Prey Analysis in the Diet of Some Ponerine Ants (Hymenoptera: Formicidae) and Web-building Spiders (Araneae) in Coffee Plantations in Chiapas, Mexico

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by

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ABSTRACT

A census of the prey captured by seven common web–building spiders (*Cyclosa caroli*, *Gasteracantha cancriformis*, *Leucauge mariana*, *L. venusta*, *Anelosimus jucundus*, *Achaearanea tesselata*, and an undetermined species of Linyphiidae) and two dominant ponerine ant species (*Ectatomma ruidum* and *E. tuberculatum*) was carried out over a two–year period in different coffee plantations, in the Mexican state of Chiapas. A total of 4,334 prey items were recovered, of which near to 70% were identified to family level and classified according to their feeding habits. For each of the predators, the bulk of the prey belonged to the four most abundant orders of insects (Hymenoptera, Diptera, Homoptera and Coleoptera) known to be associated with Neotropical coffee plantations.

The comparison by computed coefficients of both diet breath and diet overlap indicated some degree of similarity between the two ant species, and between the six spider species. Moreover, spiders that used webs that function in a similar manner as insect traps (both araneids and the tetragnathid on one side, both theridiids and the linyphiid on the other side) showed more similar diets. Each predator appeared to have an unique feeding niche within the coffee agroecosystem: for all of the 28 comparisons made between pairs of species, diet overlap (C) values were far lower than the theoretical value of +1 corresponding to complete overlap. Each species also differed in its response to prey availability although the frequency of predation on most types of prey appeared to be positively correlated with their relative abundance in the biotope. This correlation was especially obvious within the Hymenoptera.

Of the 159 families identified, 30 (38.1% of all the identified prey) were recognized as containing species known to be pests of coffee plants. Herbivores, detritivores and polyphagous arthropods constituted the major part of prey for ants and spiders alike (82.9% of all

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identified prey for the web–building spiders against 89.9% for the ponerine ants), while only 11.9% of all identified prey corresponded to families that are beneficial (from an agricultural view point) as predators, parasitoids, or possible pollinators. These results, along with the absence of serious native coffee pests in the study area, confirm the beneficial economic impact of web–building spiders and carnivorous ants as generalist predators in Neotropical coffee agroecosystems.

Key words: Ant–spider communities, generalist predators, feeding ecology, diet overlap, coffee agroecosystem.

INTRODUCTION

Ants and spiders are among the most common generalist predators (Hölldobler & Wilson 1990; Young & Edwards 1990) and have a marked impact on the terrestrial ecosystems in which they live (Kajak *et al.* 1972; Nyffeler *et al.* 1994a). Due to their stabilizing and/or regulating influence on pest insect populations, these predators are of particular interest for conservation biological control in agroecosystems (Riechert & Lockley 1984; Nyffeler & Benz 1987; Carroll & Risch 1990; Way & Khoo 1992). Their influence in Neotropical agroecosystems of economic importance (like coffee, cocoa, sugar cane, or maize), remains poorly studied, even though certain species are known to be very common in these habitats (Robinson & Robinson 1974; Young 1986; Ibarra-Núñez 1990; Perfecto 1990; Perfecto & Snelling 1995; Ibarra-Núñez & García-Ballinas 1998). As generalist predators, ants and spiders not only prey upon pest insects, but also on insects of neutral economic status or on beneficial ones (Nyffeler *et al.* 1994a). Consequently, determination of the range of captured prey, prey feeding habits (*i.e.* their economic status 'pest' or 'beneficial'), and their relative frequency in the diet of the most common species of these predator groups, can be regarded as of fundamental importance for an evaluation of the impact of such predators. Moreover, this information may facilitate the identification of the main target prey for a given predator and permit the degree of specialization of each predator to be determined.

Coffee (mainly *Coffea arabica* and *C. canephora*) is the second most important perennial culture in Mexico. With 280,597 hectares of plantations, Chiapas is the largest producer in Mexico. Due to the economic relevance of coffee production, and in order to estimate the real impact of natural generalist predators in a perennial Neotropical agroecosystem, we studied the predatory influence of various ants and web–building spiders on invertebrate populations associated with coffee in Chiapas.

MATERIALS AND METHODS

Study area

Our study was performed in the Soconusco region, the main agricultural zone of Chiapas, Mexico. The sampling areas were located in four coffee plantations with diverse shade trees: 1) The Experimental Station of the INIFAP at Rosario Izapa, Tuxtla Chico (ca. 14°58'N, 92°09'W, 430m elevation), 18 km E–NE of Tapachula; 2) Finca "Irlanda", Huehuetan (ca. 15°10'N, 92°21'W, 780m elevation), 65km N–NW of Tapachula; 3) Finca "Hamburgo", Tapachula (ca. 15°10'N, 92°19'W, 950m elevation), 62km N–NW of Tapachula; 4) Finca "Santa Elena", Tapachula (ca. 15°05'N, 92°16'W, 700m elevation), 32km N-NE of Tapachula.

Over a two–year period, we sampled the prey caught by nine predator species: two dominant ponerine ants (Lachaud 1990; Valenzuela *et al.* 1995), and seven common web–building spiders (Ibarra-Núñez 1990; Ibarra-Núñez & García-Ballinas 1998). The studied species were *Ectatomma ruidum*, *E. tuberculatum* (Formicidae, Ponerinae), *Cyclosa caroli*, *Gasteracantha cancriformis* (Araneae, Araneidae), *Leucauge mariana*, *L. venusta* (Araneae, Tetragnathidae, these being two very close species that cannot be differentiated as immatures and, as such, were considered jointly as a single predator group in this study), *Anelosimus jucundus*, *Achaearanea tesselata* (Araneae, Theridiidae), and one undetermined species (Araneae, Linyphiidae, probably *Lepthyphantes* sp.), reported here as "Linyphiidae sp. 1". Both *Ectatomma* species nest in the ground and forage individually, but *E. ruidum* searches for prey exclusively at the leaf–litter level, whereas *E. tuberculatum* performs most of its foraging activity on coffee plants and shade trees. Nevertheless, both ant species visit also extrafloral nectaries and transport sugary liquids (Weber 1946; Lachaud 1990; Altshuler 1999) and, therefore, *E. ruidum* is able to forage on small shrubs. Some differences also exist between the spider species according to their foraging strategies: *C. caroli*, *G. cancriformis*, *L. mariana* and *L. venusta* build two–dimensional orb–webs, whereas *A. jucundus*, *A. tesselata* and the undetermined Linyphiidae build three–dimensional space-webs.

The spiders and their prey were sampled each month, between February 1993 and December 1994, by searching all the webs found in a plot containing 10 to 12 coffee plants. Web owners and their prey remains were preserved in a vial with 70% ethanol and the collecting data were recorded. For ant prey items, samples were collected over the course of three weeks for each species, at two periods of the year (dry

and rainy seasons). Prey were gently recovered with forceps from individual foraging ants belonging to different colonies while returning to their nest, and preserved in ethanol. All prey were identified at the family level except for a number of very damaged specimens, identified only to order or to class. The total number of recovered prey (identified or not) was recorded.

In order to define the effect of these predators, we studied the possibility of a correlation between the trophic habits of the captured prey and their relative frequency in the predator diet. According to the classification proposed by Daly *et al.* (1978) and Borror *et al.* (1989), the collected prey were clustered, at family level, in one of the following categories: herbivores, nectarivores (include pollen feeders), detritivores (include fungivores), predators, parasites (include parasitoids), and polyphages. An additional category, the "abstainers", corresponding to non–feeding adult insects with aquatic immatures not associated with coffee (e.g. Ephemeroptera), was also considered. Due to the diversity of feeding habits in various families of insects (e.g. Staphylinidae comprise predators, parasites, fungivores, etc.), only the most representative feeding category was retained for each family.

Data analysis

On the basis of prey records for the eight predator species, we attempted to evaluate the competitiveness and predatory impact of these species comparing them by means of different indices commonly used in such community or diversity studies: diet breadth, diet overlap and prey selectivity (Colwell & Futuyma 1971).

Diet breadth. Diet breadth (H'), indicating the degree of diversity of each specific diet, was calculated on basis of the Shannon–Weaver formula (Shannon & Weaver 1949):

$H' = - \Sigma\ pij\ ln\ pij$

where pij is the frequency of capture of prey taxon j (order or family) by predator species i (calculated from Table 1). The diet evenness (H'/ H'max), characterizing the breadth homogeneity of the diet (Hurtubia 1973), was calculated using the following formula:

$H' / H'\ max = H' / ln\ R$

where R is the number of prey taxa (orders or families) (see Nyffeler & Sterling 1994). The values of this index range from 0 indicating that only one prey taxon was captured, to a maximum of +1 indicating that all prey taxa were used evenly. Statistical comparison of diet breadth were made according to Poole (1974) and Nyffeler & Sterling (1994) using a *t*–test (see Nyffeler & Sterling (1994) for a detailed description of the statistical method).

Diet overlap. Diet overlap (C) of two predator species, permits the evaluation of the degree to which their ecological niches differ. This was calculated using the method of Colwell & Futuyma (1971), developed by Nyffeler & Sterling (1994) for the comparison of the feeding niches of polyphagous spiders in cotton plantations:

$C_{1,2} = 1 - 1/2 \Sigma \mid (p1j - p2j) \mid$

where p1j and p2j is the frequency of capture of prey taxon j (order or family) by predator species 1 and 2 respectively (calculated from Table 1). An overlap value was calculated for each of the possible 28 species pairs. A value of 0 indicates no overlap and +1 indicates complete overlap.

Because of possible asymmetrical diet overlap between two species (the diet of a species may completely overlap that of a second species, whereas the diet of the second species may only partially overlap that of the first species), specific overlap must be calculated for species 1 onto 2 and also for species 2 onto 1 (Nyffeler & Sterling 1994). Specific diet overlap for two given species was calculated using the formula (Ludwig & Reynolds 1988; Nyffeler & Sterling 1994):

$Z_{1,2} = - 2 N_1 \ln (SO_{1,2})$

$Z_{2,1} = - 2 N_2 \ln (SO_{2,1})$

where N1 is the number of prey in the first sample (species 1), and N2 is the number of prey in the second sample (species 2), and where

$SO_{1,2} = e^{[\Sigma(p1j \ln p2j) - S (p1j \ln p1j)]}$

$SO_{2,1} = e^{[\Sigma (p2j \ln p1j) - S (p2j \ln p2j)]}$

where p1j and p2j is the frequency of capture of prey taxon j (order or family) by predator species 1 and 2 respectively (calculated from Table 1). The test statistic has a chi-square distribution (with df = number of prey taxa (R) - 1) (see Petraitis (1979), Ludwig & Reynolds (1988) and Nyffeler & Sterling (1994) for more details on the calculation of statistical parameters). For values of Z higher than the critical value for chi-square at P = 0.001, the null hypothesis of complete overlap was rejected. Specific diet overlap was tested for each of the 28 predator species pairs.

Prey selectivity. In order to determine whether some prey taxa were captured selectively, Ivlev's index of electivity (IE) was calculated (Ivlev 1961):

$IE = (pj - qj) / (pj + qj)$

where pj is the frequency of prey taxon j (order or family) in the diet of the predator species under consideration, and qj is the frequency of this prey taxon in the potential prey population. A value of 0 indicates that the capture of the prey taxon under consideration is proportional to the frequency of this taxon in the habitat, all values above 0 indicate

a selective over–predation of this prey taxon from the pool of available prey, and all values below 0 indicate a selective under–predation of this prey taxon. The frequency of the available prey orders and families in coffee plantations was assessed from extensive samplings from the aerial part of the coffee plants made each month for three years, with a D-Vac suction device in 'Finca Irlanda' and in 'Finca Hamburgo' (see Ibarra *et al.* 1995). As with any collection method, suction samples tend to be biased, in this case against very mobile, larger flying insects, which may well escape at a disproportionate rate. More over, due to the sampling technique used, only available prey present on coffee plants were considered and some prey taxa, like Halotaxida and Isopoda which only occurred in the leaf litter, could not be taken into account. As a consequence, *E. ruidum* that concentrates its foraging activity on the leaf litter was not considered in the comparison of prey selectivity. Nevertheless, despite these different limitative constraints, the D–Vac suction samples were considered as sufficiently representative of the natural prey availability.

RESULTS

Diversity of prey species and diet evenness

A total of 4,334 prey items were recovered. The total prey range was very large, involving 159 invertebrate families spread over 30 orders, mostly arthropods: 156 families within 28 orders (Appendix 1). As would be expected for generalist predatory species, within each predator's diet, prey diversity was also very large, ranging from 40 families (14 orders) for *A. tesselata*, to 84 families (19 orders) for the Linyphiidae sp.1.

In all cases, the diet evenness (H'/H'max) was superior to 0.5, indicating an absence of prey specialization (Table 1). Whatever the prey grouping taken into consideration (orders or families), the analysis of this prey diversity for the eight predator species showed a trend of increasing evenness (H'/H'max) with increasing diet breadth (H'). Nevertheless, according to the prey grouping level taken into consideration, some differences were observed among the predator species. At the level of prey orders (Table 1A), pairwise comparisons indicated significant differences between the orb-weaver spiders (*G. cancriformis*, *L. mariana/venusta* and *C. caroli*), which shared the lowest diet breadth values and the highest prey specialization, and the space-web weavers (the Linyphiidae sp.1, *A. tesselata* and *A. jucundus*) which had the highest diet breadth values and the lowest prey specialization. The two ponerine ant species presented intermediate values. At the level of prey

Table 1. Comparison of diet breadth (H' ± variance) of the eight species of predators, calculated from the prey frequency in each diet (Appendix 1).H' values followed by the same letter are not significantly different (P > 0.05) by pairwise *t*-test comparison. A: prey grouped at the level of order; B: prey grouped at the level of family.

(A)	R	H' ± variance	H'/H'max
G. cancriformis	8	1.1339 ± 0.0025 b	0.5453
L. mariana/venusta	13	1.5060 ± 0.0052 a	0.5871
C. caroli	13	1.5180 ± 0.0027 a	0.5918
E. tuberculatum	16	1.7701 ± 0.0050 e	0.6384
R. ruidum	19	1.9634 ± 0.0012 d	0.6668
Linyphiidae sp. 1	19	2.0485 ± 0.0006 c	0.6957
A. tesselata	14	2.0566 ± 0.0054 c d	0.7793
A. jucundus	17	2.1044 ± 0.0047 c d	0.7428
(B)	R	H' ± variance	H'/H'max
E. tuberculatum	42	2.0526 ± 0.0093 e	0.5492
E. ruidum	61	2.3575 ± 0.0053 d	0.5735
C. caroli	43	2.6838 ± 0.0072 a	0.7136
L. mariana/venusta	53	2.8813 ± 0.0090 a b	0.7257
A. tesselata	40	2.9262 ± 0.0123 a b	0.7933
A. jucundus	50	3.0453 ± 0.0095 b c	0.7784
G. cancriformis	42	3.1117 ± 0.0056 b c	0.8325
Linyphiidae sp. 1	84	3.1982 ± 0.0017 c	0.7218

families (Table 1B), such a separation between spider species according to the structure of their web was not so clear, but the diet breadth of the two ponerine ant species appeared significantly reduced and more specialized than that of the spiders.

As a whole, the orders with the greatest number of families preyed upon were: Diptera (31 families), Hymenoptera (22), Coleoptera (18), Homoptera (17), and Psocoptera (14). Among the prey families, 30 (*i.e.* 18.9% of all families, representing 28.7% of all the collected prey and 38.1% of the identified prey) have been reported as containing species recognized as pests for the coffee plants (Appendix 1): 19 families for Latin America, and 11 for other continents (Le Pelley 1968, 1973). Homoptera showed the highest number (10) of prey families reported as pests.

Comparison of the feeding niche of predator species

Each predator diet was characterized by a specific combination of the orders of the most frequently captured prey (Table 2). Estimates of diet overlap for each of the 28 predator species pairs (Table 3) showed that each species had its own feeding niche within the coffee agroecosystem. For all of the 28 species pairs comparisons, diet overlap (C) values were far from the theoretical value of +1 corresponding to complete overlap. They ranged from 0.36 to 0.80 (overall mean = 0.55 ± 0.02 SE) for prey grouped at the level of order (Table 3A), and from 0.14 to 0.59 (overall

Table 2. Main prey taxa (> 5% within one predator diet) predated upon by each predator species and their relative frequency (%) in the diet. When present at a frequency lower than 5%, orders are reported as (+), and as (-) when totally absent.

Prey Orders	*C. caroli*	*G. cancriformis*	*L. mar./ven.*	*A. jucundus*	*A. tesselata*	Lin. sp. 1	*E.ruidum*	*E.tuberculatum*
Hymenoptera	40.0	43.7	23.5	20.7	13.7	19.8	29.3	52.5
Diptera	20.3	36.2	49.7	7.7	15.8	24.6	13.6	+
Homoptera	+	+	6.5	28.8	19.2	20.3	6.6	+
Coleoptera	+	7.9	+	9.5	8.2	+	10.3	5.8
Sub-total[1]	*66.7*	*90.3*	*82.7*	*66.7*	*56.8*	*66.7*	*59.7*	*65.9*
Thysanoptera	13.6	+	+	+	23.3	5.6	+	+
Halotaxida	-	-	-	-	-	-	17.9	7.1
Collembola	+	-	+	12.2	-	+	-	-
Isoptera	-	-	-	+	-	+	+	9.1
Cryptostigmata	+	-	+	+	+	7.9	-	-
Psocoptera	+	+	+	+	+	7.5	-	+
Lepidoptera	+	+	+	+	+	+	5.4	+
No. prey records	*487*	*318*	*294*	*222*	*146*	*1684*	*819*	*364*

[1]This subtotal takes into account all the prey belonging to the four most abundant insect orders (Hymenoptera, Diptera, Homoptera, and Coleptera) present in coffee agroecosystems in the study area, even if their respective frequency in the diet is less than 5% and if the corresponding valve does not appear in this table.

Table 3. Coefficient of diet overlap among eight species of predators, calculated from the prey frequency in each diet (Appendix 1). A: prey grouped at the level of order; B: prey grouped at the level of family. Cc: *Cyclosa caroli*; Gc: *Gasteracantha cancriformis*; Lm/v: *Leucauge mariana/venusta*; Aj: *Anelosimus jucundus*; At: *Achaeranaea tesselata*; Lsp 1: undetermined Linyphiidae; Er: *Ectatomma ruidum*; Et: *E. tuberculatum*.

(A)	Cc	Gc	Lm/v	Aj	At	Lsp 1	Er	Et
Cc	-	0.80	0.61	0.45	0.60	0.61	0.55	0.63
Gc	0.80	-	0.71	0.43	0.44	0.53	0.57	0.62
Lm/v	0.61	0.71	-	0.50	0.52	0.68	0.52	0.40
Aj	0.45	0.43	0.50	-	0.66	0.68	0.52	0.43
At	0.60	0.44	0.52	0.66	-	0.72	0.50	0.36
Lsp 1	0.61	0.53	0.68	0.68	0.72	-	0.49	0.37
Er	0.55	0.57	0.52	0.52	0.50	0.49	-	0.61
Et	0.63	0.62	0.40	0.43	0.36	0.37	0.61	-
Mean	0.61	0.59	0.56	0.52	0.54	0.58	0.54	0.49
±SE	0.04	0.04	0.04	0.04	0.05	0.05	0.02	0.04
(B)	Cc	Gc	Lm/v	Aj	At	Lsp 1	Er	Et
Cc	-	0.50	0.59	0.30	0.49	0.46	0.28	0.28
Gc	0.50	-	0.54	0.26	0.28	0.43	0.21	0.21
Lm/v	0.59	0.54	-	0.31	0.36	0.55	0.25	0.25
Aj	0.30	0.26	0.31	-	0.49	0.41	0.21	0.20
At	0.49	0.28	0.36	0.49	-	0.50	0.50	0.14
Lsp 1	0.46	0.43	0.55	0.41	0.50	-	0.21	0.21
Er	0.28	0.21	0.25	0.21	0.50	0.21	-	0.57
Et	0.28	0.21	0.25	0.20	0.14	0.21	0.57	-
Mean	0.41	0.35	0.41	0.31	0.39	0.40	0.32	0.27
±SE	0.05	0.05	0.05	0.04	0.06	0.05	0.06	0.06

mean = 0.36 ± 0.03 SE) for prey grouped at the level of family (Table 3B).

Although the analysis of diet overlap at the prey order level (Table 3) appeared to indicate some degree of similarity of feeding niches between some species pairs (e.g. between *C. caroli* and *G. cancriformis*, *G. cancriformis* and *L. mariana/venusta*, or the Linyphiidae sp.1 and *A. tesselata*), no complete overlap was detected. In all cases, the calculated chi-square greatly exceeded the critical value at P = 0.001, and this result was even stronger for prey grouped at the level of family. However, given either type of prey grouping (orders or families), intermediate levels of overlap were observed between the two ant species (C = 0.61 and 0.57 respectively) on one hand, and between the six spider species (mean C = 0.60 ± 0.03 SE and 0.43 ± 0.03 SE respectively) on the other hand, indicating some degree of similarity within each category of predators. Diet overlap between ant and spider species was moderately

lower (mean C = 0.50 ± 0.03 SE for prey grouped at the level of order and 0.24 ± 0.03 SE for prey grouped at the level of family). Moreover, as already noted in the comparison of spider diet breadth, the comparison of these species feeding niches indicated that spiders that used similar types of webs had more similar diets. The two araneids and the tetragnathid species which spin orb–webs had high indices of diet overlap (mean C = 0.71 ± 0.05 SE and 0.54 ± 0.03 SE respectively according to the prey order/family level), as did the two theridiids and the linyphiid species (mean C = 0.69 ± 0.02 SE and 0.47 ± 0.03 SE respectively) which spin space–webs. This contrasts with lower overlap values for species pairs using different types of webs (mean C = 0.53 ± 0.03 SE and 0.38 ± 0.03 SE respectively).

For each of the eight predators, the bulk of the prey (56.8% to 90.3%) belonged to the four most abundant orders of insects associated with Neotropical coffee (Morón & López 1985; Ibarra-Núñez 1990): Hymenoptera (13.7% to 52.5%), Diptera (4.7% to 49.7%), Homoptera (2.0% to 28.8%), and Coleoptera (2.0% to 10.3%) (Table 3). At a more specific level, other important prey items included Thysanoptera for *C. caroli*, *A. tesselata* and the Linyphiidae sp. 1, Collembola for *A. jucundus*, Cryptostigmata and Psocoptera for the Linyphiidae sp. 1, Isoptera for *E. tuberculatum*, Lepidoptera for *E. ruidum* and Halotaxida for both *Ectatomma* species.

The families that suffered the highest percentages of predation (Table 4) were: Formicidae (Hymenoptera, 16.6% of all 4,334 collected prey), Cecidomyiidae (Diptera, 6.3%), Lumbricidae (Halotaxida, 4.0%), Aphididae (Homoptera, 3.9%), and Thripidae (Thysanoptera, 3.9%). Some families were predated by seven of the eight predators (Appendix 1), namely Cixiidae (Homoptera), Phlaeothripidae (Thysanoptera), Cecidomyiidae and Chironomidae (Diptera), whereas Diaspididae (Homoptera), Thripidae (Thysanoptera), Scolytidae (Coleoptera) and Sciaridae (Diptera) were captured by all six spider predators. The Formicidae (Hymenoptera) and Cicadellidae (Homoptera) were the only families consistently preyed upon by all eight predators.

Prey selectivity and predatory impact

On the basis of the analysis of 101,326 arthropods collected in coffee plantations (Ibarra-Núñez *et al.* 1995, unpublished data), which served as the reference for prey availability in coffee agroecosystems of the study region, each predator species showed a specific response to prey availability determined by Ivlev's index of electivity (IE) (Table 5). Considering only those prey orders consistently present (*i.e.* those with a frequency higher than 0.5 %), the three orb weavers showed a marked

Table 4. Main prey families (> 5% within one predator diet) predated upon by each predator species and their relative frequency (%) in the diet. When present at a frequency lower then 5%, families are reported as (+), and as (-) when totally absent.

Prey Orders	*C. caroli*	*G. cancriformis*	*L. mar./ven.*	*A. jucundus*	*A. tesselata*	Lin. sp. 1	*E.ruidum*	*E.tuberculatum*	Total[1]
Fomicidae (Hym.)	13.3	10.4	15.6	9.9	8.2	9.1	26.4	47.0	16.6
Cecidomyiidae (Dip.)	+	6.9	17.3	+	+	10.3	+	-	6.3
Thripidae (Thys.)	12.5	+	+	+	17.8	+	-	-	3.9
Lumbricidae (Halo.)	-	-	-	-	-	-	17.9	7.1	4.0
Aphididae (Hom.)	+	-	+	5.4	9.6	8.3	-	-	3.9
Entomobryidae (Coll.)	+	-	+	12.2	-	+	-	-	1.3
Cicadellidae (Hom.)	+	+	+	11.7	+	+	+	+	2.1
Termitidae (Isop.)	-	-	-	-	-	+	+	9.1	0.8
Chironomidae (Dip.)	+	+	8.2	+	+	+	+	-	2.3
Ptiliidae (Coleop.)	+	5.3	+	-	-	+	-	-	0.6
Sciaridae (Dip.)	+	+	5.1	+	+	+	-	-	1.5
No. prey records	*487*	*318*	*294*	*222*	*146*	*1684*	*819*	*364*	*4334*

[1]This total takes into account all the prey caught by each predator, even if their respective frequency in the diet is less than 5% and if the corresponding value does not appear in this table.

Table 5. Absolute (Aa) and relative (%a) abundance of potential prey orders, and the corresponding electivity index for six spider species and *E. tuberculatum* (*E. ruidum* not considered). For each predator species, the number of orders over–predated *vs.* under–predated are given in the last line.

Order	Aa	%a	*C. caroli*	*G. cancriformis*	*L. mar./ven.*	*A. jucundus*	*A. tesselata*	Lin. sp. 1	*E.tuberculatum*
Hymenoptera	23934	23.62	0.33	0.34	0.02	-0.05	-0.24	-0.07	0.42
Homoptera	19778	19.52	-0.78	-0.75	-0.49	0.21	0.02	0.04	-0.71
Collembola	17384	17.16	-0.95	-1.00	-0.88	-0.15	-1.00	-0.82	-1.00
Diptera	10463	10.33	0.39	0.58	0.67	-0.13	0.23	0.43	-0.33
Araneae	8844	8.73	-0.68	-0.92	-1.00	-0.72	-0.60	-0.63	-0.52
Acarida	5737	5.66	-0.65	-1.00	-0.52	-0.05	0.01	0.25	-1.00
Coleoptera	5441	5.37	-0.03	0.23	-0.25	0.29	0.24	-0.44	0.09
Orthoptera	2493	2.46	-1.00	-1.00	-0.55	-0.45	-0.26	-0.63	0.38
Thysanoptera	2474	2.44	0.73	-0.41	0.23	-0.02	0.82	0.41	-0.60
Psocoptera	2258	2.23	-0.02	-0.73	0.23	0.35	0.13	0.56	-0.57
Lepidoptera	1692	1.67	-0.75	-0.66	-0.08	-0.28	-0.39	-0.17	0.12
Hemiptera	591	0.58	-0.10	-1.00	0.10	0.60	0.43	0.31	0.68
With less than 0.5%a									
Neuroptera	216	0.21	0.06	-1.00	-1.00	0.37	0.55	0.45	0.48
Opilionida	6	0.01	-1.00	-1.00	-1.00	-1.00	-1.00	0.83	0.99
Embioptera	5	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Dermaptera	3	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.95	-1.00
Ephemeroptera	2	0.00	-1.00	-1.00	0.99	-1.00	-1.00	-1.00	-1.00
Pseudoscorpionida	2	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.99
Strepsiptera	2	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Siphonaptera	1	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Isoptera	0.01[1]	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Trichoptera	0.01[1]	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Total: 22 orders	101326	100.00	3/15	2/19	2/14	4/10	3/12	9/9	7/13

[1]In order to calculate all electivity index values, the absolute abundance of orders captured by any predator but not found in the sampling of potential prey orders was recorded with an arbitrary value of 0.01 (see Nyffeler & Strerling 1994)

positive electivity (IE = 0.31) for Diptera, Hymenoptera (*G. cancriformis* and *C. caroli*) and Thysanoptera (*C. caroli*). The three space-web weavers were characterized by a conspicuous positive electivity for Hemiptera, Psocoptera (*A. jucundus* and the Linyphiidae sp.1), Thysanoptera (*A. tesselata* and the Linyphiidae sp.1), and Diptera (the Linyphiidae sp.1). For *E. tuberculatum*, clearly positive electivity was observed for Hemiptera, Hymenoptera and Orthoptera.

Taking into account the overall effect of the six spider species and of *E. tuberculatum* on the coffee plant arthropods (Fig. 1), these predators showed a negative electivity (IE ≤ -0.31) for Collembola, Aranaea and Orthoptera, a positive electivity for Thysanoptera, Diptera, Psocoptera and Hemiptera, and an apparently passive prey selection (Ivlev's values ranging from -0.30 to +0.30) for Acarida, Coleoptera, Hymenoptera, Homoptera and Lepidoptera, that reflected the availability of these prey taxa in the environment.

Considering the Ivlev's index for the predated families of the two quantitatively most abundant orders, Hymenoptera and Homoptera, that were also important as parasitoids and polyphages (Hymenoptera) or herbivores (Homoptera), each predator showed a specific response to prey availability (Table 6). For each predator species, there were more families under-predated (IE ≤ -0.31) than over-predated (IE ≥ 0.31) in both prey orders. This was also the case for the Hymenoptera when the seven predators were considered as a whole (33 families: 11 over-

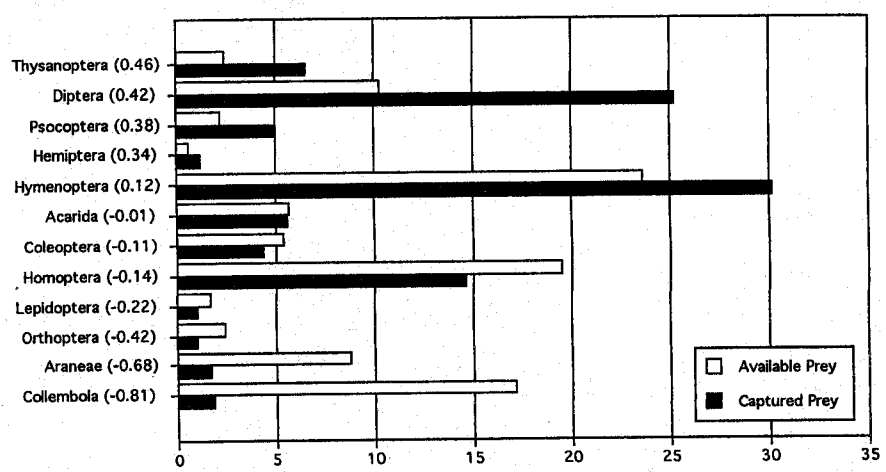

Fig. 1: Relative frequency of available and captured prey orders, with their corresponding value of the Ivlev's index of electivity. Only orders with a frequency > 5% in the biotope were considered. Due to the sampling technique used, only available prey present on coffee plants were considered and *E. ruidum*, which concentrates its foraging activity on the leaf litter, was not considered in the comparison of prey selectivity.

Table 6. Absolute (Aa) and relative (%a) abundance of potential prey families in the orders Homoptera and Hymenoptera, and the corresponding electivity index for each of six spider species and E. *tuberculatum (E. ruidum* not considered) and for all predators taken as a whole. For each predator species, the number of orders over–predated *vs.* under–predated are given in the last line.

Homoptera	Aa	%a	C. *caroli*	*G. cancriformis*	*L. mar.lven.*	*A. jucundus*	*A. tesselata*	Lin. sp.I	E. *tuberculatum*	Total
Diaspididae	12548	63.45	-0.52	-0.38	-0.69	-0.95	-0.88	-0.81	-1.00	-0.81
Coccidae	2052	10.38	-1.00	-1.00	0.26	-0.01	0.21	-0.18	-1.00	-0.12
Aphididae	1743	8.81	0.55	-1.00	-0.20	0.40	0.73	0.68	-1.00	0.63
Cicadellidae	1618	8.18	0.42	0.55	0.37	0.69	-0.34	0.21	0.74	0.38
Issidae	1063	5.38	0.58	-1.00	0.53	-1.00	-1.00	0.13	0.67	0.11
Tropiduchidae	156	0.79	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Cixiidae	110	0.56	0.89	0.93	0.91	0.90	0.87	0.28	-1.00	0.72
Delphacidae	109	0.55	-1.00	-1.00	0.83	-1.00	0.76	-1.00	-1.00	-0.09
Pseudococcidae	95	0.48	-1.00	-1.00	-1.00	0.56	-1.00	0.16	-1.00	0.18
Aleyrodidae	75	0.38	-1.00	0.95	-1.00	-1.00	-1.00	0.83	-1.00	0.78
Psyllidae	50	0.25	-1.00	0.97	-1.00	0.91	0.94	0.96	-1.00	0.95
Cercopidae	47	0.24	-1.00	-1.00	-1.00	0.75	-1.00	-1.00	0.95	0.32
Flatidae	31	0.16	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.97	0.19
Membracidae	21	0.11	-1.00	-1.00	-1.00	0.88	-1.00	0.90	-1.00	0.88
Derbidae	15	0.08	-1.00	-1.00	-1.00	-1.00	-1.00	0.86	-1.00	0.80
Ortheziidae	13	0.07	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Nogodinidae	12	0.06	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Margarodidae	7	0.04	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Achilidae	4	0.02	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Eriosomatidae	4	0.02	-1.00	-1.00	0.99	-1.00	-1.00	-1.00	-1.00	0.84
Dictyopharidae	3	0.02	-1.00	-1.00	0.99	-1.00	-1.00	-1.00	-1.00	0.88
Cicadidae	0.01[1]	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Total: 22 families										
	19776	100.00	4 / 18	4 / 18	6 / 14	8 / 13	4 / 17	5 / 12	4 / 18	11 / 6

[1]In order to calculate all electivity index values, the absolute abundance of orders captured by any predator but not found in the sampling of potential prey orders was recorded with an arbitrary value of 0.01 (see Nyffeler & Sterling 1994).

Table 6. cont.

Hymenoptera	Aa	%a	C. *caroli*	*G. cancriformis*	*L. mar.lven.*	*A. jucundus*	*A. tesselata*	Lin. sp.I	E. *tuberculatum*	Total
Formicidae	18940	79.48	-0.09	-0.35	0.00	-0.07	-0.06	-0.06	0.06	-0.05
Platygasteridae	945	3.97	0.21	0.61	-0.07	-1.00	0.19	-0.48	-1.00	-0.03
Ceraphronidae	767	3.22	-1.00	0.29	-0.30	0.32	0.57	0.49	-1.00	0.15
Braconidae	544	2.28	-1.00	-0.33	-1.00	0.16	0.44	-0.66	-1.00	-0.60
Eulophidae	460	1.93	0.52	0.57	0.46	-1.00	-1.00	-0.35	-1.00	0.12
Encyrtidae	453	1.90	0.04	0.42	-0.05	-1.00	-1.00	0.10	-1.00	-0.05
Pteromalidae	347	1.46	-1.00	-1.00	-1.00	0.36	-1.00	-1.00	-1.00	-0.82
Mymaridae	320	1.34	0.50	0.72	0.12	-1.00	-1.00	0.55	-1.00	0.40
Trichogram-matidae	207	0.87	0.65	0.46	0.33	0.56	-1.00	0.69	-1.00	0.50
Aphelinidae	180	0.76	-1.00	0.21	-1.00	-1.00	-1.00	-1.00	-1.00	-0.68
Scelionidae	134	0.56	-1.00	0.72	-1.00	-1.00	-1.00	-0.09	-1.00	0.01
Diapriidae	103	0.43	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Cynipidae	84	0.35	-1.00	0.89	-1.00	-1.00	-1.00	-1.00	0.20	0.42
Ichneumonidae	55	0.23	-1.00	0.67	0.76	0.86	-1.00	-1.00	-1.00	0.30
Eupelmidae	48	0.20	0.82	-1.00	-1.00	-1.00	-1.00	0.64	-1.00	0.48
Signiphoridae	42	0.18	-1.00	-1.00	-1.00	0.95	-1.00	0.78	-1.00	0.61
Bethylidae	34	0.14	0.87	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.34
Apidae	26	0.11	-1.00	0.83	0.88	0.93	-1.00	0.62	0.98	0.93
Eurytomidae	24	0.10	0.91	0.92	-1.00	-1.00	-1.00	0.80	-1.00	0.79
Perilampidae	22	0.09	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Vespidae	22	0.09	-1.00	-1.00	-1.00	0.94	-1.00	-1.00	0.70	0.51
Tetracampidae	18	0.08	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Agaonidae	12	0.05	0.98	0.92	0.94	-1.00	0.98	0.90	-1.00	0.93
Dryinidae	10	0.04	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Chalcididae	9	0.04	0.93	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	0.58
Sphecidae	9	0.04	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00

Table 6. Continued on next page.

Table 6. Cont.

Hymenoptera	Aa	%a	C. *caroli*	G. *cancriformis*	L. *mar.lven.*	A. *jucundus*	A. *tesselata*	Lin. sp.l	E. *tuberculatum*	Total
Pompilidae	4	0.02	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Torymidae	4	0.02	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Eucharitidae	2	0.01	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Mutilidae	2	0.01	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Tiphiidae	2	0.01	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Halictidae	1	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Rhopalosomatidae	1	0.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Total: 33 families										
	23831	100.00	8 / 22	11 / 20	5 / 23	7 / 24	3 / 28	8 / 22	2 / 29	11 / 15

predated, 15 under–predated and 7 predated according to their availability). The situation was reversed, however, for the Homoptera, with more families conspicuously over-predated than under–predated (22 families: 11 over–predated, only 6 under–predated and 5 predated according to their availability). Considered as a whole, the predators in this study showed a trend of positive electivity for Homoptera and a trend of negative electivity for the parasitic Hymenoptera. Moreover, the relation between the frequency of prey capture and the relative abundance of the prey families in the biotope was higher for Hymenoptera than for Homoptera. The 8 most important hymenopteran families (each one accounting for more than 1% of all 23,831 available hymenopteran insects) reported from coffee plantations in the study area (cf. Table 6) were: Formicidae, Platygasteridae, Ceraphronidae, Braconidae, Eulophidae, Encyrtidae, Pteromalidae and Mymaridae, representing 95.6% of all the determined hymenopteran items collected by D-Vac sampling coffee plants. Our data indicated that 5 of these (Formicidae, Platygasteridae, Ceraphronidae, Eulophidae and Encyrtidae), accounting for 84.3% of the 696 determined hymenopteran prey captured by these predators (*E. ruidum* not considered, see material and methods), were captured according to their relative abundance in coffee agroecosystems. In contrast, of the 5 most important homopteran families (each one accounting for more than 1% of all 19,776 available homopteran insects):

Diaspididae, Coccidae, Aphididae, Cicadellidae and Issidae, representing 96.2% of all the determined homopteran items available, only 2 (Coccidae and Issidae), accounting for only 14.8% of the 431 determined homopteran prey captured by the six spider species and *E. tuberculatum*, were caught according to their relative abundance. Whereas the family Diaspididae was the most abundant as potential homopteran prey, it was significantly underpredated (IE = -0.81), probably because juveniles and adult females are sessile and well protected by bodily secretions and only adult males, that are winged, are available as prey to web–building spiders.

Each of the 159 identified families was ascribed to a trophic category, with the exception of three dipteran families (Asteiidae, Diastatidae and Sinneuridae) and the two undetermined families of Astigmata and Mesostigmata, whose feeding habits are unknown (Appendix 1). The calculation of the Ivlev's index for the trophic groups again indicated (Table 7) differences among the seven predator species (*E. ruidum* being excluded). Nevertheless, taken as a whole, these predators showed a positive electivity for the nectarivores, a negative electivity for the predators and an apparent passive electivity for all other trophic categories which were quantitatively predated according to their relative abundance.

Considering the total prey recovered, *i.e.* the overall diet of the predator community, prey diversity (expressed as the number of families preyed upon within each trophic category) was greatest among herbivores and detritivores, and lowest among polyphages, nectarivores, and abstainers (Table 8). However, in terms of quantity of prey recovered for each predator species (expressed as the number of prey items captured), polyphagous arthropods along with herbivores and detritivores, constituted the major part of the captured prey (64.0%), while other trophic categories (parasitoids, predators, nectarivores, and abstainers) clearly suffered lower predation (Table 8). The strong predation upon polyphage, herbivore and detritivore arthropods is even more evident (85.0%) if we do not take into account the large proportion of prey specimens not identified at family level, for which it was not possible to determine their feeding habits.

With the exception of *G. cancriformis*, which showed an appreciable degree of predation of parasitoids, the impact on polyphage, herbivore and detritivore arthropods was confirmed at the level of each predator species. The predation rate upon this type of prey fluctuated between 43.1% of all the collected prey (for *C. caroli*) to 81.6% (for *E. tuberculatum*). However, the apparently greater predatory impact of ponerine ants upon this kind of prey was probably an artifact linked to the variability

Table 7. Absolute (Aa) and relative (%a) abundance of potential prey trophic categories, and the corresponding electivity index for each of the six spider species and *E. tuberculatum* (*E. ruidum* not considered) and for all predators taken together (Total).

Trophic categories	Aa	%a	*C. caroli*	*G. cancriformis*	*L. mar./ven.*	*A. jucundus*	*A. tesselata*	Lin. sp.1	*E. tuberculatum*	Total
Herbivores	31363	31.32	0.09	-0.03	0.12	0.17	0.27	0.20	-0.44	0.12
Detritivores	28476	28.43	-0.30	-0.22	-0.17	0.01	-0.12	-0.01	-0.12	-0.08
Polyphages	21268	21.24	0.05	-0.12	-0.03	-0.26	-0.35	-0.28	0.43	-0.04
Predators	10926	10.91	-0.40	-0.83	-0.92	-0.09	-0.29	-0.46	-0.37	-0.45
Parasitoids	5820	5.81	0.32	0.65	0.11	-0.13	-0.06	0.01	-0.66	0.13
Abstainers	2099	2.10	0.58	0.49	0.67	-0.58	-0.42	0.17	-1.00	0.28
Nectarivores	197	0.20	-1.00	0.44	0.79	0.48	0.63	-0.12	0.93	0.69

in the number of prey with unknown feeding habits. This number varied according to the predator species (from 7.4% for *E. tuberculatum* to 43.3% for *C. caroli*), due to the habit of various spiders to crush their prey prior to consumption, which made their identification more difficult. Taking into account only the prey with known feeding habits, the predatory impact of both groups of predators on recognized or potential insect pests was very similar: 82.9% for the web–building spiders against 89.9% for the ponerine ants.

DISCUSSION

As generalist predators, most ants and spiders have been reported feeding on a wide range of prey (Nentwig 1987, Hölldobler & Wilson 1990, Wise 1993). This was confirmed by the prey diversity identified in the diet of the eight studied predators, ranging from 40 to 84 families depending on the predator in question. Not all these predators, however, showed an equal capacity for subduing prey and each predator's diet showed a specific combination of prey orders. Nentwig (1987) stated that the differences in prey spectrum among web-building spiders are essentially linked to differences in their web structure, to the presence or not of an attack-wrap behavior which enables them to immobilize prey without direct contact, and to the possible use of cooperative hunting in social species. As a consequence, araneids, tetragnathids and theridiids, which build relative large webs, can include in their prey spectrum larger prey than the linyphiid species for which an important proportion of its diet comprised small prey such as Diptera, Homoptera, Thysanoptera, Cryptostigmata and Psocoptera. Neverthe-

Table 8. Diet distribution (%), for each predator species, according to the feeding habits of the prey. The values between parenthesis correspond to the corrected percentages relative to the total number of collected prey with known feeding habits (see text for detailed explanation).

Feeding habits categories	Families concerned	C. *caroli*	G. *cancriformis*	L. *mar.lven.*	A. *jucundus*	A. *tesselata*	Lin. sp.I	E. *ruidum*	E. *tuberculatum*	Global
Herbivores	46	21.1 (37.3)		18.2 (29.6)	31.3 (39.5)		35.1 (44.1)	43.8 (54.7)		3 6 . 3
(47.1) 17.8 (23.2)		11.3 (12.2)		27.5 (36.6)						
Polyphages	5	13.3 (23.6)	10.4 (16.8)	16.0 (20.2)	9.9 (12.4)	8.2 (10.3)	9.2 (11.9)	27.5 (35.7)	49.5 (53.4)	17.1 (22.6)
Detritivores	47	8.6 (15.2)	11.3 (18.4)	16.0 (20.2)	23.0 (28.8)	17.8 (22.2)	21.5 (27.9)	24.5 (31.9)	20.9 (22.6)	19.4 (25.8)
Sub-total [1]	98	43.1 (76.1)	39.9 (64.8)	63.3 (79.8)	68.0 (85.3)	69.9 (87.2)	67.0 (87.0)	69.8 (90.8)	81.6 (88.1)	64.0 (85.0)
Parasitoids	21	6.4 (11.2)	17.0 (27.6)	5.8 (7.3)	3.6 (4.5)	4.1 (5.1)	4.6 (5.9)	0.4 (0.5)	1.1 (1.2)	4.6 (6.1)
Predators	28	2.7 (4.7)	0.6 (1.0)	0.3 (0.4)	7.2 (9.0)	4.8 (6.0)	3.1 (4.0)	5.1 (6.7)	4.7 (5.0)	3.5 (4.6)
Abstainers	3	4.5 (8.0)	3.8 (6.1)	8.5 (10.7)	0.5 (0.6)	0.7 (0.9)	2.3 (2.9)	0.1 (0.2)	0.00 (0.00)	2.3 (3.1)
Nectarivores	4	0.00 (0.00)	0.3 (0.5)	1.4 (1.7)	0.5 (0.6)	0.7 (0.9)	0.1 (0.2)	1.5 (1.9)	5.2 (5.6)	0.9 (1.2)
Unknown[2]	3	43.3	38.4	20.7	20.3	19.9	22.9	23.1	7.4	24.7
No. prey records	*159*	*487*	*318*	*294*	*222*	*146*	*1684*	*819*	*364*	*4334*

[1]This sub-total takes into account all the prey belonging to herbivore, polyphage and detritivores feeding categories. [2] he percent values associated to the prey with unknown feeding habits correspond to the three identified dipteran families with unknown feeding habits (Asteiidae, Diastatidae and Sinneuridae) and to unidentified prey families.

less, spider prey are often of small size, with an optimal prey length ranging from 50% to 120% of the spider length in the case of web-building spiders (Nentwig & Wissel 1986). Our data indicate that, contrary to various reports of frequent predation of large and difficult prey by orb weavers (Robinson & Robinson 1970, Uetz *et al.* 1978, Nyffeler & Benz 1978, Howell & Ellender 1984), small items are most commonly present in the diet of all the web-building spiders herein studied. This agrees with the observations of Shelly (1983, 1984) and Nentwig (1985) on araneids in Panama.

Compared to spiders, large insects (such as lepidopteran, bees and grasshoppers) contribute to a greater proportion of the diet of the two ponerine ants. These ants may also take other large prey such as opilions, chilopods, diplopods, dragonflies, large beetles (Chrysomelidae, Melolonthidae, Scarabaeidae), crustaceans, mollusks (snails, slugs) and annelids (earthworms). As for the web–building spiders, however, the major part of their diet comprises small prey items such as Hymenoptera (mostly ants), Diptera, Homoptera, small Coleoptera, Isoptera and small Halotaxida (less than 20mm in length). While the majority of ant species are expected to regularly prey upon large items, due to nestmate recruitment and cooperative prey retrieval, the workers of both ponerine species we studied are essentially solitary foragers (Lachaud *et al.* 1984, Valenzuela *et al.* 1995). As a consequence, recruitment and group retrieving scarcely occurred during hunting in *E. ruidum* (Lachaud 1985; Pratt 1989; Schatz *et al.* 1997) and are unknown in *E. tuberculatum* (Dejean & Lachaud 1992). Laboratory and field observations (Schatz *et al.* 1997) have indicated that the optimal weights and sizes of the prey collected by *E. ruidum* range from 4 to 20 mg in weight and from 7 to 15mm in length, *i.e.* from 50% to 250% the ant weight and from 100% to 200% the ant length, corresponding to the load an individual worker can manage on its own.

The main prey taxa for both classes of predators are: Hymenoptera, Diptera, Homoptera and Coleoptera, accounting for 56.8% to 90.3% of all the prey items collected. These orders correspond to the four most abundant orders of insects associated with coffee in the Soconusco region (Morón & López 1985; Ibarra-Núñez 1990; Ibarra-Núñez & García-Ballinas 1998) and, more generally, to Neotropical agroecosystems (see Janzen (1973) for Costa Rica and the Caribbean zone, and Nentwig (1985) for Panama). Coleoptera, Hymenoptera, Homoptera and Diptera were also the major insect orders captured by two orb-weavers, *Mecynogea lemniscata* and *Metepeira labyrinthea* (78.4% and 89.4% respectively), in forested areas of central Maryland in USA (Wise & Barata 1983). Nyffeler & Sterling (1994) reported similar pattern of prey

capture by nine species of common web-building spiders in cotton crops in the United States, where the most predated orders were Homoptera (44.4%), Hymenoptera (32.5%), Diptera (10.9%), and Coleoptera (8.6%).

The principal prey of our study species obviously reflect the habitats in which they live and forage: the soil and the branches of trees for the ants, whereas the spiders limit themselves to foliage inhabiting prey or small aerial prey. For generalist predators like ants or spiders, the frequency of relative predation on any prey, is generally proportional to their relative abundance (see Dejean, 1991, Wise 1993). In as far as the prey grouping level selected for data analysis was large enough (orders or trophic categories), our results confirmed the existence of such a proportional effect between the frequency of prey capture by the eight studied predators and the relative abundance of the prey families in the biotope. With a finer level of prey grouping (families), such a correlation was not so clear, perhaps due to the very low abundance of many families. Within the two quantitatively most abundant orders present in coffee agroecosystems, only 3 out of 33 hymenopteran families and 5 out of 22 homopteran families showed a relative abundance in the biotope (on the basis of all available prey) greater than 0.5%. Nevertheless, for the more abundant families, the agreement between the frequency of relative predation on a given prey and its relative abundance is also noteworthy. This is especially obvious with the Formicidae. Out of the 159 families involved in the global range of predated arthropods, 11 present a frequency of predation greater than 1% of all 4,334 collected prey and account for 44.1% of this total. Five of these 11 families (Chironomidae, Cecidomyiidae, Aphididae, Cicadellidae and Formicidae) have been reported representing 37.8% of the total potential prey associated with coffee orchards in the Soconusco region (Ibarra-Núñez 1990), and appear, from our results, as representing 31.1% of all recovered prey. Even if a large part of the predation is focused on Cecidomyiidae, Thripidae, Aphididae, Entomobryidae and Cicadellidae for the spiders, and on Lumbricidae and Termitidae for the ponerine ants, Formicidae were an important item in the diet of each one of the eight studied predators (8.22% to 46.98%) and this family, on its own, accounted for 16.6% of all collected prey. The major part of the ants caught in spiders' webs were winged sexual forms (*Crematogaster*, *Pseudomyrmex*, *Camponotus*). Ants caught by *E. ruidum* were essentially (84.3%) wingless workers (*Pheidole*, *Adelomyrmex*, *Camponotus*, *Paratrechina*) and those caught by the arboricolous *E. tuberculatum* were of both forms with more than a third part of winged sexual (*Camponotus*, *Crematogaster*, *Atta*). Almost all these ant genera are considered as more or less important pests or potential pests in

Neotropical agroecosystems (see Vinson 1986; Vander Meer *et al.* 1990; Williams 1994).

Virtually all species of generalist predators that prey on economically important pests also possess some potential disadvantages (Way & Khoo 1992; Nyffeler *et al.* 1994a) and their use in pest management must be weighed against possible negative effects such as predation upon beneficial insects and/or protection of some pests. The need for detailed studies on the predatory role and economic impact of spiders and ants in natural agroecosystems is well recognized (Whitcomb 1974; Finnegan 1974; Riechert & Lockley 1984; Carrol & Risch 1990; Way & Khoo 1992; Nyffeler *et al.* 1994a). There are, however, almost no data, at family level, concerning the type of prey trapped by each group of generalist predators. Only a few studies provide partial information on some of the arthropods families preyed upon by generalist spiders (Robinson & Robinson 1970; Nentwig 1980, 1985, 1987; Wise & Barata 1983; Nyffeler *et al.* 1989, 1994a, b; Nyffeler & Sterling 1994) or by generalist ants (Lévieux 1977; Risch & Carroll 1982; Dejean 1991; Dejean *et al.* 1993, 1999; Valenzuela *et al.* 1994, 1995). Among the prey captured by the eight predators in the present study, 1,243 (28.7% of all prey collected and 38.1% of all identified prey) corresponded to families containing species that have been reported as coffee pests in Latin America (1,202) or in other continents (41). On the other hand, only 390 (9.0% of all the prey and 11.9% of all identified prey) correspond to families that are beneficial as predators, parasitoids, or possible pollinators (150, 200 and 40 prey items, respectively). For both ants and spiders, herbivore, detritivore and polyphage arthropods, representing 81.0% of the potential determined prey collected on coffee plants (Table 7), constituted the major part of the prey caught (with a mean of 85.0% of all the determined prey captured) while nectarivores, abstainers, predators and parasitoids, representing 19.0% of the potential prey, only accounted for 15.0% of all the determined prey. With the exception of *G. cancriformis* and *E. tuberculatum*, for which the values are very similar, for each one of the other studied predators, the proportion of herbivore prey alone was always higher than the proportion of predators, parasitoids and nectarivores combined (between 1.6 and 4.3 times as large).

In the coffee plantations where this study was performed, the negative effects of both web-building spiders and ponerine ants on beneficial arthropods are clearly counteracted by their activity in killing numerous recognized or potential pest insects. It is noteworthy that, apart from damage due to the coffee berry borer *Hypothenemus hampei*, which was introduced to Mexico in 1978 (Baker 1984) and almost totally

lacks native predators (but see Pérez-Lachaud 1998), no other coffee pests are reported as important in the Soconusco region, even though some potential pests are known to be present (various species of scolytids, aphids, coccids and Lepidoptera). This absence of serious native coffee pests in the study area may be, at least in part, attributable to the collective predatory impact of the rich ant and spider fauna.

ACKNOWLEDGMENTS

This work was supported by the Mexican research programs no. 0574P-N and 28869-N from CONACyT. We are grateful to T. Williams for a critical reading of the manuscript and for improving the English text.

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Appendix 1. List of prey orders and families, and diet distribution (in number of prey items and percent of total prey items at the ordinal level) for the eight studied predators. For each prey family, the feeding habits are reported as well as their occurrence as potential coffee pests in Latin America (la) or other continents (oc). Abs: abstainer; Det: detritivore; Her: herbivore; Nec: nectarivore; Par: parasitoid; Pre: predator; Pol: polyphage; Unk: unknown feeding habits. Cc: *Cyclosa caroli*; Gc: *Gasteracantha cancriformis*; Lm/v: *Leucauge mariana/venusta*; Aj: *Anelosimus jucundus*; At: *Achaearanea tesselata*; Lsp1: undetermined Linyphiidae; Er: *Ectatomma ruidum*; Et: *E. tuberculatum*.

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
ARANEAE		1.44%	0.31%	0.00%	1.35%	2.05%	1.90%	2.56%	2.47%	76
9 (5.66%)										(1.75%)
Anyphaenidae	Pre						1			1
Araneidae	Pre					3				3
Clubionidae	Pre	1						1		2
Ctenidae	Pre							1	1	2
Dictynidae	Pre								1	1
Lycosidae	Pre							9		9
Pholcidae	Pre						3			3
Salticidae	Pre	2			3		14	5	2	26
Theridiidae	Pre						5	1		6
Unidentified	Pre	4	1				9	4	5	23
OPILIONIDA		0.00%	0.00%	0.00%	0.00%	0.00%	0.06%	0.49%	1.10%	9
3 (1.89%)										(0.21%)
Cosmetidae	Det-Pre								1	1
Phalangiidae	Det-Pre							3	3	6
Triaenonychidae	Det-Pre							1		1
Unidentified	Det-Pre						1			1
PSEUDOSCORPIONIDA		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.27%	1
1 (0.63%)										(0.02%)
Monosphyronida	Pre								1	1
ASTIGMATA		0.00%	0.00%	0.00%	0.45%	0.00%	0.00%	0.00%	0.00%	1
1 (0.63%)										(0.02%)
Unidentified	Unk				1					1
CRYPTOSTIGMATA		0.21%	0.00%	0.68%	2.25%	3.42%	7.90%	0.00%	0.00%	146
3 (1.89%)										(3.37%)
Camisiidae	Det			1						1
Ceratozetoidea	Det						14			14
Galumnidae	Det	1		1	1	5	2			10
Unidentified	Det				4		117			121

Appendix 1. Continued:

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
MESOSTIGMATA 1 (0.63%)		0.00%	0.00%	1.02%	0.45%	0.68%	0.83%	0.00%	0.00%	19
(0.44%)	Unidentified	Unk				3	1	1	14	
		19								
PROSTIGMATA 3 (1.89%)		0.82%	0.00%	0.00%	1.80%	1.37%	0.42%	0.00%	0.00%	17 (0.39%)
Bdellidae	Pre	3				1		1		5
Cunaxidae	Pre	1				1		1		3
Trombidiidae	Pre					2		2		4
Unidentified	Unk						2	3		5
GEOPHILOMORPHA 1 (0.63%)		0.00% (0.12%)	0.00%	0.00%	0.00%	0.00%	0.00%	0.61%	0.00%	5
Unidentified	Pre							5		5
SCUTIGEROMORPHA 2 1 (0.63%)		0.00%	0.00%	0.00% (0.05%)	0.00%	0.00%	0.00%	0.00%	0.55%	
Unidentified	Pre								2	2
DIPLOPODA 1 (0.63%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.85%	0.00%	7 (0.16%)
Polydesmidae	Det							7		7
COLLEMBOLA 2 (1.26%)		0.41%	0.00%	1.02%	12.16%	0.00%	1.66%	0.00%	0.00%	60 (1.38%)
Entomobryidae	Det	1			2	27		25		55
Sminthuridae	Det	1			1			3		5
THYSANURA 2 (1.26%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.24%	0.00%	2 (0.05%)
Lepismatidae	Det							1		1
Nicoletiidae	Det							1		1
EPHEMEROPTERA 1 (0.63%)		0.00%	0.00%	0.34%	0.00%	0.00%	0.00%	0.00%	0.00%	1 (0.02%)
Unidentified	Abs									1
ODONATA 1 (0.63%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.12%	0.00%	1 (0.02%)
Unidentified	Pre	1	1							

Appendix 1. Continued.

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
ORTHOPTERA 5 (3.14%)		0.00%	0.00%	0.68%	0.90%	1.37%	0.53%	1.59%	4.95%	46 (1.06%)
Acrididae	Her(oc)			1		1			3	5
Blattellidae	Pol							4	3	7
Gryllidae	Pol (la)			1			1	2	6	10
Tetrigidae	Her								2	2
Tettigonidae	Her (la)							2	2	4
Unidentified	Unk				2	1	8	5	2	18
ISOPTERA 1 (0.63%)		0.00%	0.00%	0.00%	0.45%	0.00%	0.06%	0.12%	9.07%	36 (0.83%)
Termitidae	Det (la)						1	1	33	35
Unidentified	Det				1					1
PSOCOPTERA 14 (8.81%)		1.85%	0.31%	3.40%	4.50%	2.74%	7.48%	0.00%	0.55%	162 (3.74%)
Amphipsocidae	Det	2	1				1			4
Archipsocidae	Det						5			5
Caeciliidae	Det	1		5			49		1	56
Ectopsocidae	Det	1		1	4		18			24
Epipsocidae	Det				1		6			7
Lachesillidae	Det	2		1			10			13
Lepidopsocidae	Det						1			1
Liposcelidae	Det	1		2	1	1				5
Mesopsocidae	Det					1	1			2
Pachytroctidae	Det						1			1
Polypsocidae	Det						1			1
Pseudocaeciliidae	Det						1			1
Psocidae	Det			1	2	2	7			12
Psyllipsocidae	Det								1	1
Unidentified	Det	2			2		25			29
DERMAPTERA 1 (0.63%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.12%	0.12%	0.00%	3 (0.07%)
Forficulidae	Det						2			2
Unidentified	Det							1		1
HEMIPTERA 8 (5.03%)		0.41%	0.00%	0.68%	2.25%	1.37%	1.07%	1.83%	2.75%	54 (1.25%)

Appendix 1. Continued:

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
HEMIPTERA Continued.										
Anthocoridae	Pre					1	3			4
Coreidae	Her (oc)								2	2
Cydnidae	Her							1	1	2
Lygaeidae	Her				1				2	3
Miridae	Her (oc)	1		2	1	1	1	1		7
Pentatomidae	Her (oc)							8	1	9
Reduviidae	Pre				2		1		2	5
Tingidae	Her (oc)						1	2		3
Unidentified	Unk	1			1		12	3	2	19
HOMOPTERA 17 (10.69%)		2.05%	2.52%	6.46%	28.83%	19.18%	20.31%	6.59%	3.02%	536 (12.37%)
Aleyrodidae	Her (la)		1				12			13
Aphididae	Her (la)	3		1	12	14	140			170
Cercopidae	Her (la)				1				1	2
Cicadellidae	Her (la)	2	2	3	26	1	38	11	6	89
Cicadidae	Her (la)				2			2		4
Cixiidae	Her	1	1	2	6	2	3	2		17
Coccidae	Her (la)			3	6	4	22			35
Delphacidae	Her			1		1				2
Derbidae	Her						3			3
Diaspididae	Her (la)	2	2	2	1	1	20			28
Dictyopharidae	Her			1						1
Eriosomatidae	Her			1						1
Flatidae	Her (oc)							1	1	2
Issidae	Her (la)	2		3			21	2	3	31
Membracidae	Her				1		6	30		37
Pseudococcidae	Her (la)				1		2			3
Psyllidae	Her		1		3	2	35	2		43
Unidentified	Her		1	2	5	3	40	4		55
THYSANOPTERA 3 (1.89%)		13.55%	0.94%	3.74%	2.25%	23.29%	5.58%	0.24%	0.55%	217 (5.01%)
Merothripidae	Det					1				1
Phlaeothripidae	Det	5	2		1	7	26	2	2	45
Thripidae	Her	61	1	11	4	26	66		1	69
Unidentified	Unk						2			2

Appendix 1. Cont.

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
NEUROPTERA 2 (1.26%)		0.21%	0.00%	0.00%	0.45%	0.68%	0.53%	0.00%	0.55%	14 (0.32%)
Chrysopidae	Pre	1					9		2	12
Hemerobiidae	Pre				1					1
Unidentified	Pre					1				1
COLEOPTERA 18 (11.32%)		4.31%	7.86%	3.06%	9.46%	8.22%	2.02%	10.26%	5.77%	227 (5.24%)
Anthicidae	Pol						1			1
Brentidae	Her							1		1
Buprestidae	Her (oc)							1		1
Chrysomelidae	Her (la)				1		1	9	9	20
Coccinellidae	Pre				3					3
Cucujidae	Pre				2	1	1			4
Curculionidae	Her (la)						1	5		6
Elateridae	Her				1		1	1		3
Lampyridae	Pre							1		1
Lathridiidae	Det				2	3	6			11
Melolonthidae	Her (la)							1		1
Platypodidae	Det		1							1
Ptiliidae	Det	4	17	5			1			27
Scarabaeidae	Det							10	4	14
Scolytidae	Her (la)	10	4	1	1	1	5			22
Scydmaenidae	Det			1						1
Staphylinidae	Pre						1	7		8
Tenebrionidae	Her (oc)							2		2
Unidentified	Unk	7	3	2	11	7	16	46	8	100
TRICHOPTERA 1 (0.63%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.06%	0.00%	0.00%	1 (0.02%)
Unidentified	Abs						1			1
LEPIDOPTERA 2 (1.26%)		0.21%	0.31%	1.36%	0.90%	0.68%	1.13%	5.37%	1.92%	79 (1.82%)
Pyralidae	Her (oc)							1		1
Frenatae	Her							2		2
Unidentified	Her	1	1	4	2	1	19	41	7	76

Appendix 1. Continued:

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
HYMENOPTERA		40.04%	43.71%	23.47%	20.72%	13.70%	19.77%	29.30%	52.47%	1233
22 (13.84%)										(28.45%)
Agaonidae	Her	4	1	1		1	2			9
Aphelinidae	Par		1							1
Apidae	Nec		1	1	1		1	6	17	27
Bethylidae	Par	2								2
Braconidae	Par		1		1	1	1			4
Ceraphronidae	Par		5	1	2	2	20			30
Chalcididae	Par	1								1
Cynipidae	Her		5						1	6
Encyrtidae	Par	2	4	1			5	1		13
Eucharitidae	Par							1		1
Eulophidae	Par	6	6	3			2			17
Eupelmidae	Par	2					2			4
Eurytomidae	Par	2	2				2			6
Formicidae	Pol (la)	65	33	46	22	12	153	216	171	718
Ichneumonidae	Par		1	1	1			1		4
Mymaridae	Par	4	7	1			10			22
Platygasteridae	Par	6	14	2		1	3			26
Pteromalidae	Par				1					1
Scelionidae	Par		3				1			4
Signiphoridae	Par				2		3			5
Trichogram-matidae	Par	4	2	1	1		10			18
Vespidae	Pre				1			7	1	9
Unidentified	Unk	97	53	11	14	3	118	8	1	305
DIPTERA		20.33%	36.16%	49.66%	7.66%	15.75%	24.58%	13.55%	4.67%	942
31 (19.50%)										(21.74%)
Agromyzidae	Her (oc)		8							8
Anisopodidae	Det			1						1
Asteiidae	Unk			2						2
Bibionidae	Nec							1		1
Calliphoridae	Det								1	1
Cecidomyiidae	Her	16	22	51	3	5	173	1		271
Ceratopogonidae	Par	1	4	6		2	10		1	24
Chamaemyiidae	Pre					1				1
Chironomidae	Abs	22	12	24	1	1	37	1		98
Chloropidae	Her		5	2				1		8
Culicidae	Par						8		3	11
Diastatidae	Unk			1		1				2
Dolichopodidae	Pre		1	1						2
Drosophilidae	Det			2		1		2		5

Appendix 1. Continued.

ORDER No. families (% total no. families) Family	Feeding habits	*Cc*	*Gc*	*Lm/v*	*Aj*	*At*	Lsp1	*Er*	*Et.*	No. prey items / Order
DIPTERA Continued.										
Empididae	Pre	1					1			2
Ephydridae	Her		3							3
Muscidae	Det		2				2	3	2	9
Mycetophilidae	Det	2		3			1			6
Phoridae	Det		2	4			3		1	10
Piophilidae	Det								1	1
Pipunculidae	Par	1								1
Psychodidae	Det	1			1	3	9			14
Scatopsidae	Det		2			1	1			4
Sciaridae	Det	18	7	15	4	1	21			66
Simuliidae	Par		4	1						5
Sinneuridae	Unk		1							1
Sphaeroceridae	Det		2	1			1			4
Stratiomyidae	Nec						1	2	1	4
Syrphidae	Pol							3		3
Tephritidae	Her (la)							8		8
Tipulidae	Nec			3		1		3	1	8
Unidentified	Unk	37	40	29	8	6	146	86	6	358
UNIDENTIFIED INSECTS		14.17%	7.86%	4.42%	3.15%	5.48%	3.98%	5.01%	2.20%	238 (5.49%)
Unidentified	Unk	69	25	13	7	8	67	41	8	238
ISOPODA 1 (0.63%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	2.69%	0.00%	22 (0.51%)
Oniscidae	Det							22		22
PULMONATA 2 (1.26%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.49%	0.00%	4 (0.09%)
Slugs	Her (oc)							1		1
Snails	Her (la)							3		3
HALOTAXIDA 1 (0.63%)		0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	17.95%	7.14%	173 (3.99%)
Lumbricidae	Det							147	26	173
TOTAL NO. FAMILIES 159		43	42	53	50	40	84	61	42	4334 100.00%
TOTAL NO. ORDERS 30		13	8	13	17	14	19	19	16	