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Nyffeler, Martin; Benz, Georg

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Department of Entomology, Swiss Federal Institute of Technology, ETH-Zentrum, Zurich,
Switzerland

Foraging ecology and predatory importance of a guild of orb-weaving spiders in a grassland habitat¹

By M. NYFFELER and G. BENZ

Abstract

In an abandoned grassland ecosystem (megaphorbe meadow: Valeriano-Filipenduletum, *Carex acutiformis* Ehrh. type) in Eastern Switzerland, orb-weaving spiders dominated the spider community of the field layer (ca 60 % of the yearly total of spiders in sweep samples). The orb-weavers of this grassland comprised predominantly the six species *Argiope bruennichi* (Scop.), *Araneus quadratus* Clerck, *Araneus diadematus* Clerck, *Nuctenea cornuta* (Clerck), *Meta segmentata* Clerck, and *Tetragnatha extensa* (L.), which combined formed a guild of insectivorous predators. The orb-weaving spiders in that grassland captured a variety of insect taxa (generalist predators); their major prey were Diptera (diverse species) and Homoptera (primarily leafhopper *Stenocranus major* [Kbm.] and aphids of the *Anoecia corni* group). Araneae constituted a very small fraction (< 0.5 %) in the orb-weavers' prey, indicating that araneophagy (cannibalism and interspecific predation) is insignificant for the nutrition of this orb-weaver guild. Considerable prey overlap between the spider species was found, suggesting that the six orb-weavers basically utilized the same insect taxa as diets. Major predator activities of this orb-weaver guild occurred in the second half of summer. At that time of the year total numbers of all orb-weavers averaged between 1.7 and 4.3 ind./m² in five grassland patches (overall mean of the habitat = 3 ind./m²). In the second half of summer the orb-weaving spiders daily spun an overall web area of ca. 0.1 m²/m² ground area (range of five grassland patches: 0.07–0.15 m² web area/m² ground area). An extrapolation of the overall mean of the entire grassland habitat indicates that the orb-weaver guild daily spun an estimated web area of ca. 1000 m²/ha ground area. Such a large web area evidently is death trap for large numbers of grassland insects. Data of this paper and of literature indicate that spiders in such undisturbed grassland ecosystems exert a high predation pressure on insect populations. Among the insects killed by this orb-weaver guild were also agricultural pests such as the aphids *Aphis fabae* Scop., *Myzus persicae* Sulz., *Hyalopterus pruni* Geoffr., *Rhopalosiphum padi* L., and *Sitobion avenae* F.

1 Introduction

Orb-weaving spiders (families Araneidae and Tetragnathidae) often are abundant in little disturbed grassland habitats (LOHMEYER and PRETSCHER 1979; NYFFELER and BENZ 1987a, b). Some orb-weaver species (genus *Araneus* and *Argiope*) preferentially inhabiting abandoned grasslands belong to the largest spiders of the temperate zone. In late summer, when these large-sized orb-weavers are mature and daily spin orbs of large diameters (up to 60 cm Ø, WIEHLE 1931), they become especially eye-catching to the field ecologist. Besides grasslands, other habitats such as crop fields, apple orchards, forests, and tropical plantations were observed to be populated by orb-weaving spiders in considerable numbers (ROBINSON and ROBINSON 1974; NATON 1976; LESAR and UNZICKER 1978; NYFFELER, unpubl.). Previously numerous studies about predation of orb-weaving spiders in various habitats were published (KAJAK 1965; ROBINSON and ROBINSON 1970, 1974; NYFFELER 1983; NYFFELER and BENZ 1978, 1980, 1981a, 1982a; UETZ et al. 1978; OLIVE 1980, 1981a, b; BROWN 1981; HORTON and WISE 1983; NENTWIG 1983a, b, 1985a, b; WISE

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and BARATA 1983; PASQUET 1984; NYFFELER et al. 1989, a.o.). Nevertheless, many questions about these spiders' ecological role as mortality agents of insects remain open.

In order to learn more about the predatory role of orb-weaving spiders a project was started, in which prey kill by an orb-weaver guild in a Swiss grassland was studied during one summer season. Our study basically focussed on the following two topics:

1. Evaluation of foraging (prey capture etc.) of the orb-weaver guild from spring to late summer.
2. Evaluation of the web area/m² ground area daily spun by orb-weavers in late summer (predatory impact is a function of the web area/m² ground area).

The species composition of the foliage-dwelling spider community of the investigated grassland habitat is published elsewhere (NYFFELER and BENZ 1987a).

2 Materials and methods

2.1 Study area

The study was carried out in an abandoned grassland habitat (of ca ½ ha) located ca 3.5 km south-east of the International Airport Zurich-Kloten, near the river Glatt (national grid coordinates: 685.65/253.65) from June to September. It refers to a megaphorbe meadow (Valeriano-Filipenduletum, *Carex acutiformis* Ehrh. type; "Hochstaudenried" in German literature. In parts this meadow is strongly eutrophic (with *Phalaris arundinacea* L.). It is infested partially with weeds, partially with shrubs. To some extent there are transitions to hay meadows. The reed borders on a forested area (initial stage of an *Acer-Fraxinus* forest).

Since this habitat represents a mosaic of patches with differing vegetation architecture, we divided the habitat for the purpose of the population density assessment into five "types of patch" (table 4A):

- Open grass area (above)
- Open grass area (below)
- Wayside (above)
- Wayside (below)
- Shrubs at periphery of grass area.

2.2 Assessment of population densities and spatial distribution patterns

On September 2, the spider population densities (n_i) were assessed by counting the numbers of orb-weavers within 150 small patches, each of 1 m × 1 m (30 randomly selected samples taken in each of the five "types of patch"). Overall mean density (no. ind./m²) is the total number of spiders of the five times 30 samples, divided by 150. (Assessed data compiled in table 4A).

Vertical web distribution within the field layer was assessed by measuring the distance between orb-hub and ground with a meter stick. (Assessed data represented in table 5 and fig. 1).

2.3 Assessment of catching area per spider

In this study, the catching area per spider (a) was calculated as an approximately circular area with the following formula:

$$a = \pi * (d/2)^2, \quad (1)$$

where d = diameter (in cm) of the catching area of a web. Since most orb-weaving spiders spin slightly asymmetrical orb-webs (NENTWIG 1985a), it follows that mostly horizontal diameter $\neq$ vertical diameter. In this study, we measured horizontal diameter and vertical diameter of an orb-web, and from these two values we calculated the arithmetical mean used as estimate of parameter d in formula 1. (Assessed data compiled in table 3).

2.4 Assessment of the web area/m² ground area spun by the orb-weavers

How large is the web area daily spun by orb-weaving spiders per space unit (cm² web area/m² ground area)? The average web area/ground area ($\bar{A}_i$) was calculated for the i^{th} species of the orb-weaver guild with the following formula:

$$\bar{A}_i = \bar{n}_i * \bar{a}_i, \quad (2)$$

where $\bar{n}_i$ and $\bar{a}_i$ are respectively avg. population density (no. spiders/m², table 4A) and avg. catching area per spider (in cm², table 3) of i^{th} of the 6 orb-weaver species. (Computed data compiled in table 4B).

Hence, the average web area ($\bar{A}_G$) of the entire orb-weaver guild per space unit is:

$$\bar{A}_G = \sum_{i=1}^6 \bar{A}_i, \quad (3)$$

where $\bar{A}_i$ is the average web area/ground area of the i^{th} of $i = 1, 2, \dots, 6$ orb-weaver species. (Computed data compiled in table 4B).

2.5 Assessment of the spiders' prey

Evidence of predation by orb-weavers in this study was obtained indirectly by removing the remains of previously killed arthropods from the spiders' webs. All arthropods found dead in spider webs were considered prey. It may be questioned whether all arthropod carcasses found in spider webs actually represent these predators' food or whether some of them died in the webs without being preyed upon. From the point of view of pest control only the number of insects killed is relevant, not the number of insects consumed. However, all insect groups considered prey of orb-weaving spiders in this paper (tables 6–8) were observed to be actually eaten in the laboratory (NENTWIG 1983a) or field (NYFFELER and BENZ, unpubl.), and prey data presented in this paper can therefore be considered to be the orb-weaving spiders' food. Prey items were collected from webs with forceps, and preserved in 70 % ETOH. They were later identified and counted under a dissecting microscope. Of the prey groups "Cicadina" and "Aphidina", samples were sent to specialists for exact identification. (List of identified Homoptera presented in table 10).

In order to examine to what extent the syntopic spider species used the available prey recourses in common, prey overlap was assessed. For this purpose, a resource matrix was set up (sensu MÜHLENBERG 1976). In our "feeding niche-system", the compared spider species are looked upon as resource users and the components in the spiders' prey are considered as resource classes. The overlap coefficient $\hat{C}\lambda$ was calculated by means of the formula of MORISITA, modified by HORN (1966):

$$\hat{C}\lambda = \frac{2 \sum_{i=1}^S x_i y_i}{\sum_{i=1}^S x_i^2 + \sum_{i=1}^S y_i^2}, \quad (4)$$

where S is the total number of food items, x_i and y_i are proportions of the i^{th} item in the prey spectra of spider species x and y . Values of $\hat{C}\lambda$ range from zero to 1.0 (from entirely different to identical prey spectra). (Calculated values presented in table 9).

To get a figure of the spiders' prey killing capacity, numbers of prey items found per web were recorded; those figures are considered to be minimum estimates of the spiders' daily prey capture rates (see table 12).

3 Results

3.1 The orb-weaver guild

Orb-weaving spiders were the numerically dominant spider group in the investigated grassland (overall, ca. 60 % of the yearly total of spiders sampled by sweeping the field layer) (table 1). Three large-sized species (*Argiope bruennichi* [Scop.], *Araneus quadratus* Clerck, and *Araneus diadematus* Clerck) and three medium-sized species (*Nucteana cornuta* [Clerck], *Meta segmentata* Clerck, and *Tetragnatha extensa* [L.]) predominated among the orb-weavers of this habitat, combined forming a guild of insectivorous predators. These six orb-weaver species were observed to be foraging diurnally and nocturnally (table 2). The web of the six spider species is described in table 3. The orb-weaver guild of this study is composed of one species (*N. cornuta*) reproducing from spring to autumn (tending towards a "time generalist"), one stenochronous species reproducing in spring (*T. extensa*), and four stenochronous species reproducing in late summer/autumn (*A. bruennichi*, *A. quadratus*, *A. diadematus*, *M. segmentata*) (table 2). Major predator activities of this orb-weaver guild occurred in the second half of summer (August/September), when the three large-sized species *A. bruennichi*, *A. quadratus*, and *A.*

Table 1. Relative abundance of spiders of various foraging behaviours in a grassland habitat in Eastern Switzerland, assessed by sweep sampling (immatures plus adults)

The table is based on a species list from NYFFELER and BENZ (1987a)

Foraging behaviour	June 12 %	June 28 %	July 17 %	August 14 %	Sept. 20 %	Mean %
Orb-weaving spiders	56.9	55.9	65.6	64.9	55.6	59.8
Space web spiders ^a	25.6	13.3	12.6	12.7	25.0	17.8
Hunting spiders ^b	13.1	29.8	18.3	21.4	15.6	19.6
Unid. spiders	4.4	1.0	3.5	1.0	3.9	2.8
Total	100	100	100	100	100	100

^a "Space web spiders" refers to all web-building spiders which do not construct orb-webs. –

^b "Hunting spiders" refers to all spiders foraging without a catching web.

Table 2. Body size, time of maturity, and time of the day of foraging in six orb-weaving spiders

Spider species	Adult female length (cm)	Time of maturity ^a	Time of the day of web construction	Time of the day of prey capture ^c
<i>Argiope bruennichi</i>	11–14	VIII–IX (stenochronous)	early morning	<i>day and night</i>
<i>Araneus quadratus</i>	9–15	VIII–X (stenochronous)	early morning ^b	<i>day and night</i>
<i>Araneus diadematus</i>	10–12	VIII–X (stenochronous)	early morning	<i>day and night</i>
<i>Nuctenea cornuta</i>	6–8.5	I–XII (eurychronous)	evening	<i>day and night</i>
<i>Meta segmentata</i>	5–8	VIII–X (stenochronous)	early morning	<i>day and night</i>
<i>Tetragnatha extensa</i>	8–11	V–VII (stenochronous)	evening	<i>day and night</i>

^a Data from CROME (1961). – ^b Morning (according to WIEHLE 1931), evening (according to KAJAK 1965). – ^c Preferred time in italics, estimated according to our observations.

diadematus were mature and spun strong webs with average diameters of ca. 24–26 cm (average catching areas of 450–550 cm²) (table 3).

3.2 Population densities of the orb-weavers

Population densities of the six orb-weaver species in five patches within the investigated grassland habitat in the second half of summer are compiled in table 4A. The most abundant species at that time was *T. extensa* whose population densities averaged in the five patches between 0.1 and 3.1 ind./m² (overall mean of habitat = ca. 1 ind./m²). Also quite abundant were *A. quadratus* and *M. segmentata* (in each species overall mean = 0.7 ind./m²). Less abundant were *A. bruennichi* (overall mean = 0.4 ind./m²), *A. diadematus* (overall mean = 0.2 ind./m²), and *N. cornuta* (overall mean = 0.1 ind./m²). Total numbers of all orb-weavers in the second half of summer averaged between 1.7 and 4.3 ind./m² in the five different grassland patches (overall mean of the habitat = 3 ind./m²) (table 4A).

Table 3. Comparison of web characteristics of six orb-weaving spiders inhabiting a grassland habitat in Eastern Switzerland (August/September)
The catching areas have been calculated as approximately circular areas

Spider species	Deviation of web plane from vertical (angle in °) ^a	Number of spiral turns ^a $\bar{x}$ (range)	Mesh size ^b (cm) $\bar{x}$	Web diameter ^c (cm) $\bar{x} \pm SE$	Catching area (cm ²) $\bar{x} \pm SE$
<i>Argiope bruemichi</i>	0–10	26 (19–30)	0.5	24.26 $\pm$ 0.91 25.05 $\pm$ 0.92	489.49 $\pm$ 36.38 518.68 $\pm$ 36.14
<i>Aranus quadratus</i>	0–10	26 (20–31)	0.5	22.76 $\pm$ 1.23 24.37 $\pm$ 0.88	444.98 $\pm$ 47.62 490.34 $\pm$ 35.59
<i>Aranus diadematus</i>	15–45	32 (28–40)	0.3	22.85 $\pm$ 1.27 28.61 $\pm$ 1.01	425.02 $\pm$ 48.99 673.72 $\pm$ 47.27
<i>Nuctenea cornuta</i>	0–30	24 (15–28)	0.3 ^d , 0.6 ^e	15.49 $\pm$ 1.81 ^f 14.45 $\pm$ 1.82 ^f	234.90 $\pm$ 51.98 221.19 $\pm$ 44.50
<i>Meta segmentata</i>	45–90	26 (20–29)	0.3	14.24 $\pm$ 0.99 15.06 $\pm$ 0.75	172.15 $\pm$ 22.61 197.18 $\pm$ 20.77
<i>Tetragnatha extensa</i>	15–45	17 (16–20)	0.4 ^g	15.71 $\pm$ 2.81 —	231.13 $\pm$ 84.79 —

^a Data from literature (KÖNIG 1951). — ^b Distance between spiral turns. — ^c Arithmetical mean of horizontal and vertical diameters. — ^d Measured on immatures in Sept. — ^e After NENTWIG (1983b). — ^f Mixed stages; adult web ϕ = 25 cm. — ^g Value from literature (WIEHLE 1963). — ^h No measurements.

Table 4. Population parameters of six orb-weaving spiders in a grassland habitat in Eastern Switzerland (early September)

A: Population densities (no. ind./m² ground area) of orb-weaving spiders in five different grassland patches. Each mean value ($\bar{x}$ based on 30 samples (each of 1 m × 1 m ground area). B: Web area/ground area of orb-weaving spiders in five grassland patches, calculated by means of formulas 2 and 3 (using data of Tables 3 and 4A)

A. Spider species	Open grass area (above)	Open grass area (below)	Wayside (above)	Wayside (below)	Shrubs at periphery of grass area
	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$
<i>Argiope bruennichi</i>	0.37 ± 0.12	0	0.73 ± 0.18	0.83 ± 0.17	0
<i>Araneus quadratus</i>	1.00 ± 0.16	0.73 ± 0.17	1.27 ± 0.20	0.23 ± 0.09	0.03 ± 0.03
<i>Araneus diadematus</i>	0	0.03 ± 0.03	0.07 ± 0.05	0	0.93 ± 0.26
<i>Nuctenea cornuta</i>	0.17 ± 0.07	0.13 ± 0.08	0.33 ± 0.10	0.07 ± 0.05	0
<i>Meta segmentata</i>	0.10 ± 0.06	0.27 ± 0.11	0.23 ± 0.09	0.47 ± 0.11	2.17 ± 0.40
<i>Tetragnatha extensa</i>	0.10 ± 0.07	3.13 ± 0.44	1.27 ± 0.23	0.13 ± 0.06	0.17 ± 0.07
Total	1.73 ± 0.23	4.30 ± 0.53	3.90 ± 0.42	1.73 ± 0.30	3.30 ± 0.38
Overall mean = 3.0					
B. Spider species	Open grass area (above)	Open grass area (below)	Wayside (above)	Wayside (below)	Shrubs
	cm ² web area/m ² ground area				
<i>Argiope bruennichi</i>	191.91	0	378.64	430.50	0
<i>Araneus quadratus</i>	490.34	357.95	622.73	112.78	14.71
<i>Araneus diadematus</i>	0	20.21	47.16	0	626.56
<i>Nuctenea cornuta</i>	37.60	28.75	72.99	15.48	0
<i>Meta segmentata</i>	19.72	53.24	45.35	92.67	427.88
<i>Tetragnatha extensa</i>	23.11	723.44	293.54	30.05	39.29
Total	762.68	1183.59	1460.41	681.48	1108.44
Overall mean = 1039					

3.3 Web area/m² ground area

Based on data of tables 3 and 4A, the web area daily spun by the orb-weaving spiders was estimated in the second half of summer. At that time of the year, the orb-weaving spiders daily spun web areas averaging in various habitat patches between 0.07 and 0.15 m²/m² ground area (overall mean of the habitat = 0.1 m² web area/m² ground area) (table 4B).

3.4 Vertical web distribution patterns

The vertical distribution of orb-webs within the grassland field layer is shown in the figure (July to September) and table 5 (early September). Orb-webs were found from directly above the ground up to the top of the field layer (table 5). As the figure shows, a vertical segregation of different orb-weaver species within the field layer was observed. A statistical analysis of the data shown in the figure gave significant differences in the mean values of *A. bruennichi*, *A. quadratus*, and *N. cornuta* from July to September ($p < 0.01$, Mann-Whitney U test, 2-tailed); exception, in September the mean values of *A. quadratus* and *N. cornuta* were not found to differ significantly ($p > 0.05$).

The weighed average ($\bar{x}^2$, table 5) is an estimate of the overall vertical web distribution of the orb-weaver guild. Population densities of table 4A (open grass area) were used as weighing factors for the calculation of $\bar{x}^2$. The $\bar{x}^2$ distribution indicates that ca. 50 % of all

Table 5. Vertical distribution of a guild of orb-weaving spiders within a grassland habitat in Eastern Switzerland (data from early September; exception, *T. extensa* measured in July)

N = number of webs measured

Height of orb hub above the ground (cm)	<i>Argiope bruennichi</i> N = 40 %	<i>Meta segmentata</i> N = 50 %	<i>Araneus quadratus</i> N = 52 %	<i>Araneus diadematus</i> N = 68 %	<i>Nuctenea cornuta</i> N = 40 %	<i>Tetragnatha extensa</i> N = 37 %	$\bar{x}$ %	$\bar{x}^*$ %
225–250	0	0	0	1.47	0	0	0.25	0.01
200–225	0	0	0	0	0	0	0	0
175–200	0	0	0	0	5.00	8.11	2.19	4.59
150–175	0	0	0	8.82	7.50	16.22	5.42	9.11
125–150	0	4.00	0	6.62	15.00	22.97	8.10	13.33
100–125	0	7.00	8.65	25.00	16.25	16.22	12.19	12.53
75–100	0	15.00	45.19	29.41	16.25	22.97	21.47	27.14
50– 75	25.00	34.00	43.27	22.06	35.00	13.51	28.81	25.12
25– 50	62.50	35.00	2.88	6.62	5.00	0	18.67	7.09
0– 25	12.50	5.00	0	0	0	0	2.92	1.07

$\bar{x}$ = mean value, $\bar{x}^*$ = weighted average; population densities of Table 4A ("open grass area") used as weighing factors.

orb-webs were placed at a height of 50–100 cm above ground, suggesting that within the open grass area a considerable portion of the predation pressure due to orb-weavers was exerted within the height range of 50–100 cm above ground. At heights of less than 25 cm and more than 150 cm above ground, the predation pressure exerted by orb-weaving spiders was negligible.

3.5 Prey spectrum

The prey of ther orb-weaver guild was exclusively composed of organisms of the class Arthropoda (> 99 % Insecta) (tables 6–8). The following insect taxa prevailed in the prey of the investigated orb-weaver guild (table 6, pooled data of all spiders): Diptera (68.8 % by numbers), Cicadina (9.3 %) Aphidina (8.2 %), and Hymenoptera (7.0 %); these four insect taxa combined constituted > 90 % of all prey items (based on a total of 7480 prey items). In lower numbers Trichoptera (2.0 %), Coleoptera (1.2 %), and Thysanoptera (0.7 %) were found as prey in spider webs. In contrast to this, the six insect taxa Ephemeroptera, Heteroptera, Orthoptera, Planipennia (Chrysopidae), Mecoptera (Panorpidae), and Lepidoptera were rarely entangled in spider webs (each category constituting < 0.5 % of the total prey). In the case of Lepidoptera and Mecoptera (Panorpidae), repeated escapes from orb-webs were observed (NYFFELER and BENZ 1980, 1981a). Furthermore, Araneae constituted a very small fraction (< 0.5 %) in the orb-weaving spiders' prey. A comparison of the six orb-weavers' trophic diversity² reveals species-specific differences in the degree of polyphagy (table 6). Low trophic diversity values were found in two species (*N. cornuta*, *T. extensa*), a slightly higher value in one species (*A. quadratus*), and rather high values in three species (*A. bruennichi*, *A. diadematus*, *M. segmentata*).

If we calculate the overall trophic diversity of the spider guild as a function of the time of year (based on pooled prey records of the six spider species per moth), we receive a trend of increasing trophic diversity with the progressing season (table 8); trophic diversity

² Trophic diversity (sensu HURTUBIA 1973) calculated with SHANNON-WEAVER's information theory formula

$$H' = \sum_{i=1}^s p_i \ln p_i,$$

where p_i is the proportion of the i^{th} prey category used.

Table 6. Prey spectrum and trophic diversity of six orb-weaving spiders in a grassland habitat in Eastern Switzerland
Pooled data of one summer season

Prey	<i>Argiope bruennichi</i>	<i>Araneus quadratus</i>	<i>Araneus diadematus</i>	<i>Nuctenea cornuta</i>	<i>Meta segmentata</i>	<i>Tetragnatha extensa</i>	Total
Diptera s	587	1494	496	1603	201	590	4971 } (68.8 %)
Diptera m/l	50	24	16	6	77	4	177 } (9.3 %)
Cicadina	246	172	56	3	204	15	696 } (8.2 %)
Aphidina	74	94	104	190	111	44	617 } (0.03 %)
Other Homoptera	0	0	1	1	0	0	2 } (7.0 %)
Apidae	43	22	6	1	0	0	72 } (2.0 %)
Formicidae (apter.)	6	1	2	0	6	0	15 } (1.2 %)
Other Hymenopt. s	67	149	124	7	25	5	377 } (0.7 %)
Other Hymenopt. m/l	35	7	11	0	3	0	56 } (0.3 %)
Trichoptera	0	0	1	100	2	45	148 } (0.2 %)
Coleoptera	13	17	10	39	0	8	87 } (0.2 %)
Thysanoptera	20	12	2	17	2	2	55 } (0.2 %)
Ephemeroptera	3	3	0	11	8	1	26 } (0.2 %)
Lepidoptera	1	3	4	5	0	0	13 } (0.2 %)
Heteroptera	1	2	10	0	0	0	13 } (0.04 %)
Panorpidae	1	0	2	0	0	0	3 } (0.03 %)
Chrysopidae	0	1	0	0	0	1	2 } (0.03 %)
Orthoptera	2	0	0	0	0	0	2 } (0.1 %)
Araneae	4	1	1	1	0	2	9 } (0.1 %)
Total ident. prey	1153	2002	846	1984	639	717	7341 (+139 unid.)
Trophic diversity (H') ^a	1.59	0.99	1.39	0.78	1.57	0.75	—

^a Trophic diversity (sensu HURTUBIA 1973) calculated with SHANNON-WEAVER's information theory formula $H' = -\sum_{i=1}^s p_i \ln p_i$, where $p_i = z_i/N$; N is total number of identified prey items, z_i is the number of individuals in the i^{th} prey category. s = small, m/l = medium to large prey species.

Table 7. Prey spectrum (in % by numbers) of six orb-weaving spiders in a grassland habitat in Eastern Switzerland

Prey	<i>Argiope bruennichi</i>			<i>Araneus quadratus</i>			<i>Araneus diadematus</i>			<i>Nuctenea cornuta</i>			<i>Meta segmentata</i>			<i>Tetragnatha extensa</i>		
	Aug.	Sept.	July	Aug.	Sept.	July	Aug.	Sept.	May	June	July	Aug.	Sept.	May	June	July		
Diptera s	44.7	68.2	88.2	75.4	70.0	57.1	60.6	83.0	75.4	80.8	85.1	27.4	39.3	88.8	82.2	57.5		
Diptera m/l	5.3	0.4	0	1.8	0.9	1.8	2.2	2.8	0	0.2	0	14.2	5.5	1.1	0	0.8		
Apterous ants	0.5	0.4	0	0.1	0	0.3	0	0	0	0	0	1.3	0	0	0	0		
Bees	4.6	0	0	1.0	1.3	0.7	0.7	0	0	0.1	0	0	0	0	0	0		
Other Hymenopt. s ^a	5.1	7.9	0.6	7.5	8.2	13.7	18.3	0	0.5	0.2	1.9	4.3	2.7	0	1.2	0.8		
Other Hymenopt. m/l	3.5	0.8	0	0.4	0.3	1.5	0	0	0	0	0	0.6	0	0	0	0		
Winged aphids	4.5	11.5	4.6	1.8	6.2	13.0	7.3	10.6	4.2	12.2	8.4	15.9	18.6	3.6	4.5	15.8		
Apterous aphids	0.3	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0		
Cicadina	24.8	6.3	0	9.0	9.5	6.5	6.6	0.7	0.2	0.1	0	31.2	31.1	3.6	1.5	0		
Thysanoptera	2.0	0.4	0	0.4	0.6	0.1	0	0.7	0.6	0.7	3.7	0.4	0	0	0.6	0		
Heteroptera	0.1	0	0	0.1	0.1	1.2	0.7	0	0	0	0	0	0	0	0	0		
Orthoptera ^b	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Lepidoptera	0	0.4	1.3	0	0.1	0.6	0	0	0.2	0.3	0	0	0	0	0	0		
Trichoptera	0	0	0	0	0	0.1	0	0	12.5	1.9	0.9	0.4	0	0	4.8	24.2		
Chrysopidae	0	0	0.6	0	0	0	0	0	0	0	0	0	0	0	0.3	0		
Scorpionflies	0.1	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0		
Coleoptera	1.0	1.6	1.3	1.0	0.6	1.2	0.7	0.7	4.0	1.1	0	0	0	0.7	1.8	0		
Ephemeroptera	0.3	0	0	0.3	0.1	0	0	0	0	1.0	0	1.5	0.5	0.4	0	0		
Salicidae	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Other spiders ^c	0.2	0.4	0	0.1	0	0.1	0	0	0	0.1	0	0	0	0.4	0	0.8		
Undt. prey	2.6	1.6	3.3	0.9	2.0	1.7	2.9	1.4	2.4	1.4	0	2.3	2.2	1.4	3.0	0		
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100		
No. prey items	929	252	153	708	1140	722	137	141	618	1150	107	471	183	276	331	120		
No. webs	95	24	7	47	59	129	11	26	47	64	11	309	75	138	156	53		
No. observation days	5	2	1	3	4	6	1	3	5	6	2	7	3	3	5	5		

a Winged individuals. – b One adult specimen of *Roeseliana roeseli* (Hgb.). – c Web-builders. s = small, m/l = medium to large prey species.

^a Winged individuals. - ^b One adult specimen of *Roeseliana roeseli* (Hgb.). - ^c Web-builders. s = small, m/l = medium to large prey species.

Table 8. Seasonal patterns of trophic diversity of an orb-weaver guild (pooled data of six spider species) in a grassland habitat in Eastern Switzerland (May to September)

Prey taxa	May %	June %	July %	August %	September %
Diptera	89.5	79.9	80.9	59.8	68.5
Cicadina	2.6	0.6	0.1	16.9	11.3
Aphidina	6.2	4.5	11.8	8.2	8.6
Hymenoptera		0.8	0.4	11.8	10.0
Trichoptera		9.8	3.6	0.1	
Coleoptera	1.0	3.3	1.1	0.9	0.7
Thysanoptera	0.2	0.8	0.6	1.0	0.5
Ephemeroptera	0.2		0.8	0.4	0.1
Lepidoptera		0.1	0.4	0.1	0.1
Heteroptera				0.4	0.1
Planipennia		0.1	0.1		
Mecoptera				0.1	
Orthoptera				0.1	
Other Homoptera			0.1	0.03	
Araneae	0.2		0.1	0.2	0.1
Total	100	100	100	100	100
Trophic diversity (H') ^a	0.45	0.78	0.73	1.24	1.04

^a Trophic diversity (sensu HURTUBIA 1973) calculated with SHANNON-WEAVER's information theory formula. Only prey items considered which could be identified at order level at least.

Table 9. Prey overlap ($\hat{C}\lambda$ values) within a guild of six orb-weaving spiders

Based on data of Table 6

	<i>A. bruennichi</i>	<i>A. diadematus</i>	<i>A. quadratus</i>	<i>N. cornuta</i>	<i>T. extensa</i>	<i>M. segmentata</i>
<i>A. bruennichi</i>	—					
<i>A. diadematus</i>	0.94	—				
<i>A. quadratus</i>	0.92	0.96	—			
<i>N. cornuta</i>	0.85	0.93	0.98	—		
<i>T. extensa</i>	0.85	0.92	0.98	1.00	—	
<i>M. segmentata</i>	0.88	0.67	0.67	0.60	0.60	—
Average overlap ^a	0.89	0.88	0.90	0.87	0.87	0.68
mean (of 15 pairings' overlap values) = 0.85						

^a Each average overlap represents a mean value of five species pairings between an orb-weaver species and the 5 other guild members.

was found to have increased from May ($H' = 0.45$) to August ($H' = 1.24$) and then to have slightly declined in September ($H' = 1.04$).

Considerable prey overlap between the six orb-weaver species (at the level of identified prey taxa, table 6) was found in this study ($\hat{C}\lambda \geq 0.60$, in all tested species pairs) (table 9)³, indicating that the six spiders basically utilized the same insect groups as prey, though in somewhat differing proportions. However, some significant food differences between the six orb-weavers – which assumedly reflect interspecific differences of foraging parameters (see tables 2–5, and fig.) – could be noticed (tables 6 and 7): For instance, honey bees were

³ Overlap values presented in table 9 may be overestimates compared with calculation at species level.

Vertical distribution of three orb-weaving spiders in a grassland habitat (July to September). Mean value $\pm$ 1 SE (vertical bar), numbers in the graphic indicate the no. of webs observed

quite frequently killed by *A. bruennichi* (almost 5 % of total prey by numbers in August), but made up only a low portion (≤ 1 %) in the prey of the other five orb-weaver species (table 7). Hymenoptera (as a whole group) constituted < 1 % of the prey of *N. cornuta* and *T. extensa*, but > 5 % of the prey of the other four orb-weaver species (table 6). Contrary, Trichoptera constituted a considerable fraction (respectively 5 and 6 %) in the prey of *N. cornuta* and *T. extensa*, but were rare (< 0.5 %) in the prey of the other four spider species (table 6). *N. cornuta* and *T. extensa* both spin their webs in the evening (table 2), which evidently favours the capture of insects flying at dusk and during the night (e.g. Trichoptera); the other four orb-weavers spin their webs in the morning (table 2), which may explain the higher proportion of diurnally foraging insects (e.g. Hymenoptera) in their prey.

Cicadina (primarily *Stenocranus major* [Kbm.] [table 10]) – which are jumpers – made up > 20 % in the prey of *M. segmentata* and *A. bruennichi*, but < 10 % in the prey of the other four orb-weaver species (table 6). As many as 44 cicadas were found entangled at one time in a single web of *A. bruennichi*. Data of this study suggest that orb-weavers living close to the ground (*M. segmentata*, *A. bruennichi*, table 5) tend to capture a higher proportion of jumping insects (Cicadina, Orthoptera), while orb-weavers living in the higher strata of the field layer tend to capture a higher proportion of flying insects (e.g.

Diptera) (table 11). The same pattern was observed in another study on orb-weavers inhabiting abandoned grasslands (see NYFFELER and BENZ 1978).

Table 10. Species of Cicadina (A) and Aphidina (B) in the prey of orb-weaving spiders
Observations in a grassland habitat in Eastern Switzerland (August/September)

A. Cicada species	<i>Argiope bruennichi</i>		<i>Araneus quadratus</i>		<i>Araneus diadematus</i>		<i>Meta segmentata</i>		Total		Σ	Σ %
	Aug.	Sept.	Aug.	Sept.	Aug.	Sept.	Aug.	Sept.	Aug.	Sept.		
<i>Stenocranus major</i>	160	12	64	102	35	8	140	56	399	178	577	94.9 %
<i>Kelisia punctulum</i>	2			4	5		2		9	4	13	2.1 %
<i>Mocuellus metrius</i>	3			2					3	2	5	0.8 %
<i>Cicadula quadrinotata</i>		2					1		1	2	3	0.5 %
<i>Cicadella viridis</i>		2							0	2	2	0.3 %
<i>Lepyronia coleoptrata</i>	1				1				2	0	2	0.3 %
<i>Javesella pellucida</i>							1		1	0	1	0.2 %
<i>Evacanthus interruptus</i>							1		1	0	1	0.2 %
<i>Dicranotropis hamata</i>	1								1	0	1	0.2 %
<i>Aphrodes bicinctus</i>	1								1	0	1	0.2 %
<i>Empoasca spec.</i>					1				1	0	1	0.2 %
Typhlocybinae							1		1	0	1	0.2 %
Total	168	16	64	108	42	8	146	56	420	188	608	100.0 %

B. Aphid species	<i>A. bruennichi</i>	<i>A. quadratus</i>	<i>A. diadematus</i>	<i>M. segmentata</i>
<i>Anoecia corni</i> ^a	many	many	many	many
<i>Rhopalosiphum padi</i>	+	+	+	
<i>Sitobion avenae</i>		+		
<i>Sitobion sp.?</i>	+			
<i>Aphis fabae</i>		+	+	+
<i>Aphis sp.</i>			+	
<i>Myzus persicae</i>		+		
<i>Hyalopterus pruni</i>	+			
<i>Rhopalomyzus lonicerae</i>			+	
<i>Linosisiphon galiophagum</i>				+
<i>Dysaphis spp.</i>		+		

^a *Anoecia* sp. of the *A. corni* group. Thelaxidae are host alternating with migration between *Cornus sanguinea* L. (I) and sweet grasses (II). The many captures point to mass migrations.

Table 11. Selection of "type" of prey (in %) by six orb-weaving spiders in a grassland habitat in Eastern Switzerland

"Type" of prey	<i>Meta segmentata</i> (N = 639)	<i>Argiope bruennichi</i> (N = 1153)	<i>Araneus quadratus</i> (N = 2002)	<i>Araneus diadematus</i> (N = 846)	<i>Tetragnatha extensa</i> (N = 717)	<i>Nuctenea cornuta</i> (N = 1984)
Flying insects ^a	66.8	77.4	91.3	93.0	97.6	99.8
Jumping arthropods ^b	31.9	21.6	8.6	6.6	2.1	0.2
Wingless, non-jump. ^c	1.3	1.0	0.1	0.4	0.3	0.05
Total	100	100	100	100	100	100

^a Diptera, Aphidina (winged), Thysanoptera, Heteroptera, Lepidoptera, Trichoptera, Chrysopidae, Panorpidae, Coleoptera, Ephemeroptera, Apidae, and "other Hymenoptera". – ^b Cicadina, Orthoptera, and Salticidae. – ^c Aphidina (wingless), Formicidae (wingless), and web-building spiders.

3.6 Numbers of prey items/web

Numbers of prey items entangled per web were counted on several days in the evening (table 12). Orb-weavers tend to rebuild their webs daily and each time eat the old thread mass with all attached insects to recycle the web proteins (PEAKALL 1964; NENTWIG 1985b); prey items counted per web can therefore be considered to be prey captured by the spider on that day. However, since web-building spiders have the habit of dropping some

Table 12. Average numbers of prey items/web ($= \bar{x}$) of orb-weaving spiders in a grassland habitat in Eastern Switzerland (N = number of webs)

$\bar{x}$ values presented in this table are minimum estimates of the avg. numbers of prey organisms killed/web/day (on rainless days)

Spider species	Sample	Sample size	No. prey items/web $\bar{x}$
<i>Nuctenea cornuta</i>	1 ^a	(N = 15)	11.7
	2 ^a	(N = 9)	13.4
	3 ^a	(N = 9)	29.7
	4 ^b	(N = 10)	10.4
	5 ^b	(N = 9)	20.8
	6 ^b	(N = 25)	23.9
<i>mean = 18.3</i>			
<i>Araneus quadratus</i>	1 ^b	(N = 7)	21.9
	2 ^c	(N = 27)	11.1
	3 ^c	(N = 11)	15.2
	4 ^c	(N = 6)	15.7
	5 ^d	(N = 20)	16.9
	6 ^d	(N = 25)	17.5
	7 ^d	(N = 12)	27.0
<i>mean = 17.9</i>			
<i>Argiope bruennichi</i>	1 ^c	(N = 21)	7.9
	2 ^c	(N = 55)	10.1
	3 ^c	(N = 19)	10.9
	4 ^d	(N = 21)	10.5
<i>mean = 9.9</i>			

^a In June. – ^b In July. – ^c In August. – ^d In September.

prey carcasses from the web after the meal (TURNBULL 1973), and since in this study we were not able to observe prey capture and feeding continuously around the clock, data presented in table 12 must be considered to be minimum estimates of the real daily prey capture rates.

Table 12 suggests that the prey capture rate of *N. cornuta* and *A. quadratus* may have been 10–20 insects/web/day (at least) in summer. In comparison to this, the prey capture rate of *A. bruennichi* may have been 10 insects/web/day (at least) in the second half of summer. In a few particularly well exposed orb-webs, a much higher number of insects could be counted. Occasionally, more than 100 prey organisms (small insects) entangled at one time were counted per orb-web, indicating that orb-weaving spiders have a high killing power (see below).

3.7 Predatory importance of the spiders

Among the spiders' prey there were economically neutral arthropods (assumedly most prey organisms, tables 6 and 7), beneficials (1% honey bees), and pests (agriculturally harmful aphids). Eight percent of the total prey were Aphidina (table 6), demonstrating the orb-weavers' potential as predators of this economically interesting group of plant-sucking insects. The majority of aphids entangled in orb-webs were *Anoecia* sp. of the

economically neutral *Anoecia corni* group (table 10), which are known to be host alternating with migration between *Cornus sanguinea* L. (I) and sweet grasses (II). Besides, the orb-weaving spiders were observed to be predaceous on agriculturally harmful aphids such as *Rhopalosiphum padi* L., *Sitobion avenae* F., *Aphis fabae* Scop., *Hyalopterus pruni* Geoffr., and *Myzus persicae* Sulz. (table 10) (see also NYFFELER and BENZ 1982b).

4 Discussion

4.1 Prey of orb-weaving spiders

The investigated orb-weavers were observed to utilize a variety of insect taxa as prey (generalist predators, tables 6 and 7), which is in agreement with previous prey analysis of orb-weaving spiders (see BILSING 1920; KAJAK 1965; ROBINSON and ROBINSON 1970, 1974; NYFFELER and BENZ 1978, 1979; WISE and BARATA 1983, a. o.). In this study, the orb-weavers' prey was exclusively composed of Arthropoda, whereby Insecta constituted > 99 % of these spiders' prey. Araneophagy (cannibalism and interspecific predation) is a predatory behavior often observed in spiders (BRISTOWE 1958; PÖTZSCH 1966; NYFFELER et al. 1987a, b). However, in this study a very small fraction (< 1 %) of the spiders' prey were Araneae, indicating that araneophagy is of no significance for the nutrition of this orb-weaver guild. Likewise prey analysis by other researchers indicate that araneophagy is of little importance for the nutrition of orb-weaving spiders (BILSING 1920; KAJAK 1965; ROBINSON and ROBINSON 1970, 1974; ENDERS 1974; NYFFELER and BENZ 1978; UETZ et al. 1978; HORTON and WISE 1983, a. o.).

Considering the spiders' prey by numbers (tables 6 and 7), it is evident that adult Diptera (mostly small species) composed the major prey group, while Homoptera and Hymenoptera were the prey categories second and third in importance. Furthermore, Coleoptera and Trichoptera were also quite frequently captured by the spiders. The same pattern of a predominance of Diptera, Homoptera, Hymenoptera, and Coleoptera in the prey of web-building spiders was observed in other grassland habitats (KAJAK 1965; NYFFELER and BENZ 1978; NENTWIG 1980). In some studies on orb-weaving spiders of the genus *Argiope* (e.g. *A. bruennichi*), additionally Orthoptera were mentioned as a major prey component (see below). Trichoptera seem not to be a typical component in the prey of grassland spiders; but in this study large numbers of Trichoptera were observed swarming in the evening in the top zone of the grassland, which is located next to the river Glatt (stream ecosystems are known to be populated by Trichoptera larvae in large numbers, ODUM 1971).

Diptera, Homoptera, Hymenoptera, and Coleoptera occur within the grassland field layer in higher numbers than other potential prey groups (table 13); the prevalence of these four insect taxa in the spiders' prey evidently reflects the potential prey composition in grasslands.

One guild member, *A. bruennichi*, was often quoted in literature for its specific predatory behaviour of utilizing grasshoppers as a major food source (see above) and therefore was considered to tend towards a specialized predator of grasshoppers (WIEHLE 1931; MARPLES 1935; CROME and CROME 1961; LOHMEYER and PRETSCHER 1979; GILLANDT and MARTENS 1980). In Eastern Switzerland there are grassland habitats where *A. bruennichi* was observed utilizing grasshoppers as a major food source (NYFFELER 1982), which agrees with the classic opinion about this spider's feeding habits; in those habitats grasshoppers constituted according to NYFFELER (1982) an estimated $\frac{2}{3}$ to $\frac{3}{4}$ of the total prey biomass of *A. bruennichi*. However, as tables 6 and 7 show, grasshoppers constituted only a very small fraction (< 0.5 % by number) of the prey of *A. bruennichi* in the abandoned grassland near the Airport Kloten. Thus, the prey spectrum of *A. bruennichi* assessed in this study differs considerably from the previously known feeding

Table 13. Major arthropod groups (potential prey of spiders, % by numbers) within the field layer of European grasslands

Based on literature data

Arthropod taxa	BONESS (1953) ^a (West Germany)	PERTERER and THALER ^b (1976) ^b (Austria)	PASQUET (1984) ^c (France)	KAJAK (1965) ^d (Poland)
	%	%	%	%
Diptera	43.1	37.7–88.1	81.6–90.9	ca. 60
Homoptera	{ 17.7	1.2–34.5	{ 1.8– 8.8	ca. 25
Heteroptera		0.1– 0.4		–
Hymenoptera	8.9	3.6–15.2	4.0– 6.1	ca. 8
Coleoptera	4.7	3.2– 9.5	0.3– 2.1	ca. 2
Other Arthropoda	25.6	3.6– 9.0	1.8– 3.0	ca. 5
Total	100	100	100	100

^a Sweep sampling. – ^b Water traps placed in the field layer. – ^c Colour traps placed in the field layer. – ^d Sticky traps placed in the field layer.

habits of this spider species (see also NYFFELER and BENZ 1978, 1981b, 1982c); data of this study are characterizing *A. bruennichi* as a generalist predator with a broad “feeding niche” (high trophic diversity value, “feeding niche” sensu KREBS 1986, table 6). Likewise the related American species *Argiope aurantia* Lucas – which also inhabits abandoned grasslands – was observed to be a generalist predator (NYFFELER et al. 1987c).

Data of table 8 indicate a trend of increasing diversity in the orb-weavers’ prey with the progressing summer season. The same pattern of an increasing trophic diversity with the progressing summer season was also found in other prey analyses of web-building spiders (TURNBULL 1960; KAJAK 1965). In a study conducted in a Polish grassland, KAJAK (1965) distinguished between the orb-weavers’ “period of uniform food” in spring/early summer and the “period of varied food” in summer.

4.2 Prey capture rates of orb-weaving spiders

In this study, prey capture rates of large orb-weaving spiders in summer were estimated at roughly 10–20 prey organisms killed/web/day (minimum estimates, table 12). This is of the same magnitude as data from literature.

For instance, in a rye field in Eastern Switzerland NYFFELER and BENZ (1979) found that an average of 14.3 prey organisms/web/day were captured by *N. cornuta* in summer.

In a Polish grassland, KAJAK (1965) assessing the prey capture rate of orb-weavers found that *N. cornuta* killed an average of 13.8 prey organisms/web/day in spring, whereafter the daily number of captured prey declined.

In a grassland in France, PASQUET (1984) estimated that in late summer *Araneus marmoreus* Clerck caught an average of 14.1 prey organisms/web/day, while *A. bruennichi* caught an estimated average of 4.3 prey organisms/web/day.

These are overall values of well and badly placed webs. However, orb-weaving spiders are capable of killing much higher numbers of prey organisms by means of their large webs. In particularly favourable web sites, their capability of killing prey in excess occasionally results in extraordinary high capture rates. As many as 1000 small insects have been found entangled at one time in a single orb-web (KIRCHNER 1964; NATON 1976). NYFFELER (1982) reports that seven relatively voluminous grasshoppers (family Acrididae) were entangled at one time in a single web of *A. bruennichi*. These observations evidence the high killing power of orb-weaving spiders (see below).

4.3 Predatory importance of spiders in grassland ecosystems

In this study, the overall orb-weaver density amounted to ca. 3 webs/m² ground area in the second half of summer. At that time of year the orb-weaver guild daily spun an estimated web area of ca 1000 m²/ha ground area.

Comparatively, in an undisturbed grassland habitat in West Germany average numbers of large orb-weavers (*Argiope bruennichi*) of respectively 6 and 3 ind./m² ground area were found in two succeeding summers (LOHMEYER and PRETSCHER 1979); from that we assessed that in LOHMEYER and PRETSCHER's grassland in the two summers an estimated web area of respectively ca. 3000 and 1500 m²/ha ground area were daily spun by orb-weavers (valid for August/September, based on an individual catching area of 500 cm² per female of *A. bruennichi* as given in table 3).

Assuming that a female *A. bruennichi* may kill in August and September an average of ca. 10 insects/day (on rainless days, table 12), it follows that in a grassland populated by 3–6 adult female *A. bruennichi*/m² (see above), an estimated number of 30–60 insects/m² ground area/day may be killed by these orb-weavers. Extrapolated over an entire meadow, this corresponds to an estimated prey kill due to orb-weavers of the magnitude of roughly ½ million insects/ha ground area/day. However, in a situation where the inherent killing potential (see above) would be fully utilized, theoretically even much higher numbers of insects could be destroyed per space and time unit. By multiplying the known maximum prey capture rate (ca. 1000 insects killed/web/day) with the observed population density of 6 large orb-webs/m² ground area (see above), we assess a theoretical maximum killing capacity due to orb-weavers of ca. 400 million insects/ha ground area/week; this corresponds with a biomass of 400 kg/ha/week, assuming 1 mg fresh weight per prey item. This is a purely speculative value probably not realized anywhere in nature; nevertheless, this theoretical consideration indicates that such a large web area is death trap for large numbers of insects and evidently exerts a high predation pressure on the grassland arthropod community. According to TURNBULL's (1973) rough estimate, 47 500 kg prey biomass/ha/year would be killed by spiders; we feel that this is strongly exaggerated. ROBINSON and ROBINSON's (1974) estimate of 160 kg (fresh weight)/ha/year killed by the web-building spiders of a tropical coffee plantation seems more realistic.

Experimental evidence for the high predation pressure exerted by large orb-weaving spiders on grassland arthropods was provided by Polish researchers (KAJAK et al. 1968). In exclusion experiments by means of field cages they could demonstrate that on "plots with spiders" losses in the yield of vascular plants caused by grasshoppers were two times smaller than on "plots without spiders".

In another study, Polish researchers evaluated prey kill of spiders within the field layer of an undisturbed grassland habitat near Warsaw (KAJAK 1971; KAJAK et al. 1971); the consumption estimated for all field layer-spiders (including many orb-weavers) in two succeeding years amounted to respectively 2482 and 3244 mg (dry weight)/m² ground area per season. Supposing that 1 kg dry weight equals approx. 4 kg fresh weight of prey (EDGAR 1971, assessed in *Drosophila* flies that 0.27 mg dry weight equals 1 mg wet weight), we calculated that prey kill due to the field layer-spiders in that Polish grassland may have been respectively ca. 100 and 130 kg (fresh weight)/ha ground area/year. KAJAK and OLECHOWICZ (1970) estimated that web-building spiders eliminated 25–40 % of the adult Diptera in undisturbed grassland.

Another comparable study on grassland spiders was conducted in the Southern USA by VAN HOOK (1971), who estimated that in an undisturbed grassland ecosystem prey kill by spiders amounted to 6.76 kcal/m²/year (which may be roughly 50 kg fresh weight/ha/year, according to our estimate), and that predation by spiders accounted for 21 % of total prey mortality. VAN HOOK (1971) suspected that spiders were the dominant invertebrate predator in that undisturbed grassland ecosystem.

In conclusion, in uncultivated grassland ecosystems where spiders can forage and reproduce relatively undisturbed, spiders seem to play an important ecological role as mortality agents of grassland arthropods and in terms of community energy flow, evidenced by their high prey kill capacity.

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Zusammenfassung

Nahrungsökologie und Prädatorenbedeutung der Radnetzspinnengilde eines Graslandhabitates

In einem in der Ostschweiz gelegenen unbewirtschafteten Graslandhabitat (Hochstaudenried: Valeriano-Filipenduletum, Ausbildung mit *Carex acutiformis* Ehrh.) wurden die Prädatorenaktivitäten und -bedeutung einer Radnetzspinnengilde untersucht. Diese Spinnengilde setzte sich aus den sechs Arten *Argiope bruennichi* (Scop.), *Araneus quadratus* Clerck, *Araneus diadematus* Clerck, *Nuctenea cornuta* (Clerck), *Meta segmentata* Clerck und *Tetragnatha extensa* (L.) zusammen. Diese Radnetzspinnengilde entfaltete den Hauptanteil ihrer Prädatorenaktivität in der zweiten Sommerhälfte, wenn große Arten (Gattungen *Argiope* und *Araneus*) reif wurden und große, starke Fangnetze bauten. Die durchschnittliche Besiedlungsdichte betrug in der zweiten Sommerhälfte ca. 3 Radnetzspinnen/m², wobei diese Spinnen täglich schätzungsweise 0.1 m² Netzfläche/m² Bodenfläche spannen (= 1000 m² Netzfläche/ha Bodenfläche pro Tag). Man darf annehmen, daß eine so gewaltige Netzfläche Todesfalle für unzählige Beutetiere ist und folglich einen großen Prädatorendruck auf die Beutepopulationen ausübt. Eine Nahrungsanalyse ergab, daß diese Radnetzspinnen beinahe ausschließlich insektivore Prädatoren sind (> 99 % Insekten in der Beute; Nahrungsgeneralisten mit Hauptbeute Diptera und Homoptera). Von Interesse ist, daß sich – gemäß unserer Nahrungsanalyse – unter den von der Radnetzspinnengilde getöteten Insekten die landwirtschaftlich schädlichen Blattläuse *Aphis fabae* Scop., *Myzus persicae* Sulz., *Hyalopterus pruni* Geoffr., *Rhopalosiphum padi* L. und *Sitobion avenae* F. befanden.

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Authors' address: Dr. sc. nat. MARTIN NYFFELER and Prof. Dr. phil. GEORG BENZ, Department of Entomology, Swiss Federal Institute of Technology, ETH-Zentrum, CH-8092 Zurich, Switzerland