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PREY SELECTION OF SPIDERS IN THE FIELD

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ABSTRACT. In this article, an overview of the general feeding patterns of common agroecosystem spiders is presented. Five groups of web-weavers (Tetragnathidae, Araneidae, Theridiidae, Linyphiidae, Dictynidae) and five groups of hunters (small-sized Oxyopidae, large-sized Oxyopidae, Thomisidae, Salticidae, Lycosidae) are analyzed comparatively (based on 40 prey analyses previously published by various European and US authors). Fewer than 10 insect orders, as well as the order Araneae, make up the bulk of the prey of these spiders. Web-weavers and hunters both basically feed on the same prey orders, but in different proportions. The observed differences reflect in part the very diverse range of life styles and foraging modes exhibited by the various spider groups and, to some extent, differences in prey availability. Web-weavers are almost strictly insectivorous (insects constituting $> 99\%$ of total prey). Hunters, however, exhibit a mixed strategy of insectivorous and araneophagic foraging patterns (insects constituting $\approx$75–90% of total prey). Diet breadth computed with the Inverted Simpson Index was, on average, significantly higher in the hunting spiders than the web spiders. There seems to be a consistent trend of greater diet breadth of the hunters compared to the web-weavers in agroecosystems. Overall, spider individuals of small size (including large percentages of immatures) numerically dominate the faunas of field crops, and these feed primarily on tiny prey ($<$ 4 mm in length).

Information on how prey selection in the field operates is a prerequisite to a quantitative assessment of the spiders' potential as biological control agents in agroecosystems. Prey selection has been defined by Hassell (1978) as follows: ''Preference for a particular prey is normally measured in terms of the deviation of the proportion of that prey attacked from the proportion available in the environment.'' Most authors who studied the prey of spiders failed to record the availability of potential prey in the environment probably due to technical difficulties. Thus, corresponding data on the actual and potential prey are scarce; and, consequently, only a limited number of prey selection studies on spiders following Hassell's approach exist (e.g., Uetz et al. 1978).

Another approach to searching for patterns of prey selection is to analyze a large set of data on the actual prey of different spider groups (with very differing life styles and foraging modes) and to compare the degree to which utilization of the various prey taxa differs. Numerous published field studies on the actual prey of spiders are available for such an investigation (see reviews by Nyffeler 1982; Nentwig 1987; Riechert & Harp 1987; Wise 1993; Nyffeler el al. 1994a, b). In the current investigation, five groups of web-weavers (Tetragnathidae, Araneidae, Theridiidae, Linyphiidae, Dictynidae) and five groups of hunters (small-sized Oxyopidae [i.e., *Oxyopes salticus*], large-sized Oxyopidae [i.e., *Peucetia viridans*], Thomisidae, Salticidae, Lycosidae), representing nine families, are analyzed comparatively. These selected groups are among the most common spider predators in agroecosystems (Nyffeler et al. 1994b) and, thus, are of particular interest from the point of view of biological control. Descriptions of the life styles and foraging modes of these 10 spider groups are given by Rypstra (1982), Nentwig (1987), Wise (1993), and Nyffeler et al. (1994a, b).

METHODS

For each of the 10 spider groups the relative taxonomic composition of the diets (mean $\pm$ SE of 4 different prey analyses) was assessed (Tables 2, 3). Overall, 40 different prey analyses (based on observational data from 31 published studies [see Table 1]) have been processed. To determine relative feeding specialization, the diet breadth B (= diversity of arthropod orders in the diet) was computed for each spider group by means of the Inverted Simpson Index (see Levins 1968; Colwell & Futuyma 1971) (Table 4). Diet breadth is inversely related to ecological specialization

Table 1.—Field studies used for the assessment of the relative taxonomic composition of the diets of ten spider groups. Habitats: SO = soybean, CO = cotton, PE = peanuts, AA = alfalfa, WW = winter wheat, OA = oats, MA = maize, MM = mown meadow, VE = vegetables, NC = noncrop.

Spider group	Habitat	Area	Author(s)
Tetragnathidae			
Tetragnatha laboriosa	SO	USA	LeSar & Unzicker (1978)
Tetragnatha laboriosa	SO	USA	Culin & Yeargan (1982)
Tetragnatha laboriosa	CO	USA	Nyffeler et al. (1989)
Tetragnatha extensa	WW	Europe	Nyffeler & Benz (1979)
Araneidae			
Acanthepeira stellata	CO	USA	Nyffeler et al. (1989)
Argiope aurantia	CO	USA	Nyffeler et al. (1987a)
Neoscona arabesca	CO	USA	Nyffeler et al. (1989)
Neoscona arabesca	SO	USA	Culin & Yeargan (1982)
Theridiidae			
Latrodectus mactans	CO	USA	Nyffeler et al. (1988a)
Achaearanea riparia	WW	Europe	Nyffeler & Benz (1988a)
Theridion impressum	WW	Europe	Nyffeler (1982)
Theridion impressum	OA	Europe	Nyffeler & Benz (1979)
Linyphiidae			
various Erigoninae	MA	Europe	Alderweireldt (1994)
various Erigoninae	WW	Europe	Sunderland et al. (1986)
various Erigoninae	WW	Europe	Nyffeler & Benz (1988b)
various Erigoninae	MM	Europe	Nyffeler (1982)
Dictynidae			
Dictyna segregata	CO	USA	Nyffeler et al. (1988b)
Dictyna arundinacea	WW	Europe	Heidger & Nentwig (1989)
Dictyna arundinacea	NC	Europe	Heidger & Nentwig (1986)
Dictyna montana	NC	Africa	Nentwig (1987)
Oxyopidae (small-sized)			
Oxyopes salticus	CO	USA	Nyffeler et al. (1987b)
Oxyopes salticus	CO	USA	Nyffeler et al. (1992a)
Oxyopes salticus	CO	USA	Lockley & Young (1987)
Oxyopes salticus	PE	USA	Agnew & Smith (1989)
Oxyopidae (large-sized)			
Peucetia viridans	CO	USA	Nyffeler et al. (1987c)
Peucetia viridans	CO	USA	Nyffeler et al. (1992a)
Peucetia viridans	NC	USA	Turner (1979)
Peucetia viridans	NC	USA	Randall (1982)
Thomisidae			
Misumenops spp.	PE	USA	Agnew & Smith (1989)
Misumenops spp.	CO, NC	USA	Dean et al. (1987)
Xysticus emertoni	NC	USA	Morse (1983)
Xysticus spp.	MM	Europe	Nyffeler & Breene (1990a)
Salticidae			
Phidippus audax	CO, NC	USA	Dean et al. (1987)
Phidippus audax	CO, NC	USA	Young (1989)
Phidippus audax	VE	USA	Riechert & Bishop (1990)
Phidippus johnsoni	NC	USA	Jackson (1977)
Lycosidae			
Pardosa ramulosa	AA	USA	Yeargan (1975)
Pardosa spp.	PE	USA	Agnew & Smith (1989)
Pardosa spp.	WW	Europe	Nyffeler & Benz (1988c)
Pardosa amentata	NC	Europe	Hallander (1970)

Table 2.—Relative taxonomic composition of the diets of various web-weavers [for each spider group a mean ± SE, based on 4 different prey analyses has been computed]. [1] LeSar & Unzicker (1978); Nyffeler & Benz (1979); Culin & Yeargan (1982); Nyffeler et al. (1989). [2] Culin & Yeargan (1982); Nyffeler et al. (1987a); Nyffeler et al. (1989) [data for 2 species]. [3] Nyffeler (1982); Nyffeler & Benz (1979, 1988a); Nyffeler et al. (1988a). [4] Nyffeler (1982); Sunderland et al. (1986); Nyffeler & Benz (1988b); Alderweireldt (1994). [5] Nentwig (1987); Nyffeler et al. (1988b); Heidger & Nentwig (1986, 1989).

Diet item (in %)	Tetragnathidae[1] (*Tetragnatha*)	Araneidae[2] (*Acanthepeira, Argiope, Neoscona*)	Theridiidae[3] (*Latrodectus, Achaearanea, Theridion*)	Linyphiidae[4] (Erigoninae)	Dictynidae[5] (*Dictyna*)	Overall mean
Homoptera	51 ± 16	36 ± 7	26 ± 9	33 ± 8	21 ± 13	33 ± 5
Diptera	40 ± 17	21 ± 6	15 ± 7	9 ± 2	64 ± 15	30 ± 6
Hymenoptera	3 ± 1	7 ± 2	32 ± 17	2 ± 1	7 ± 3	10 ± 4
Collembola	0 ± 0	0 ± 0	0 ± 0	48 ± 8	0 ± 0	10 ± 5
Coleoptera	1 ± 1	24 ± 9	13 ± 4	<1 ± 0.2	1 ± 1	8 ± 3
Heteroptera	5 ± 4	3 ± 1	1 ± 1	1 ± 0.5	<1 ± 0	2 ± 1
Lepidoptera	<1 ± 0.7	3 ± 1	1 ± 1	0 ± 0	0 ± 0	<1 ± 0.4
Araneae	0 ± 0	<1 ± 0.2	<1 ± 0.5	<1 ± 0.2	<1 ± 0.2	<1 ± 0.1
Others	0 ± 0	5 ± 4	11 ± 4	6 ± 2	7 ± 2	6 ± 2
Total	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0

(Colwell & Futuyma 1971; Turner 1979). Thus, high *B*-values are characteristic for exceedingly polyphagous predators, whereas low values indicate a more specialised feeding behavior. [Here a specialist feeder is defined as one that exhibits narrow diet breadth in a particular environment.]

RESULTS AND DISCUSSION

Overall, fewer than 10 arthropod orders (Diptera, Homoptera, Hymenoptera, Heteroptera, Collembola, Coleoptera, Lepidoptera, and Araneae) make up the bulk of the prey of common agroecosystem spiders all of which are polyphagous predators (generalists) (Tables 2, 3). Dietary mixing seems to be advantageous by optimizing a balanced nutrient composition needed for survival and reproduction (Greenstone 1979; Uetz et al. 1992; Toft 1995). The various spider groups feed basically on the same orders, but in different proportions. The observed differences reflect,

Table 3.—Relative taxonomic composition of the diets of various hunters [for each spider group a mean ± SE, based on 4 different prey analyses has been computed]. [1] Lockley & Young (1987); Agnew & Smith (1989); Nyffeler et al. (1987b; 1992a). [2] Turner (1979); Randall (1982); Nyffeler et al. (1987c, 1992a). [3] Morse (1983); Dean et al. (1987); Agnew & Smith (1989); Nyffeler & Breene (1990a). [4] Jackson (1977); Dean et al. (1987); Young (1989); Riechert & Bishop (1990). [5] Hallander (1970); Yeargan (1975); Nyffeler & Benz (1988c); Agnew & Smith (1989).

Diet item (in %)	Oxyopidae[1] (*Oxyopes*)	Oxyopidae[2] (*Peucetia*)	Thomisidae[3] (*Misumenops, Xysticus*)	Salticidae[4] (*Phidippus*)	Lycosidae[5] (*Pardosa*)	Overall mean
Heteroptera	30 ± 10	18 ± 4	18 ± 11	21 ± 11	16 ± 13	21 ± 4
Diptera	14 ± 3	13 ± 5	28 ± 8	17 ± 6	21 ± 7	19 ± 3
Araneae	11 ± 4	13 ± 6	9 ± 3	16 ± 6	24 ± 9	15 ± 3
Hymenoptera	11 ± 5	35 ± 20	16 ± 6	5 ± 5	3 ± 1	14 ± 3
Homoptera	18 ± 4	1 ± 0.5	2 ± 1	14 ± 3	17 ± 5	10 ± 2
Lepidoptera	8 ± 6	9 ± 2	16 ± 7	10 ± 4	3 ± 2	9 ± 2
Coleoptera	<1 ± 0.3	6 ± 1	6 ± 2	13 ± 7	3 ± 2	6 ± 2
Collembola	0 ± 0	0 ± 0	<1 ± 0.2	0 ± 0	8 ± 6	2 ± 1
Others	7 ± 1	5 ± 2	5 ± 2	4 ± 2	5 ± 2	5 ± 1
Total	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0	100 ± 0

in part, the diverse range of life styles and foraging modes exhibited by the various spider groups, and to some extent differences in prey availability (see Riechert & Luczak 1982; Nentwig 1987; Nyffeler et al. 1994b).

Web-weavers are almost strictly insectivorous (insects constituting > 99% of total prey) (Table 2). Aggressive encounters among web-weavers occur quite frequently, but rarely result in predation. In a web, the potential victim gets advanced vibrational warning and can flee or be ready to repulse the attacker. During such encounters between web-weavers the inferior individual is usually chased away by its opponent (see Wise 1993). Under conditions of suitable food supply in the form of insects the web-weavers seem to minimize feeding on ‘‘dangerous prey’’ such as spiders. Hunters, however, exhibit a mixed strategy of insectivorous and araneophagic foraging patterns (insects constituting ≈75–90% of total prey) (Table 3). Field populations of several species of hunters had been found to be in a state of undernourishment (see Nyffeler & Breene 1990b). Thus, araneophagy including cannibalism (as an additional feeding strategy to insectivory) may be crucial in sustaining the hunter populations during periods of food shortage (see Wise 1993). ‘‘Eating other spiders appears to be an opportunistic occurrence, a larger or faster individual overpowering another in a chance encounter’’ (Jackson 1992).

Based on the data presented in Tables 2 and 3, the diet breadth (*B*) for spiders was computed with the Inverted Simpson Index (Table 4). The highest value was approximately five times higher than the minimum (B = 1.13 vs. 5.58), which indicates considerable between-species differences in diet breadth. Evidently the hunters exhibit on average a less specialized feeding behavior (overall mean diet breadth = 4.20 ± 0.20) compared to the web-weavers (overall mean = 2.61 ± 0.22) (Table 4), the difference between the two overall means being statistically significant (Mann-Whitney *U* test; $U_s = 52.5$; $df = 20, 20$; $P < 0.002$).

The data in Table 3 are almost exclusively based on US sources (3 out of 20 references from Europe), whereas those in Table 2 are from both European and US sources (10 out of 20 references from Europe). The US studies are generally from more southern and warmer

Table 4.—Diet breadth (*B*) of five groups each of web-weaving spiders and hunting spiders; higher values indicate a less specialized feeding behavior (same data used as in Tables 2, 3).

Spider group	Diet breadth *B*	
	Mean ± SE	Range
Web-weavers:		
Tetragnathidae	1.87 ± 0.40	1.24–2.96
Araneidae	3.42 ± 0.28	2.86–4.19
Theridiidae	3.20 ± 0.60	1.70–4.52
Linyphiidae	2.55 ± 0.30	1.85–3.20
Dictynidae	2.00 ± 0.42	1.13–3.00
Overall mean	2.61 ± 0.22	
Hunters:		
Oxyopidae (*Oxyopes*)	4.42 ± 0.58	2.76–5.44
Oxyopidae (*Peucetia*)	4.34 ± 0.34	3.42–4.86
Salticidae	4.38 ± 0.33	3.45–4.89
Thomisidae	3.95 ± 0.44	3.09–5.17
Lycosidae	3.90 ± 0.69	2.65–5.58
Overall mean	4.20 ± 0.20	

latitudes than the European ones (so far, most studies on the natural diets of hunters in crops available in the literature are from the southern US). Furthermore, the majority of US studies were conducted in structurally complex crops such as cotton and soybean fields, whereas most European studies were from cereal crops with a less complex (i.e., prevailingly vertical) vegetation structure. Differences in geographic latitude as well as vegetation structure could influence the prey availabilities. Thus, the question arises whether the result of a greater diet breadth of the hunters observed in this study (Table 4) eventually is due to biases in the data set (the web and hunting spiders being studied in different crops and continents). To rule out this possibility, hunters and web-weavers should be analysed under comparable conditions (i.e., in the same field with identical prey availabilities).

Studies in which both hunters and web-weavers were evaluated in the same fields were published by Nyffeler (1982), Nyffeler & Sterling (1994), and Bardwell & Averill (1997). Based on these studies the diet breadth of web spiders and hunting spiders was assessed comparatively (Table 5). In Nyffeler's (1982) study in winter wheat fields near Zurich, Switzerland, hunters (represented by *Pardosa* spp. wolf spiders) had a greater diet

Table 5.—Diet breadth (*B*) of web-weaving spiders vs. hunting spiders in winter wheat, cotton, and cranberry, based on data from: [1] Nyffeler (1982); [2] Nyffeler & Sterling (1994); [3] Nyffeler et al. (1992a); [4] Bardwell & Averill (1997).

Crop	Foraging strategy	Spider species	Diet breadth *B*
WHEAT:	Web-weavers	*Tetragnatha extensa*[1]	1.24
		Theridion impressum[1]	2.90
		Erigoninae (pooled data)[1]	3.10
		Achaearanea riparia[1]	3.70
	Hunters	*Pardosa* spp. (pooled data)[1]	4.48
COTTON:	Web-weavers	*Tetragnatha laboriosa*[2]	1.36
		Latrodectus mactans[2]	1.70
		Dictyna segregata[2]	2.37
		Neoscona arabesca[2]	2.86
		Acanthepeira stellata[2]	3.29
	Hunters	*Oxyopes salticus*[3]	4.73
		Oxyopes salticus[2]	4.76
		Peucetia viridans[2,3]	4.86
CRANBERRY:	Web-weavers	(pooled data)[4]	3.17
	Hunters	(pooled data)[4]	4.69

breadth than the web-weavers (represented by orb weavers, sheet web-weavers, and tangle web-weavers) (Table 5). Likewise, in Texas cotton fields, the numerically dominant hunters (*Oxyopes salticus* and *Peucetia viridans*) exhibited greater diet breadth than several species of web-weavers (Table 5) (see Nyffeler et al. 1992a; Nyffeler & Sterling 1994). Furthermore, the data presented by Bardwell & Averill (1997) from cranberry bogs in Massachusetts suggest that the hunting spiders exhibited greater diet breadth than the web-weavers (pooled data for all hunters vs. web-weavers) (Table 5). Thus, in agroecosystems there seems to be a consistent trend of greater diet breadth of hunters compared to web-weavers regardless of crop type or geographic region investigated.

How do we explain this difference? Web spiders are stationary predators that wait for food to come to them (i.e., ‘sit-and-wait’ strategy). The prime requirement for the ‘sit-and-wait’ strategy is a food that moves (Turnbull 1973). A large proportion of web spiders spin aerial webs, with which they filter the aerial plankton (see Kajak 1965; Chacon & Eberhard 1980; Nentwig 1980). Others spin webs adapted to capture walking, crawling, or jumping prey (Turnbull 1973). Most web-weavers depend largely on relatively few prey groups available in high numbers in a particular environment (see Bristowe 1941; Turnbull 1960; Nyffeler & Benz 1979, Sunderland et al. 1986; Nentwig 1987; Alderweireldt 1994). In contrast, hunting spiders, by and large, seem to be less restricted in their diet (see Turnbull 1973). Representatives of various hunting spider families (e.g., Oxyopidae, Salticidae, Thomisidae, Lycosidae) have been reported to feed on both moving and motionless prey, which is indicative of a more mobile foraging strategy (see Nyffeler et al. 1990; Jackson & Tarsitano 1993). It is quite possible that the greater diet breadth of the hunting spiders (Table 4) simply reflects their greater opportunities to actively seek out suitable food due to their higher mobility (see Turnbull 1973).

There is observational evidence that hunting spiders can narrow their diet breadth significantly at times when a suitable prey type becomes locally superabundant relative to other prey (see Kiritani et al. 1972; Dean et al. 1987; Nyffeler et al. 1992b, 1994b). Thus, the greater diet breadth observed in the hunters (Table 4) does not necessarily imply that they require a more diverse diet than the web-weavers. It may instead show that they have a better chance of finding suitable food than web-weavers in agroecosystems (Young & Edwards 1990). However, there are exceptions to the rule (Turner & Polis 1979). Several members of the hunter families Thomisidae, Salticidae, Clubionidae, Gnaphosidae and Zodariidae are known to specialize on ants (see Nentwig 1986, 1987).

Most spiders feed on prey that are small relative to their own size (prey length ≤ spider length) (Wise 1993). Feeding experiments with a variety of spider species and a model prey (crickets) conducted in the laboratory revealed that the optimal prey length ranges from 50–80% of the spiders' own length (Nentwig 1987). Nentwig's laboratory data are fully supported by observations in the field (Hayes & Lockley 1990; Nyffeler et al. 1987b, c, 1992a). Overall, spider individuals of small size (including large percentages of immatures) numerically dominate the faunas of field crops, and these feed primarily on tiny prey organisms (< 4 mm in length) (LeSar & Unzicker 1978; Young & Edwards 1990; Nyffeler et al. 1994a).

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