage is more associated than pure taxa assemblages (Table 5). Considering specific species pairs, the number of CUs is a measure of negative association. Higher number of CUs was found between myrmicine ants and ant associated spiders. In *Z. rubidum* we found no CU with any of the ant genera. The CU pattern of spider-ant species pairs is given in Table 5.

Discussion

The main purpose of the present study was to reveal if known ant associated spiders respond to the distribution of ants in an ecologically measurable way. The results certainly support the hypothesis, that non-random co-occurrence patterns exist in the field between ants and ant associated spiders. Although associations were rather broad, they were influenced by spider and ant characteristics, from which ant defence type seemed to be the most important. For our purposes the Sas Hill in Budapest proved to be a very good location where we could sample 11 ant associated species. This is important, because most ant associated species are relatively rare (Cushing, 1997; Pekar, 2004b; Pekar, 2004a; Nelson & Jackson, 2009; Cushing, 2012; Nelson & Jackson, 2012), and to study their ecology and relations to other taxa is therefore not easy.

Measuring the association pattern indicated by ants and ant associated spiders first of all gave us the result that associations are not at the lowest taxonomic resolution of the present study (spider species and ant genera), but at the higher

Table 3. Spearman correlation coefficients (ϱ) of ant associated spiders and ant genera in the trap-season dataset. Row header contains ant genera, (abbreviated names, c.f. Table 2). ■ marked ants are myrmicine, unmarked ones are formicine ants. Spiders marked with ♣ are ant-eaters, unmarked ones are ant-mimics. The number of ● symbols marks the strength of the correlation (denoted by: ● – 0.1-0.19, ●● – 0.2-0.29, ●●● – 0.3-0.39, ●●●● >0.4). All marked correlations were significant at $P<0.05$.

Spider/Ant	*Micaria dives*	*Phrurolithus festivus*	*Phrurolithus szilyi*	*Callilepis schuszteri* ♣	*Zodarion rubidum* ♣
Lepto. ■	-0.04	0.1	0	0.21 ●●	0.17 ●
Messo. ■	-0.04	0.03	0.13	0.02	-0.06
Myrmi. ■	0.01	0.07	-0.11	-0.1	0
Solen. ■	0.1	-0.05	0.14	-0.05	0.01
Temno. ■	0.02	0.09	0.01	0	0.13
Tetra. ■	0.07	-0.01	0.01	-0.04	0
Bothr.	-0.04	0.11	0.02	-0.04	-0.01
Campo.	0.28 ●●	0.15 ●	0.24 ●●	0.23 ●●	0.37 ●●●
Formi.	0.17 ●●	0.15 ●	0.20 ●●	0.23 ●●	0.53 ●●●●
Lasiu.	0.11	0.11	0.16 ●	0.01	0.54 ●●●●
Plagi.	0.21 ●●	0.09	0.18 ●	0.14 ●	0.29 ●●
Tapin.	0.19 ●	0.13	0.32 ●●●	0.09	0.34 ●●●

Table 4. Observed C-scores, standard effect size (S. E. S.) and significance level of co-occurrence analysis on trap and trap season datasets.

Composition	Trap S.E.S.	Trap P	Trap (C-score)	Trap-Season S.E.S.	Trap-Season P	Trap-Season (C-score)
Only spider	-1.8	0.02	3.42	-1.1	0.13	15.53
Only ant	-2.1	0.01	2.31	-3.2	0.0002	11.82
Spider + ant	-3.2	0.0002	1.67	-3.5	0.0001	10.04

level of functional and morphological groups. At these higher levels the two statistical methods, measuring positive and negative associations, gave congruent results.

Our results are also in agreement with observations about the moderately narrow diet of ant-eating spiders. These spiders are specialised on consuming not a single ant species, but rather a broader spectrum of species, such as genera or subfamily (Pekar, 2004; Pekar et al., 2012). Based on spider response to olfactory cues produced only in a narrow range of genera, in a recent study Cardenas et al. (2012) argue that *Z. rubidum* - previously thought as an "ant generalist" - in fact, preys mostly on the genera *Lasius* and *Formica*. Our field results support this notion.

It was proved that spider and ant size are marginally significant factors in the association, most probably for different reasons in ant-mimicking and ant-eating spiders. On one hand, preying on ants is risky because of the defences, which favours a higher spider/ant size ratio, but for the same reason large ant-eaters can be less associated with ants because they may have a broader diet. On the other hand, ants below a certain size might not be preferred, because preying on them results in lower profit (less nutrition in preferred body parts) compared to cost (Pekar, 2004b; Pekar et al., 2010; Cushing, 2012). In *Z. rubidum* we know from case studies that the spider shows preference for similar sized or larger ants (Pekar, 2004b). Probably for other ant-eaters, size ratio with prey plays similar role. In ant mimics size plays important role because appropriate size enchases the accuracy of the mimic, making it more effective.

The strongest pattern found was, that both ant-mimicking and ant eating spiders showed positive association with formicine ants and neutral or negative association with myrmicine ants, as it was confirmed by both statistical approaches. In ant-mimicking spiders the reason could be that the numerical dominance of formicine ants makes these ants a better model for Batesian-mimicry (Schowalter, 2006). The strength of the association was the strongest in ant-eating spiders, where the reason for co-occurrence pattern could be the difference how they are able to cope with different defences: thick cuticle, propodeal spikes and sting with neurotoxins vs. formic acid (Blum, 1992; Bolton, 2003).

The aim of the present study was to reveal spider-ant association patterns from a field study. This is an alternative and complementary approach to laboratory studies, where preference is tested under highly artificial circumstances, and relatively little can be said about their realisation in the field. The specificity of spider-ant association proved to be relatively broad in the field, with ant associated spiders correlating with more than one ant genera. In the present study we uncovered a non-random pattern of co-occurrence, where - possibly for different reasons for ant-mimicking and ant-eating spiders - the most substantial pattern was a stronger association with fomicine than with mymicine ants.

Acknowledgements

Table 5. The number of checkerboard units (CU) of ant associated spiders and ant genera in the trap-season dataset. Row header contains ant genera (names abbreviated, c.f. table 2). ■ marked ants are Myrmicine, unmarked ones are Formicine ants. Spiders marked with ♣ are ant-eaters, unmarked ones are ant-mimics. Numbers show the number of CUs observed for the species pair. the number of CUs is visually represented by the number of ● symbols (no symbol – <4, ● – 4-5, ●● – 6-7, ●●● – 8-9).

Spider/Ant	*Micaria dives*	*Phrurolithus szilyi*	*Phrurolithus festivus*	*Callilepis schuszteri* ♣	*Zodarion rubidum* ♣
Lepto.■	6 ●●	0	2	6 ●●	0
Messo.■	3	2	8 ●●●	0	0
Myrmi. ■	5 ●	5 ●	2	6 ●●	0
Solen. ■	4 ●	4 ●	9 ●●●	4 ●	0
Temno. ■	8 ●●●	2	0	6 ●●	0
Tetra. ■	0	0	0	0	0
Bothr.	3	6 ●●	8 ●●●	6 ●●	0
Campo.	0	0	0	0	0
Formi.	0	0	0	0	0
Lasiu.	0	0	0	0	0
Plagi.	0	0	0	0	0
Tapin.	0	0	0	0	0

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