

The foliage-dwelling spider community of an abandoned grassland ecosystem in eastern Switzerland assessed by sweep sampling¹

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The foliage-dwelling spiders of an abandoned grassland ecosystem (Valeriano-Filipenduletum, *Carex acutiformis* EHRH. type) in eastern Switzerland were studied from June to September by the sweeping technique. A total of 632 adult specimens representing 22 identified species had been collected by sweeping (based on totally ca. 2000 single sweeps). More than two thirds of the sampled adult spiders were females. At all times, more immature than adult spiders were captured (overall, 83% immatures). Among the 3756 collected spiders (immatures plus adults), the six families Agelenidae, Araneidae, Micryphantidae, Pisauridae, Salticidae, and Tetragnathidae prevailed in the sweep net samples (combined ca. 90% of all spiders). The five species *Evarcha arcuata* (CLERCK), *Hylyphantes nigrinus* (SIMON), *Neottiura bimaculata* (L.), *Pisaura mirabilis* (CLERCK), and *Tetragnatha extensa* (L.) constituted combined > 80% of all adult spiders sampled by sweeping. The web-building spiders *T. extensa* and *H. nigrinus* were the two species most frequently captured. Adults of large orb-weaving spiders (*Argiope bruennichi* [SCOPOLI], *Araneus quadratus* CLERCK, and *Araneus diadematus* CLERCK) were abundant in the investigated grassland habitat (assessed by web counts), but obviously underproportionately represented in the sweep net samples. Considering the total number of spiders (immatures plus adults) per 100 single sweeps, a strong increase from spring to late summer was noticed which is considered to be primarily due to egg-laying of the most dominant species in spring followed by hatching of the spiderlings in the course of the summer. Since spiders are abundant predators in this grassland ecosystem (ca. 0.1 m² web area/m² ground area, alone due to orb-weavers in August/Sept.), they may be important mortality agents of grassland arthropods.

INTRODUCTION

In the last three decades numerous investigations had been conducted on spiders in grassland habitats in Europe (DUFFEY, 1962; KAJAK, 1960, 1962, 1965, 1971, 1978) and North America (TURNBULL, 1966; VAN HOOK, 1971; DONDALE, 1971, a. o.). Studies on grassland spiders had also been carried out in Switzerland (MAURER, 1974, 1975; NYFFELER & BENZ, 1978, 1979). However, little has been published on the spider faunas of the field layer of Swiss grasslands assessed by sweep sampling. Therefore, the foliage-dwelling spider community of an abandoned grassland habitat in eastern Switzerland was studied with the sweeping technique, and the results of this study are presented here.

MATERIALS AND METHODS

The studies were carried out from June to September in an abandoned grassland habitat which is located ca. 3.5 km south-east of the International Air-

¹ This research was supported by the Swiss National Science Foundation, Grant 3.0020.76.

port Zurich-Kloten, near the river Glatt (national grid coordinates: 685.65/253.65). It refers to a megaphorbe meadow² (Valeriano-Filipenduletum, *Carex acutiformis* EHRH. type). 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).

Spiders were collected by means of a sweep net with an upper diameter of 40 cm and a length of 75 cm. Sweep net collections were made on June 10–12 (500 single sweeps), June 26–28 (500 single sweeps), July 16–18 (500 single sweeps), August 9–14 (260 single sweeps), and September 17–20 (200 single sweeps). In order to have comparable values, the data were later converted into “number of spiders/100 single sweeps”. The sampled spiders were carefully taken out of the sweep net with the help of tweezers, killed and preserved in 70% ethanol. Later they were identified in the laboratory under a dissecting microscope.

Genital preparations were made of female spiders which could not definitely be identified by the morphology of the epigyne alone. For this purpose, a piece of the genital area which contained the epigyne was macerated for 2 hours at 70 °C in a 10% solution of KOH. Subsequently the preparation was washed in water and ethanol, and then embedded in Euparal as a permanent mount. These genital preparations were then studied and compared with the illustrations of the vulvae in the following publications: DAHL (1931), HARM (1971), LOCKET & MILLIDGE (1951/53), REIMOSER (1937), and WIEHLE (1931, 1937, 1956, 1960, 1963). The nomenclature according to MAURER (1978) was used. At least one specimen of each spider species described in this paper was deposited in the Entomological Collection of the Swiss Federal Institute of Technology (ETH) Zurich.

RESULTS

The family structure of the foliage-dwelling spider community in the investigated grassland habitat is represented in Tables 1 and 2. Among the 3756 spiders (immatures plus adults) collected from June to September, the six families Agelenidae, Araneidae, Micryphantidae, Pisauridae, Salticidae, and Tetragnathidae prevailed in the sweep net samples (combined ca. 90% of all spiders). Tetragnathidae were the most frequently sampled family (ca. 50% of all collected spiders). Araneidae reached their highest proportion (26%) in the first half of June. In the Pisauridae the highest proportion (15%) appeared at the end of June. Micryphantidae were captured in fairly high numbers (ca. 22%) in September. Overall, orb-weaving spiders prevailed in the field layer of this grassland (Table 1). What the tables do not show is the fact that more than two thirds of the sampled adult spiders were females.

A total of 632 adult specimens representing 22 identified spider species had been sampled in this study (Table 2). The five species *Evarcha arcuata* (CLERCK), *Hylyphantes nigrinus* (SIMON), *Neottiura bimaculata* (L.), *Pisaura mirabilis* (CLERCK), and *Tetragnatha extensa* (L.) constituted combined > 80% of all adult spiders sampled by sweeping. The web-building spiders *T. extensa* and *H. nigrinus* were the two species most frequently captured.

² So-called “Hochstaudenried” of the German literature.

Tab. 1. Family structure of the foliage-dwelling spiders (immatures plus adults in %) of an abandoned grassland habitat in eastern Switzerland, assessed by sweep sampling. N = numbers of collected spiders.

	June 10-12	June 26-28	July 16-18	August 9-14	September 17-20	Total
Spider family	N=434	N=817	N=950	N=906	N=649	N=3756
	%	%	%	%	%	%
Orb-weaving spiders						
Tetragnathidae	30.65	42.23	57.16	61.48	51.31	50.88
Araneidae	26.27	13.71	8.42	3.42	4.31	9.72
Subtotal	56.92	55.94	65.58	64.90	55.62	60.60
Space web spiders						
Micryphantidae	13.59	5.75	2.63	10.49	21.73	9.77
Agelenidae	3.00	3.92	4.21	0.99	0.92	2.66
Linyphiidae	3.00	1.71	3.47	0.33	1.69	1.97
Theridiidae	5.99	1.96	2.00	0.33	0.15	1.73
Dictynidae	0	0	0.32	0.55	0.46	0.29
Subtotal	25.58	13.34	12.63	12.69	24.95	16.42
Hunting spiders						
Pisauridae	2.07	15.06	10.95	9.38	7.24	9.80
Salticidae	8.29	8.45	4.32	8.94	4.78	6.87
Thomisidae	1.84	2.57	1.89	1.99	0.77	1.86
Clubionidae	0.92	3.67	1.16	0.88	2.62	1.86
Philodromidae	0	0	0	0.22	0.15	0.08
Subtotal	13.12	29.75	18.32	21.41	15.56	20.47
Undt. spiders	4.38	0.98	3.47	0.99	3.85	2.50
Total	100	100	100	100	100	100

This foliage-dwelling spider community consisted to a considerable degree of medium to large-sized species (comp. size data in LOCKET & MILLIDGE, 1951/53). Adults of *Agelena gracilens* C. L. KOCH, *Araneus* spp., *Argiope bruennichi* (SCOPOLI), and *P. mirabilis* were the largest spiders found in this habitat. Of *Araneus quadratus* CLERCK and *A. bruennichi*, adults were only rarely caught with the sweep net (Table 2); of *A. diadematus* exclusively immature stages were captured by sweeping. *Enoplognatha ovata* (CLERCK), *Heliophanus flavipes* (HAHN), *H. nigritus*, *N. bimaculata*, *P. mirabilis*, *T. extensa*, and *Xysticus cristatus* (CLERCK) adults were found mainly in June, immature stages mostly between July and Sep-

Tab. 2. Foliage-dwelling spiders (no./100 sweeps) of an abandoned grassland habitat in eastern Switzerland, assessed by sweep sampling. Data which are not listed under imm. (= immatures) are all relating to adults.

Spider family and species		Number of spiders/100 sweeps					Total number of sampled spiders
		June 10-12	June 26-28	July 16-18	August 9-14	Sept. 17-20	
<u>Orb-weaving spiders:</u>							
Araneidae	Araneus quadratus	0	0.2	0	1.5	1.5	8
	Argiope bruennichi	0	0	0	0.4	0.5	2
	Meta segmentata	0	0	0	0	7.0	14
	Nuctenea cornuta	0.4	0	0	0.4	0	3
	Araneidae (imm.) a/	22.4	22.2	16.0	9.6	5.0	338
Tetragnathidae	Tetragnatha extensa	21.8	16.0	11.6	0.8	26.0	301
	Tetragnatha pinicola	0.2	0	0	0	0	1
	Tetragnatha spec.	1.8	0.2	0.4	0.4	0	14
	Pachygnatha clercki	0	0	0	0	0.5	1
	Tetragnathidae (imm.)	2.8	52.8	96.6	212.7	140.0	1594
<u>Space web spiders:</u>							
Linyphiidae	Linyphia triangularis	0	0	0	0.8	4.5	11
	Floronina bucculenta	0	0	0	0	1.0	2
	Linyphiidae (imm.)	2.6	2.8	6.6	0.4	0	61
Micryphantidae	Dismodicus bifrons	0.2	0.4	0	0	0	3
	Erigone dentipalpis	0	0	0.2	0	0	1
	Hylyphantes nigrinus	11.4	8.8	4.2	0.4	0.5	124
	Micryphantidae (imm.)	0.2	0.2	0.6	36.2	70.0	239
Theridiidae	Enoplognatha ovata	0	0.4	2.2	1.2	0	16
	Neottiura bimaculata	2.8	1.2	0	0	0	20
	Theridiidae (imm.)	2.4	1.6	1.6	0	0.5	29
Agelenidae	Agelena gracilis	0	0	0	2.7	3.0	13
	Agelenidae (imm.)	2.6	6.4	8.0	0.8	0	87
Dictynidae	Dictynidae (imm.)	0	0	0.6	1.9	1.5	11
<u>Hunting spiders:</u>							
Salticidae	Evarcha arcuata	2.2	2.6	1.8	6.9	4.5	60
	Heliophanus flavipes	0	1.2	0.2	0	0	7
	Salticidae (imm.)	5.0	10.0	6.2	24.2	11.0	191
Thomisidae	Xysticus cristatus	0.4	0	0.6	0	0.5	6
	Xysticus kochi	0.4	0	0	0.4	0	3
	Thomisidae (imm.)	0.8	4.2	3.0	6.5	2.0	61
Philodromidae	Philodromidae (imm.)	0	0	0	0.8	0.5	3
Pisauridae	Pisaura mirabilis	1.4	1.2	0.4	1.2	0	18
	Pisauridae (imm.)	0.4	23.4	20.4	31.5	23.5	350
Clubionidae	Clubiona reclusa	0	0.4	0	0	0.5	3
	Clubiona neglecta	0	0.2	0	0	0	1
	Clubionidae (imm.)	0.8	5.4	2.2	3.1	8.0	66
<u>Undt. spiders:</u>	(imm.)	3.8	1.6	6.6	3.5	12.5	94
Total	immatures	43.8	130.6	168.4	331.2	301.0	3124
	adults	43.0	32.8	21.6	17.4	23.5	632
	immatures and adults	86.8	163.4	190.0	348.6	324.5	3756

a/ Araneus diadematus abundant in this habitat, but with the sweep net sampled as immatures only.

tember. The contrary was true for *Linyphia triangularis* (CLERCK), *A. gracilens*, *Meta segmentata* CLERCK, *A. quadratus*, and *A. bruennichi*: immature stages were caught by sweeping in June/July, adults not before August/September. *E. arcuata* adults were found relatively often from June to September, and immature stages in August/September. These data on spiders' life-cycles are essentially in agreement with the literature data (see DAHL, 1931; WIEHLE, 1931; LOCKET & MILLIDGE, 1961/53; SCHAEFER, 1974).

At all five sampling dates, more immature than adult spiders were captured (Table 2). Overall, 83% of the spiders collected from June to September were immatures. Considering the total number of spiders (immatures plus adults) per 100 single sweeps, a strong increase from spring to late summer can be noticed. All adult spiders combined reached their density peak in June and the minimal density in August. Contrary to this, the minimal density of the immature spiders occurred in June, the maximal density in August/September. Since many of the numerically dominating spider species in this grassland are stenochronous with reproduction time in spring/summer (sensu SCHAEFER, 1974), we assume that a large part of the females laid their egg-sacs in spring and many have died soon thereafter. The spiderlings then hatched in the course of the summer which is evidenced by the increasing numbers of immatures in the sweep net samples with the progressing season.

DISCUSSION

All spider species found in this study had previously been recorded in Switzerland (BENZ, 1969; MAURER, 1978; MAURER & WALTER, 1980, 1984). Eleven species (*E. arcuata*, *Erigone dentipalpis* (WIDER), *E. ovata*, *H. flavipes*, *H. nigritus*, *L. triangularis*, *N. bimaculata*, *T. extensa*, *Tetragnatha pinicola* L. KOCH, *X. cristatus*, and *Xysticus kochi* (THORELL)) occurring in this abandoned grassland had also been sampled by sweeping the field layer of hay meadows near Zurich, Switzerland (NYFFELER, 1982). – The predominance of females in the adult spider samples agrees well with the results of HUHTA (1965) who found the sex ratio in most spider species to be 1 male to 3 females, because of the males' shorter life-span.

It appeared to us that adult large orb-weavers of the family Araneidae occurred in the abandoned grassland in fairly high numbers, but were captured rarely with the sweep net; contrary, adult medium-sized orb-weavers of the family Tetragnathidae were often recorded in this grassland by web counts and by the sweeping technique. Among the 78 adult orb-weavers sampled in late summer by sweeping, there were 31% Araneidae vs. 69% Tetragnathidae; in contrast, among the 445 adult orb-weavers assessed at the same time of the year by web counts, there were 68% Araneidae vs. 32% Tetragnathidae. The percentages of Araneidae in the total of orb-weavers assessed with the two methods differ significantly ($p < 0.001$, χ^2 -test for 2×2 contingency tables). Since web counts provide accurate estimates of the densities of both large Araneidae and medium-sized Tetragnathidae, we conclude from the results of this comparison that adult large Araneidae are underproportionately represented in sweep net samples.

Nevertheless, orb-weavers (Araneidae plus Tetragnathidae) dominated in this study the spider fauna of the field layer (overall, ca. 60% of all spiders sampled by sweeping, Table 1). Based on counts of webs/m² and measurements of

web diameters (see NYFFELER 1982), we estimated that the orb-weaving spider guild of this grassland spun in August/September an average web area of approximately $0.1 \text{ m}^2/\text{m}^2$ ground area (which corresponds to an estimated web area of about $1000 \text{ m}^2/\text{ha}$ ground area). Such a large web area evidently is an effective death trap for high numbers of flying and jumping insects, suggesting that a considerable amount of predation by spiders is going on in this abandoned grassland ecosystem (see also KAJAK, 1971).

It is likely that such abandoned grasslands – in which spiders forage and reproduce relatively undisturbed by human activity and thus may build up large populations – function as reservoirs for the re-colonization of neighbouring hay meadows and cereal fields whose foliage-dwelling spider populations have been reduced by respectively mowing and combine-harvesting.

ACKNOWLEDGEMENTS

We are grateful to Doz. Dr. K. Thaler, Zoology Dept., University of Innsbruck, Austria, who checked our spider identifications and to Professor Dr. F. Klötzli, Geobotanical Institute, The Rübel Foundation, ETH Zurich, who gave us informations on the habitat described in this paper.

ZUSAMMENFASSUNG

Die pflanzenbewohnenden Spinnen eines in der Ostschweiz gelegenen unbewirtschafteten Graslandökosystems (Hochstaudenried: Valeriano-Filipenduletum, Ausbildung mit *Carex acutiformis* EHRH.) wurden von Juni bis September mit der Käschermethode untersucht. Basierend auf total ca. 2000 einfachen Käscherschlägen wurden 632 Adulttiere gekäschert, die 22 identifizierten Spinnenarten zugehörten. Mehr als zwei Drittel der gesammelten adulten Spinnen waren Weibchen. Zu allen Zeiten wurden mehrheitlich juvenile Spinnen gefangen (gesamthaft 83% Jungtiere). Unter den 3756 gekäscherten Spinnen (Jung- und Adulttiere) herrschten die sechs Familien Agelenidae, Araneidae, Micryphantidae, Pisauridae, Salticidae und Tetragnathidae vor (zusammen ca. 90% aller Spinnen). Die fünf Arten *Evarcha arcuata* (CLERCK), *Hylyphantes nigrinus* (SIMON), *Neottiura bimaculata* (L.), *Pisaura mirabilis* (CLERCK) und *Tetragnatha extensa* (L.) stellten zusammen > 80% aller gekäscherten adulten Spinnen. Die Netzspinnen *T. extensa* und *H. nigrinus* waren die am häufigsten gefangenen Arten. Imagines grosser Radnetzspinnen (*Argiope bruennichi* (SCOPOLI), *Araneus quadratus* (CLERCK) und *Araneus diadematus* CLERCK) kamen im untersuchten Graslandhabitat häufig vor, gemäss Netzzählungen wurde ihre relative Häufigkeit mit der Käschermethode jedoch unterschätzt. Die Gesamtzahl aller Spinnen (Jung- und Adulttiere) pro 100 einfache Käscherschläge stieg vom Frühjahr bis zum späten Sommer stark an. Da Spinnen sich ausschliesslich carnivor ernähren und in diesem Graslandökosystem häufig sind (im August/September wird täglich allein durch Radnetzspinnen ca. $0,1 \text{ m}^2$ Netzfläche je m^2 Bodenfläche gesponnen), halten wir es für möglich, dass ihnen eine wichtige Bedeutung als Mortalitätsfaktoren von Graslandarthropoden zukommt.

REFERENCES

- BENZ, G. 1969. Beitrag zur Spinnenfauna der Ostschweiz. *Mitt. Schweiz. Entomol. Ges.* 42: 22–33.
 DAHL, M. 1931. Agelenidae. *Tierwelt Deutschlands* 23: 1–46. Jena: G. Fischer.
 DONDALE, C. D. 1971. Spiders of Heasman's field, a mown meadow near Belleville, Ontario. *Proc. Entomol. Soc. Ontario* 101: 62–69.
 DUFFEY, E. 1962. A population study of spiders in limestone grassland. *J. Anim. Ecol.* 31: 571–599.
 HARM, M. 1971. Revision der Gattung *Heliophanus* C. L. KOCH. *Senckenbergiana biol.* 52: 53–79.
 HUHTA, V. 1965. Ecology of spiders in the soil and litter of Finnish forests. *Annl. Zool. Fenn.* 2: 260–308.
 KAJAK, A. 1960. Changes in the abundance of spiders in several meadows. *Ekol. Polska* A 8: 199–228.
 KAJAK, A. 1962. Comparison of spider fauna in artificial and natural meadows. *Ekol. Polska* A 10: 1–20.

- KAJAK, A. 1965. An analysis of food relations between the spiders – *Araneus cornutus* CLERCK and *Araneus quadratus* CLERCK – and their prey in meadows. *Ekol. Polska A 13*: 717–764.
- KAJAK, A. 1971. Productivity investigation of two types of meadows in the Vistula Valley. IX. Production and consumption of field layer spiders. *Ekol. Polska A 19*: 197–211.
- KAJAK, A. 1978. The effect of fertilizers on number and biomass of spiders in a meadow. *Symp. Zool. Soc. London 42*: 125–129.
- LOCKET, G. H. & MILLIDGE, A. F. 1951/53. British Spiders, I/II. London: Ray Society. 310 pp., 449 pp.
- MAURER, R. 1974. Die Vielfalt der Käfer- und Spinnenfauna des Wiesenbodens im Einflussbereich von Verkehrsimmissionen. *Oecologia (Berl.) 14*: 327–351.
- MAURER, R. 1975. Epigäische Spinnen der Nordschweiz I. *Mitt. Schweiz. Entomol. Ges.* 48: 357–376.
- MAURER, R. 1978. Katalog der schweizerischen Spinnen (Araneae) bis 1977. Zoologisches Museum, Universität Zürich, 113 pp.
- MAURER, R. & WALTER, J. E. 1980. Für die Schweiz neue und bemerkenswerte Spinnen (Araneae). *Mitt. Schweiz. Entomol. Ges.* 53: 157–162.
- MAURER, R. & WALTER, J. E. 1984. Für die Schweiz neue und bemerkenswerte Spinnen (Araneae) II. *Mitt. Schweiz. Entomol. Ges.* 57: 65–73.
- NYFFELER, M. 1982. Field studies on the ecological role of the spiders as predators of insects in agroecosystems (abandoned grassland, meadows, and cereal fields). Diss. ETH Nr. 7097, 174 pp.
- NYFFELER, M. & BENZ, G. 1978. Die Beutespektren der Netzspinnen *Argiope bruennichi* (SCOP.), *Araneus quadratus* CL. und *Agelena labyrinthica* (CL.) in Ödlandwiesen bei Zürich. *Revue suisse Zool.* 85: 747–757.
- NYFFELER, M. & BENZ, G. 1979. Nischenüberlappung bezüglich der Raum- und Nahrungskomponenten bei Krabbenspinnen (Araneae: Thomisidae) und Wolfspinnen (Araneae: Lycosidae) in Mähwiesen. *Revue suisse Zool.* 86: 855–865.
- REIMOSER, E. 1937. Clubionidae oder Röhrenspinnen. *Tierwelt Deutschlands 33*: 45–99. Jena: G. Fischer.
- SCHAEFER, M. 1974. Experimentelle Untersuchungen zum Jahreszyklus und zur Überwinterung von Spinnen (Araneida). Habilitationsschrift, Universität Kiel, 223 pp.
- TURNBULL, A. L. 1966. A population of spiders and their potential prey in an overgrazed pasture in eastern Ontario. *Can. J. Zool.* 44: 557–583.
- VAN HOOK, R. I. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. *Ecol. Monogr.* 41: 1–26.
- WIEHLE, H. 1931. Araneidae. *Tierwelt Deutschlands 23*: 11–136. Jena: G. Fischer.
- WIEHLE, H. 1937. Theridiidae oder Haubennetzspinnen (Kugelspinnen). *Tierwelt Deutschlands 33*: 119–222. Jena: G. Fischer.
- WIEHLE, H. 1956. Linyphiidae – Baldachinspinnen. *Tierwelt Deutschlands 44*: 1–337. Jena: G. Fischer.
- WIEHLE, H. 1960. Micryphantidae – Zwergspinnen. *Tierwelt Deutschlands 47*: 1–620. Jena: G. Fischer.
- WIEHLE, H. 1963. Tetragnathidae – Streckspinnen und Dickkiefer. *Tierwelt Deutschlands 49*: 1–76. Jena: G. Fischer.

(received September 23, 1987)